bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Antisocial rewarding in structured populations

Miguel dos Santos*[1] and Jorge Peña†[2,3]

[1]Department of Zoology, University of Oxford, Oxford, United Kingdom
[2]Department of Evolutionary Theory, Max Planck Institute for Evolutionary Biology, Plön, Germany
[3]GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany

March 9, 2017

Abstract

Cooperation in collective action dilemmas usually breaks down in the absence of additional incentive mechanisms. This tragedy can be escaped if cooperators have the possibility to invest in reward funds that are shared exclusively among cooperators (prosocial rewarding). Yet, the presence of defectors who do not contribute to the public good but do reward themselves (antisocial rewarding) deters cooperation in the absence of additional countermeasures. Although a recent simulation study suggests that interactions in spatially structured populations are sufficient to prevent antisocial rewarding from deterring cooperation, the exact role of spatial structure on the evolution of public goods cooperation with reward funds remains unclear. To address this issue, we formulated and analyzed a game-theoretic model of social interactions in structured populations. We show that increasing reward funds facilitates the maintenance of prosocial rewarding but prevents its evolution from rare in spatially structured populations. Moreover, we demonstrate that spatial structure can sometimes select against the evolution of prosocial rewarding. Our results suggest that, even in spatially structured populations, additional mechanisms are required to prevent antisocial rewarding from deterring cooperation in public goods dilemmas.

*miguel.dossantos@zoo.ox.ac.uk
†pena@evolbio.mpg.de

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Contents

1 Introduction **2**

2 Model **5**
2.1 Public goods game with prosocial and antisocial reward funds 5
2.2 Spatial structure and evolutionary dynamics 6
2.3 Scaled relatedness 8

3 Results **10**
3.1 Infinitely large well-mixed populations 10
3.2 Spatially structured populations 10

4 Discussion **17**

Appendix A Inclusive gain function **22**

Appendix B Evolutionary dynamics for $\kappa = 0$ **22**

Appendix C Evolutionary dynamics for $\kappa \neq 0$ **23**

1 Introduction

Explaining the evolution of cooperation has been a long-standing challenge in evolutionary biology and the social sciences (Axelrod, 1984; Sugden, 1986; Frank, 1998; Lehmann and Keller, 2006; West et al., 2007; Sigmund, 2010). The problem is to explain how cooperators, whose contributions to the common good benefit everybody in a group, can prevent defectors from outcompeting them, leading to a tragedy of the commons where nobody contributes and no common good is created or maintained (Hardin, 1968).

A solution to this problem is to provide individuals with additional incentives to contribute, thus making defection less profitable (Oliver, 1980; Hilbe and Sigmund, 2010). Incentives can be either negative (punishment) or positive (rewards). Punishment occurs when individuals are willing to spend resources in order for defectors to lose even more resources (Sigmund, 2007). Punishment can be stable against defection, since rare defectors are effectively punished (Boyd and Richerson, 1992). However, to evolve from rare and resist invasion by individuals who cooperate but restrain from investing into incentives, i.e., second-order defectors, punishers must gain from punishing, for example, through reputational benefits in future interactions (Hilbe

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

and Sigmund, 2010; dos Santos et al., 2011; Hilbe and Traulsen, 2012).

Defection in collective action problems can also be prevented via positive incentives. Using rewards, cooperators can pay to increase the payoff of other cooperators. While the emergence of such behavior is usually favored, as there are very few cooperators to reward when cooperators are rare, it becomes increasingly costly as cooperators become more abundant in the population (Hauert, 2010). Hence, to resist second-order defectors, non-rewarding players must benefit less from rewards (Sasaki and Unemi, 2011). Alternatively, when both rewards and punishment are present, rewards can foster the emergence of punishment, which in turn can be stable provided second-order punishment is available (Sasaki et al., 2015).

Individuals can either decide to impose incentives unilaterally, or they can pool their effort to impose incentives collectively. When acting collectively, individuals invest into a fund used to either punish defectors or reward cooperators; in the latter scenario one speaks of "prosocial rewarding". These collective mechanisms can be viewed as primitive institutions, as group members both design and enforce the rules to administer incentives to overcome social dilemmas (Ostrom, 1990). Pool rewards (Sasaki and Unemi, 2011; Sasaki and Uchida, 2014) are particularly interesting because they involve the creation of resources, as opposed to their destruction (as in punishment). Prosocial rewarding can favor cooperation only if non-rewarding players can be sufficiently prevented from accessing reward funds so that second-order defectors benefit less from rewards than do rewarders (Sasaki and Unemi, 2011). However, the presence of "antisocial rewarders", i.e., individuals who do not contribute to the public good but reward themselves, destroys cooperation unless additional mechanisms, such as better rewarding abilities for prosocials, work in combination with exclusion (dos Santos, 2015).

Pool rewards can also be viewed as a consecutive collective action dilemma played exclusively among those players who made a similar choice in the first public goods game, i.e., cooperators with each other, and defectors with each other. The nature of such secondary collective action is not necessarily similar to that of the first public goods game, and might, for example, involve non-linear returns. Situations where individuals are involved in different levels of social dilemmas are particularly likely to happen in bacterial communities (Hibbing et al., 2010). Indeed, many species of bacteria secrete public good molecules (e.g., iron-binding siderophores and other signaling molecules), which are susceptible to exploitation from both their own and other strains (Griffin et al., 2004; Khan et al., 2006; Hughes and d'Ettorre, 2008). In addition, bacteria are also involved in within-species public goods

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

games, as some of those public good molecules can also be strain-specific (Hohnadel and Meyer, 1988; Hughes and d'Ettorre, 2008). We might then argue that the relevance of pool-reward mechanisms extends to non-human species.

A recent theoretical study challenged the view that additional mechanisms are required to prevent antisocial rewarding from deterring cooperation in public goods games [Szolnoki and Perc (2015); hereafter, SP15]. Instead, their authors showed that prosocial rewarding outcompetes antisocial rewarding if individuals interact preferentially with neighbors in a spatially structured population. Additionally, SP15 showed that increasing the amount of rewards is beneficial for prosocial rewarding. However, SP15 focused on one particular type of spatial structure (a lattice with overlapping groups), so it remains unclear whether their results generalize to a broader range of spatial models.

Here, we formulate a mathematical model of public goods with reward funds in spatially structured populations. Our model clarifies the role of spatial structure for cooperation to be favored through pool rewarding. The conditions under which cooperation is favored are derived analytically and written as functions of the parameters of the game and of the "scaled relatedness coefficient" (Lehmann and Rousset, 2010; Van Cleve, 2015), which serves as a natural measure of spatial structure. Scaled relatedness captures both the increased genetic structure and increased local competition brought about by spatial structure and hence depends on demographic assumptions of the particular model (Lehmann and Rousset, 2010; Van Cleve and Lehmann, 2013; Van Cleve, 2015; Peña et al., 2015; Mullon et al., 2016). To simplify our analysis, however, we treat scaled relatedness as an exogenous parameter. This allows us to make general predictions about the effect of spatial structure on cooperation, and to make connections between our results and the vast literature on inclusive fitness theory (Frank, 1998; Rousset, 2004; Lehmann and Rousset, 2014).

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

2 Model

2.1 Public goods game with prosocial and antisocial reward funds

We consider a collective action problem with an incentive mechanism based on reward funds following the model of SP15. Let us assume that individuals interact in groups of size n and play a linear public goods game (PGG) followed by a rewarding stage with non-linear returns. There are two types of actions available to individuals: "rewarding cooperation" (RC, or "prosocial rewarding"), whereby a benefit r_1/n is provided to all group members (including the focal) at a cost γ, and "rewarding defection" (RD, or "antisocial rewarding"), whereby no benefit is provided and no cost is payed. The parameter r_1 is the multiplication factor of the PGG, and it is such that $1 < r_1 < n$.

Individuals choosing RC or RD also invest in their own reward funds. Each reward fund yields a per capita net reward $r_2 - \gamma$ (reward benefit r_2 minus cost of contributing to the reward pool γ) provided there is at least another individual playing the same action among the $n-1$ other group members, and zero otherwise, i.e., self-rewarding is not allowed and the cost γ is payed only if the rewarding institution is created. For example, a focal individual playing RC will pay the cost and receive the reward only if there is at least another RC among its $n-1$ partners. This reflects a situation where reward funds yield non-linear returns, and is reminiscent of those of a volunteer's dilemma (Diekmann, 1985). Since the net reward $r_2 - \gamma$ does not depend on the group size n, r_2 can in principle take any value greater than, or equal to γ. Note that individuals choosing the most common action are more likely to get the reward, even under random group formation. Hence, RC can prevail as long as its frequency in the global population is above one half and rewards outweigh the net cost of contributing to the PGG. However, if self-rewarding is allowed, cooperation is never favored even when all individuals play RC (dos Santos, 2015).

With the previous assumptions, and letting without loss of generality $\gamma = 1$, the payoffs for a focal individual choosing either RC or RD when k co-players choose RC (and $n-1-k$ co-players choose RD) are respectively given by (cf. Equations 3.1, 3.2, and 3.3 in SP15):

$$c_k = \begin{cases} \frac{r_1}{n} - 1, & \text{if } k = 0 \\ \frac{r_1(k+1)}{n} + r_2 - 2, & \text{if } 1 \leq k \leq n-1 \end{cases} \tag{1}$$

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

and

$$d_k = \begin{cases} \frac{r_1 k}{n} + r_2 - 1, & \text{if } 0 \leq k \leq n-2 \\ \frac{r_1(n-1)}{n}, & \text{if } k = n-1. \end{cases} \tag{2}$$

Note that if everybody plays RC, everybody gets a payoff $c_{n-1} = r_1 + r_2 - 2$. Instead, if everybody plays RD, everybody gets $d_0 = r_2 - 1$. Since $r_2 > 1$, $c_{n-1} > d_0$ holds for all values of r_1 and r_2, which means that full prosocial rewarding Pareto dominates full antisocial rewarding: Players are collectively better if all play prosocial rewarding with probability one rather than if all play antisocial rewarding with probability one. Therefore, despite the presence of rewards available to both cooperators and defectors, the game we study retains the characteristics of a typical social dilemma where full cooperation by all individuals in the group yields higher payoffs than full defection by all individuals in the group. In such situations, it is usually expected that spatial structure facilitates the evolution of RC. As we show below, this is not always the case.

2.2 Spatial structure and evolutionary dynamics

We consider a homogeneous spatially structured population of constant and finite size N_{T} where individuals interact with $n-1$ other individuals according to the game described above. The exact type of spatial structure can follow any of a large family of models, including variants of the island model (Wright, 1931) and transitive evolutionary graphs (Lehmann et al., 2007). In this last case, and for simplicity, we assume that individuals play a single game with their k nearest neighbors, where k is the degree of the graph. This is in contrast to the original model by SP15, where individuals in addition play games "centered" on their neighbors and where the total payoff is the sum of payoffs accrued in these different games. Our approach can be extended to consider this more complicated scenario, but such an extension is beyond the scope of this paper. All that is required for our analysis to be valid is that the selection gradient can be written in a form proportional to the gain function given by Eq. (3) below. For more details on this formalism and the models of spatial structure captured by our approach, we refer to Rousset (2004); Lehmann and Rousset (2010); Van Cleve and Lehmann (2013); Van Cleve (2015); Peña et al. (2015).

We assume that individuals implement mixed strategies, i.e., they play RC with probability z and RD with probability $1-z$, and investigate the evolutionary dynamics of the phenotype z. More specifically, we consider the fixa-

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

tion probability $\rho(z,\delta)$ of a single mutant playing $z+\delta$ in a resident population of phenotype z, take the phenotypic selection gradient $\mathcal{S}(z) = (d\rho/d\delta)_{\delta=0}$ as a measure of evolutionary success (Rousset and Billiard, 2000; Van Cleve, 2015), and look into convergence stable strategies (Geritz et al., 1998) under trait substitution dynamics (Rousset, 2004)

In order to evaluate the selection gradient, we make use of standard results regarding the evolution of a continuous phenotype in a spatially structured population (Rousset, 2004). Denoting by $z_\bullet$ the phenotype of a focal individual, by $z_\circ$ the average phenotype of the individuals it socially interacts with, and by $f(z_\bullet, z_\circ)$ the fecundity of the focal individual, and further assuming that fecundity is proportional to the expected payoffs from the game, the selection gradient $\mathcal{S}(z)$ can be shown to take the form (Van Cleve and Lehmann, 2013)

$$\mathcal{S}(z) \propto \mathcal{G}(z) = \underbrace{\left.\frac{\partial f(z_\bullet, z_\circ)}{\partial z_\bullet}\right|_{z_\bullet, z_\circ = z}}_{-\mathcal{C}(z)} + \kappa \underbrace{\left.\frac{\partial f(z_\bullet, z_\circ)}{\partial z_\circ}\right|_{z_\bullet, z_\circ = z}}_{-\mathcal{B}(z)}, \tag{3}$$

where $\mathcal{G}(z)$ is the "gain function", which consists of three components: (i) the effect of the focal individual's behavior on its fecundity (i.e., the "direct effect" $-\mathcal{C}(z)$), (ii) the effect of the co-players' behavior on the focal individual's fecundity (i.e., the "indirect effect" $\mathcal{B}(z)$), and (iii) a measure of relatedness between the focal individual and its neighbors, demographically scaled so as to capture the effects of local competition (i.e., the "scaled relatedness coefficient" κ).

For the matrix game with two pure strategies as the one we consider here, the direct and indirect effects appearing in Eq. (3) can be written, up to a constant factor, as (Peña et al., 2015)

$$-\mathcal{C}(z) = \sum_{k=0}^{n-1} \binom{n-1}{k} z^k (1-z)^{n-1-k} \Delta_k, \tag{4a}$$

$$\mathcal{B}(z) = \sum_{k=0}^{n-1} \binom{n-1}{k} z^k (1-z)^{n-1-k} \Theta_k, \tag{4b}$$

where

$$\Delta_k = c_k - d_k \tag{5}$$

are the "direct gains from switching" recording the changes in payoff experienced by a focal if it unilaterally switches its action from RD to RC when

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

k co-players stick to RC and $n-1-k$ stick to RD (Peña et al., 2014), and

$$\Theta_k = k\,(c_k - c_{k-1}) + (n-1-k)\,(d_{k+1} - d_k) \tag{6}$$

are the "indirect gains from switching" recording the changes in the total payoff accrued by co-players when the focal unilaterally switches its action from RD to RC (Peña et al., 2015). Eq. (4) expresses $-\mathcal{C}(z)$ and $\mathcal{B}(z)$ as expected values of the direct and indirect gains from switching when the number of other individuals playing RC is distributed according to a binomial distribution with parameters n and z.

A necessary and sufficient condition for a mutant with phenotype $z+\delta$ to have a fixation probability greater than neutral when δ is vanishingly small is that $\mathcal{S}(z) > 0$ and hence that $-\mathcal{C}(z)+\kappa\mathcal{B}(z) > 0$ holds. This corresponds to a scaled form of the marginal version of Hamilton's rule (Lehmann and Rousset, 2010; Van Cleve, 2015). Importantly, the gain function $\mathcal{G}(z) = -\mathcal{C}(z)+\kappa\mathcal{B}(z)$ allows one to identify "convergence stable" evolutionary equilibria (Eshel, 1983, 1996; Taylor, 1989); these are given either by singular strategies z^* (i.e., the zeros of the gain function) satisfying $\mathcal{G}'(z^*) < 0$, or by the extreme points $z = 0$ (if $\mathcal{G}(0) < 0$) and $z = 1$ (if $\mathcal{G}(1) > 0$). Convergence stability is a standard way of characterizing long-term evolutionary attractors; a phenotype z^* is convergence stable if for resident phenotypes close to z^* mutants can invade only if mutants are closer to z^* than the resident (Geritz et al., 1998).

2.3 Scaled relatedness

The coefficient κ appearing in Eq. (3) is the "scaled relatedness coefficient", which balances the effects of both increased genetic relatedness and increased local competition characteristic of spatially structured populations (Queller, 1994; Lehmann and Rousset, 2010; Van Cleve and Lehmann, 2013; Van Cleve, 2015; Mullon et al., 2016). The scaled relatedness coefficient has been calculated for many models of spatial structure for which Eq. (3) applies; see Table 2 of Lehmann and Rousset (2010), Table 1 of Van Cleve and Lehmann (2013), Appendix A of Peña et al. (2015), and references therein for some examples. We also note that by identifying

$$\kappa = \frac{\sigma - 1}{\sigma + 1}, \tag{7}$$

where σ is the so-called "structure coefficient", the right hand side of Eq. (3) recovers the "canonical equation of adaptive dynamics with interaction structure" (Allen et al. (2013), Eq. 5). Table 1 of Allen et al. (2013) provides

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

several examples of models of spatial structure and their respective values of σ; transforming these values via Eq. (7), the scaled relatedness coefficients for such models can be obtained in a straightforward manner.

In general, κ takes a value between -1 and 1 depending on the demographic assumptions of the model, but it is always such that the larger it is the less genetic relatedness is effectively reduced by the extent of local competition. Importantly, the larger the magnitude of scaled relatedness κ the more important the role of the indirect effect $\mathcal{B}(z)$ in the selection gradient. For this reason, we use scaled relatedness κ as a measure of spatial structure; we hence refer in the following to an increase in κ as an increase in spatial structure.

In the following, we present some examples to illustrate the connection between explicit spatial structure models and the formalism we use here, based on the scaled relatedness coefficient. For a well-mixed population or an island model with Wright-Fisher demography (such that generations are overlapping), the value of scaled relatedness is

$$\kappa = -\frac{1}{N_{\mathrm{T}} - 1} \tag{8}$$

(Van Cleve and Lehmann (2013), Eq. B.1). Contrastingly, in an island model with n_{d} demes with N individuals each (so that $N_{\mathrm{T}} = n_{\mathrm{d}} N$) and a Moran demography (where adults have a positive probability of surviving to the next generation) scaled relatedness becomes

$$\kappa = \frac{1 - m - 2/n_{\mathrm{d}}}{N + 1 - m - 2/n_{\mathrm{d}}} \tag{9}$$

where m is the migration rate (Van Cleve and Lehmann (2013), Eq. B.2). In this case, κ is inversely proportional to the migration rate m; it follows that an island model with less migration has, according to our definition, more spatial structure. As a final example, consider a transitive evolutionary graph of size N_{T} and degree k updated with a (death-birth) Moran demography. In this case we have

$$\kappa = \frac{N_{\mathrm{T}} - 2k}{k(N_{\mathrm{T}} - 2)} \tag{10}$$

(Van Cleve and Lehmann (2013), Eq. B.5 with $m = 1$; which can also be recovered from the value of σ given in Table 1 of Allen et al. (2013) after applying the identity (7)). For this model of population structure, scaled relatedness is inversely proportional to the degree k. This means that, according to our terminology, graphs of larger degree (and hence more similar to a well-mixed population represented by a complete graph for which $k = N_{\mathrm{T}} - 1$) are then characterized by smaller spatial structure.

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

3 Results

Calculating the gains from switching by first replacing Eq. (1) and (2) into Eq. (5) and (6), then replacing the resulting expressions into Eq. (4a) and (4b), and simplifying, we obtain that the gain function for the PGG with reward funds can be written as (Appendix A)

$$\mathcal{G}(z) = \underbrace{\frac{r_1}{n} - 1 + (r_2 - 1)\left[z^{n-1} - (1-z)^{n-1}\right]}_{-\mathcal{C}(z)} + \kappa \underbrace{(n-1)\left\{\frac{r_1}{n} + (r_2 - 1)\left[z(1-z)^{n-2} - z^{n-2}(1-z)\right]\right\}}_{\mathcal{B}(z)}. \tag{11}$$

In the following, we identify convergence stable equilibria and characterize the evolutionary dynamics, first for well-mixed and then for spatially structured populations.

3.1 Infinitely large well-mixed populations

For well-mixed populations, and as $N_{\mathrm{T}} \to \infty$, the scaled relatedness coefficient reduces to zero (Eq. (8)). In this case, the gain function reduces to $\mathcal{G}(z) = -\mathcal{C}(z)$ and we obtain the following characterization of the evolutionary dynamics (Appendix B). If $r_1/n + r_2 \leq 2$, $z = 0$ is the only stable equilibrium, and RD dominates RC. Otherwise, if $r_1/n + r_2 > 2$, both $z = 0$ and $z = 1$ are stable, and there is a unique $z^* > 1/2$ that is unstable. In this case, the evolutionary dynamics are characterized by bistability or positive frequency dependence, with the basin of attraction of full RD ($z = 0$) being always larger than the basin of attraction of full RC ($z = 1$). Moreover, z^* (and hence the basin of attraction of $z = 0$) decreases with increasing r_1 and r_2. In particular, higher reward funds lead to less stringent conditions for RC to evolve. In any case, RC has to be initially common ($z > 1/2$) in order for full RC to be the final evolutionary outcome.

3.2 Spatially structured populations

Interactions in spatially structured populations (for which κ is not necessarily equal to zero) can dramatically alter the evolutionary dynamics of public goods with prosocial and antisocial rewards. In particular, we find that

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

whether or not the extreme points $z = 0$ and $z = 1$ are stable depends on how the scaled relatedness coefficient κ compares to the critical values

$$\kappa_* = \frac{n(2 - r_2) - r_1}{(n-1)r_1}, \tag{12}$$

and

$$\kappa^* = \frac{nr_2 - r_1}{(n-1)r_1}, \tag{13}$$

which satisfy $\kappa_* \leq \kappa^*$, in the following way (Fig. 1):

1. For low values of κ ($\kappa < \kappa_*$), full RD ($z = 0$) is stable and full RC ($z = 1$) is unstable.
2. For intermediate values of κ ($\kappa_* < \kappa < \kappa^*$), both full RD and full RC are stable.
3. For large values of κ ($\kappa > \kappa^*$), full RC is stable and full RD is unstable.

Note that, for a given group size n and PGG multiplication factor r_1, $\kappa_* = \kappa^*$ if and only if $r_2 = 1$, i.e., if rewards are absent. In this case, full RD and full RC cannot be both stable.

Rewards have contrasting effects on κ_* (the critical scaled relatedness value below which full RC is unstable) and κ^* (the critical scaled relatedness value above which full RD is unstable). On the one hand, κ_* is decreasing in the reward benefit r_2, so larger rewards increase the parameter space where full RC is stable. If spatial structure is maximal, i.e., $\kappa = 1$, the condition for full RC to be stable is $r_1 + r_2 > 2$, which always holds. On the other hand, κ^* is an increasing function of r_2. Hence, larger rewards make it harder for spatial structure to destabilize the full RD equilibrium, and hence for RC to increase when rare. For $\kappa = 1$, full RD is still stable whenever $r_1 < r_2$. Contrastingly, full defection can never be stable if $\kappa = 1$ in the absence of rewards (i.e., $r_2 = 1$) since, by definition, $r_1 > 1$. From this analysis we can already conclude that even maximal spatial structure does not necessarily allow RC to invade and increase when rare. In addition, a minimum critical value of scaled relatedness is required for prosocial rewarding to be stable once it is fully adopted by the entire population.

Let us now investigate singular strategies. Depending on the parameter values, there can be either zero, one, or three interior points at which the gain function (and hence the selection gradient) vanishes (Appendix C). If there is a unique singular point, then it is unstable while $z = 0$ and $z = 1$ are stable, and the evolutionary dynamics is characterized by bistability.

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

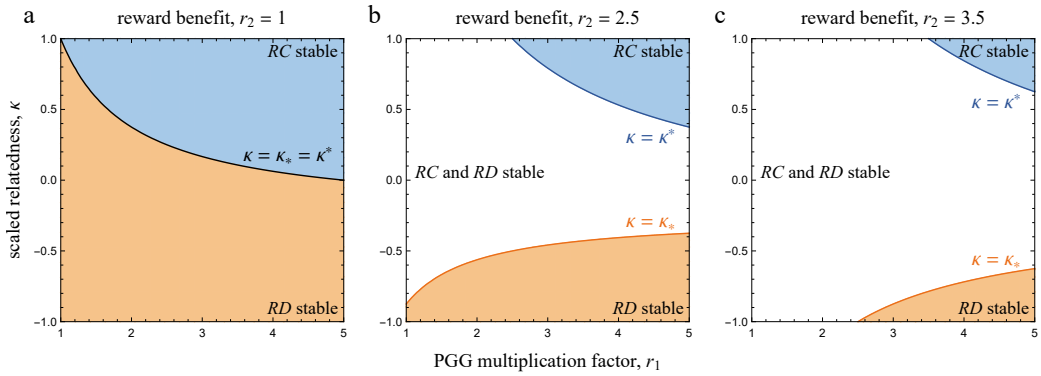

Figure 1: Phase diagrams illustrating the possible dynamical regimes of public goods games with prosocial and antisocial reward funds. Prosocial rewarding (RC) is stable if $\kappa > \kappa_*$, while antisocial rewarding (RD) is stable if $\kappa < \kappa^*$. The critical values κ_* and κ^* are functions of the public goods game multiplication factor r_1, the reward benefit r_2, and the group size n, as given by Eqs. (12) and (13). Increasing the reward benefit r_2 makes it more difficult for both prosocial and antisocial rewarding to increase from rare. Parameters: $n = 5$.

If there are three singular points (probabilities z_{L}, z_{M}, and z_{R}, satisfying $0 < z_{\mathrm{L}} < z_{\mathrm{M}} < z_{\mathrm{R}} < 1$), then $z = 0$, z_{M}, and $z = 1$ are stable, while z_{L} and z_{R} are unstable. In this case RD and RC coexist at the convergence stable mixed strategy z_{M}; a necessary condition for this dynamical outcome is both relatively large reward benefits and relatively large scaled relatedness.

We calculated the singular strategies numerically, as the equation $\mathcal{G}(z) = 0$ cannot be solved algebraically in the general case (Fig. 2 and Fig. 3). Increasing scaled relatedness generally increases the parameter space where RC is favored. Yet, there are cases where increasing scaled relatedness can hinder the evolution of RC. Specifically, when the reward benefit is considerably larger than the public goods share, increasing scaled relatedness can increase the basin of attraction of the full RD equilibrium (Fig. 2c). Also, increasing rewards can be detrimental to RC in spatially structured populations by increasing the basin of attraction of full RD (Fig. 3c, f, h, i); this is never the case when there is no spatial structure (Fig. 3a, d, g; cf. section 3.1). Finally, the best case scenario from the point of view of a rare mutant playing $z = \delta$ (where δ is vanishingly small) is in the absence of rewards (i.e., $r_2 = 1$), because that is the case where the required threshold value of scaled relatedness to favor prosocial rewarding is the lowest (i.e., where κ^* attains

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

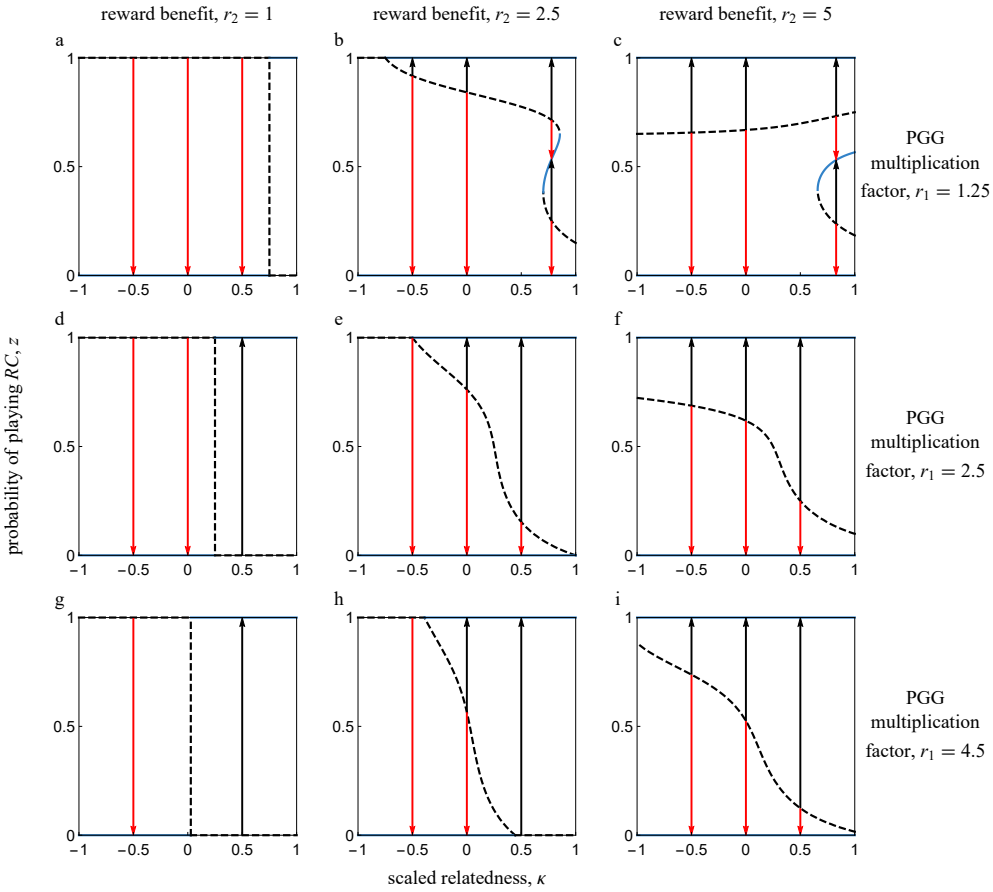

Figure 2: Bifurcation plots illustrating the evolutionary dynamics of pool rewarding in spatially structured populations. The scaled relatedness coefficient serves as a control parameter. Arrows show the direction of evolution for the probability of playing prosocial rewarding. Solid (dashed) lines correspond to convergence stable (unstable) equilibria. In the left column panels (a, d, g), rewards are absent (i.e., $r_2 = 1$). In the middle column panels (b, e, h), $r_2 = 2.5$. In the right column panels (c, f, i), $r_2 = 4.5$. In the top row panels (a, b, c), $r_1 = 1.25$. In the middle row panels (d, e, f), $r_1 = 2.5$. In the bottom row panels (g, h, i), $r_1 = 4.5$. In all panels, $n = 5$. A value of $\kappa = 0$ could correspond to an infinitely large well-mixed population (Eq. (8)); a value of $\kappa = 1/6 \approx 0.167$ could correspond to an evolutionary graph updated with a death-birth Moran model with $N_{\mathrm{T}} \gg k$ and $k = 6$ (Eq. (10)) or to an infinite island model with deme size $N = 5$ and $m \ll 1$ (Eq. (9)).

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

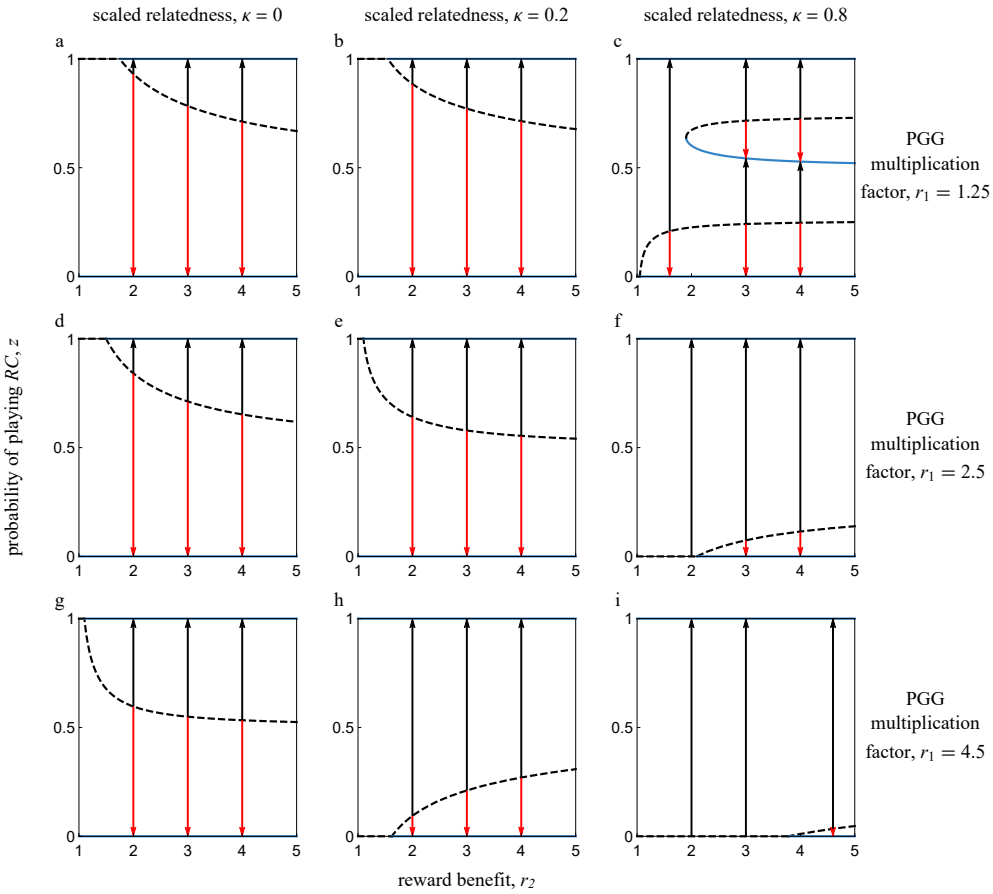

Figure 3: Bifurcation plots illustrating the evolutionary dynamics of pool rewarding in spatially structured populations. The reward benefit serves as a control parameter. Arrows show the direction of evolution for the probability of playing prosocial rewarding. Solid (dashed) lines correspond to convergence stable (unstable) equilibria. In the left column panels (a, d, g), there is no spatial structure (i.e., $\kappa = 0$). In the middle column panels (b, e, h), $\kappa = 0.2$. In the right column panels (c, f, i), $\kappa = 0.8$. In the top row panels (a, b, c), $r_1 = 1.25$. In the middle row panels (d, e, f), $r_1 = 2.5$. In the bottom row panels (g, h, i), $r_1 = 4.5$. In all panels, $n = 5$.

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

its minimum value in Eq. (13)).

In order to understand why, contrary to naive expectations, increasing spatial structure might sometimes select against RC, note first that the derivative of the gain function with respect to κ is equal to the indirect effect $\mathcal{B}(z)$. This is nonnegative if

$$\frac{r_1}{n} + (r_2 - 1)\big[\underbrace{z(1-z)^{n-2} - z^{n-2}(1-z)}_{q(z)}\big] \geq 0. \tag{14}$$

In the absence of rewards (i.e., $r_2 = 1$), condition (14) always holds. That is, increasing scaled relatedness always promotes cooperation when there are no rewards. In addition, when $0 \leq z \leq 1/2$, the function $q(z)$ is nonnegative, so that condition (14) holds and $\mathcal{B}(z)$ is positive. Hence, increasing scaled relatedness is always beneficial for RC when such behavior is expressed less often than RD. However, increasing scaled relatedness might not always favor RC when such behavior is already common in the population, i.e., if $z > 1/2$. Indeed, when the multiplication factor of the PGG is relatively small and rewards are relatively large, condition (14) is not fulfilled for some z and $\mathcal{B}(z)$ is negative for some probability of playing RC (Fig. 4).

A closer look at the indirect gains from switching Θ_k (Eq. 6) reveals why $\mathcal{B}(z)$, and hence the effect of scaled relatedness on the selection gradient, can be negative for some z. The indirect gains from switching are nonnegative for all $k \neq n-2$. For $k = n-2$ and $n \geq 4$ we have $\Theta_{n-2} = (n-1)r_1/n - r_2 + 1$, which can be negative if

$$r_2 - 1 > (n-1)r_1/n \tag{15}$$

holds. Inequality (15) is hence a necessary condition for $\mathcal{B}(z)$ to be negative for some z and for prosocial rewarding to fail to qualify as payoff cooperative or payoff altruistic [*sensu* Peña et al. (2015)]. Indeed, when condition (15) holds and hence $\Theta_{n-2} < 0$, prosocial rewarding cannot be said to be altruistic according to the "focal-complement" interpretation of altruism (Matessi and Karlin, 1984; Kerr et al., 2004). This is because the sum of the payoffs of the $n-1$ co-players of a given focal individual, out of which $n-2$ play RC and one plays RD, is larger if the focal plays RD than if the focal plays RC. We also point out that RC is not altruistic according to an "individual-centered" interpretation (Uyenoyama and Feldman, 1980; Kerr et al., 2004) or "cooperative" [*sensu* Peña et al. (2016b)] if

$$r_2 - 1 > r_1/n, \tag{16}$$

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

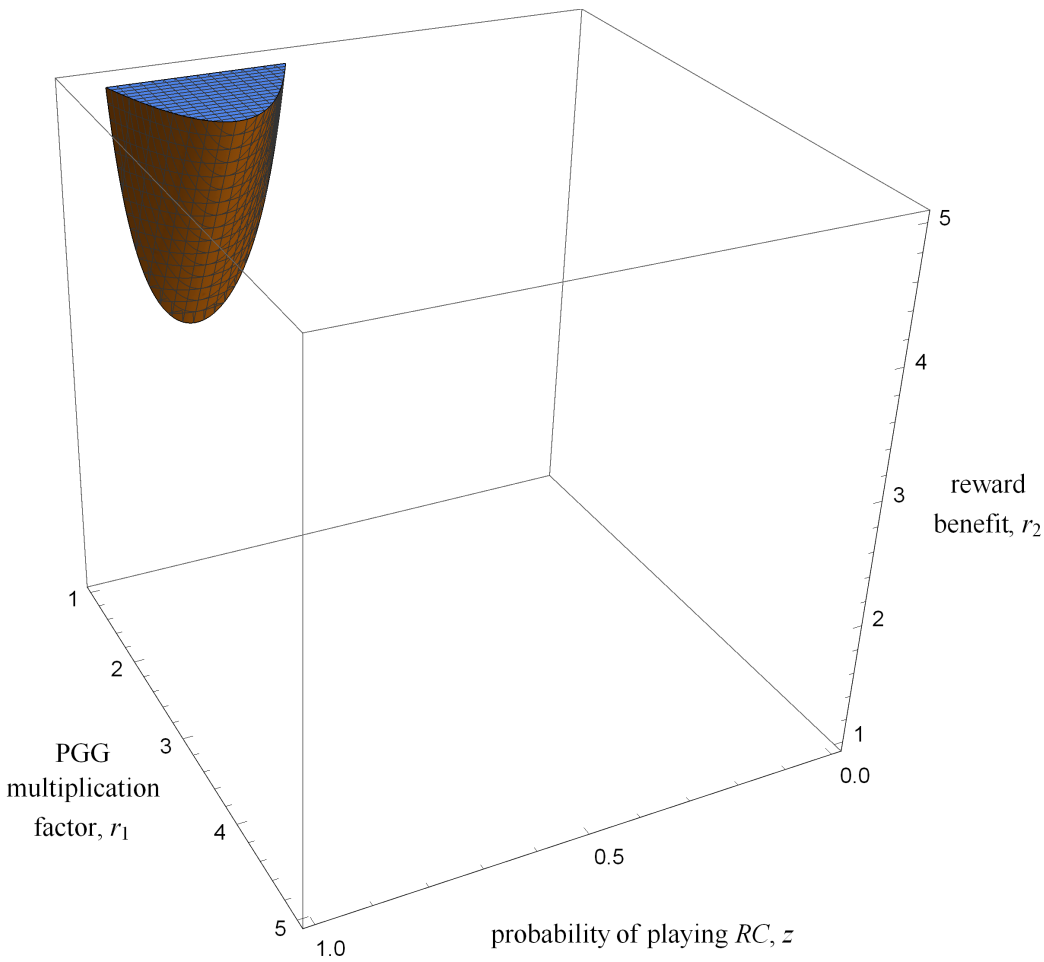

Figure 4: Parameter space where condition (14) does not hold and increasing spatial structure is detrimental to prosocial rewarding for some values of the probability of playing prosocial rewarding, z. Parameters: $n = 5$.

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

since in this case the payoff to a focal individual playing RD as a function of the number of other players choosing RC in the group, d_k (see Eq. (2)), is decreasing (and not increasing) with k at $k = n-2$. Indeed, if condition (16) holds, players do not necessarily prefer other group members to play RC irrespective of their own strategy: a focal RD player would prefer one of its $n-1$ co-players to play RD rather than play RC. In the light of this analysis, it is perhaps less surprising that for some parameters increasing spatial structure can be detrimental to the evolution of prosocial rewarding, even if prosocial rewarding Pareto dominates antisocial rewarding.

4 Discussion

We have investigated the effect of spatial structure on the evolution of public goods cooperation with reward funds. Measuring spatial structure by means of a scaled relatedness coefficient allowed us to capture both the effects of increased genetic assortment and increased local competition that characterize evolution in spatially structured populations. We have found that (i) prosocial rewarding cannot invade full antisocial rewarding unless scaled relatedness is sufficiently large, but (ii) increasing scaled relatedness can be detrimental to prosocial rewarding in cases where rewards are considerably larger than the public goods share. We have also demonstrated the contrasting effects of increasing rewards, which (iii) only benefits prosocial rewarding in well-mixed populations, but (iv) can also benefit antisocial rewarding in spatially structured populations. These results illustrate the complex nature of the evolutionary dynamics of multi-player games in the presence of spatial structure.

Our study revealed a perhaps counterintuitive result, namely, that increasing spatial structure can be detrimental to prosocial rewarding. While spatial structure generally favors the evolution of cooperation (Ohtsuki et al., 2006; Lehmann et al., 2007; Perc et al., 2013; Mullon and Lehmann, 2014; Débarre et al., 2014; Peña et al., 2016b), it can sometimes oppose it (Hauert and Doebeli, 2004; Van Cleve and Lehmann, 2013; Peña et al., 2016a). In our case, spatial structure can oppose selection because the indirect gains from switching from antisocial to prosocial rewarding can be negative. In particular, if $n \geq 4$ and exactly $n-2$ co-players choose prosocial rewarding and one co-player chooses antisocial rewarding, choosing antisocial rewarding (RD) rather than prosocial rewarding (RC) might increase (rather than decrease) the payoffs of co-players. The reason is that, in this case, by choosing RD

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

the focal player helps its RD co-player getting the reward fund, while also allowing its RC co-players to keep theirs, as the focal contribution is not critical to the creation of the prosocial reward fund. If the reward benefit is so large that Eq. (15) holds, the benefit to the single RD co-player is greater than what everybody loses by the focal not contributing to the public good, and the sum of payoffs to co-players is greater if the focal plays RD than if it plays RC. This implies that, although prosocial rewarding Pareto dominates antisocial rewarding, it does not strictly qualify as being payoff altruistic or payoff cooperative (Peña et al., 2015), hence the mixed effects of increasing spatial structure.

Our results also revealed the fact that higher values of the reward benefit r_2 make it more difficult for prosocial rewarding to invade from rare in spatially structured populations. Indeed, the critical value of scaled relatedness required for prosocial rewarding to be favored over antisocial rewarding is greater in the presence of rewards than in their absence. This is striking because rewards are meant to be mechanisms incentivizing provision in public goods games (Sasaki and Unemi, 2011; Sasaki and Uchida, 2014), rather than making collective action more difficult to emerge. Obviously, our result hinges on the assumption that prosocial rewarders and antisocial rewarders are both equally effective in rewarding themselves, i.e., that r_2 is the same for both prosocial and antisocial rewarders. Challenging this assumption by making investments in rewards contingent on the production of the public good, or by increasing the ability of prosocials to reward each other relative to that of antisocials (dos Santos, 2015), will necessarily change this picture and promote prosocial rewarding in larger regions of the parameter space.

Although higher rewards prevent the invasion of prosocial rewarding from rare, we have also shown that, once prosocial rewarding is common, higher rewards can further enhance the evolution of prosocial rewarding. These results are in line with the findings of SP15, who showed that when both spatial structure is sufficiently large (their spatial model supports cooperation even in the absence of rewards) and the initial frequency of prosocial rewarding is relatively high (i.e., 1/4 in all their simulations), larger rewards promote prosocial rewarding.

In contrast to the original model by SP15, which considered discrete strategies and strong selection, we assumed continuous mixed strategies and weak selection (Peña et al., 2015). For well-mixed populations, these different sets of assumptions lead to identical results under a suitable reinterpretation of the model variables (Peña et al., 2014). Thus, our result in section 3.1 that in this case there is a unique convergence unstable z^* in mixed strategies

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

also implies that the replicator dynamics for the two-strategy model will be characterized by an unstable rest point at the same value z^*, and corroborates the numerical results presented in section 3.(a) of SP15. By contrast, for structured populations the invasion and equilibrium conditions between discrete- and mixed-strategy game models (Grafen, 1979; Wild and Traulsen, 2007) and between weak and strong selection models (Mullon and Lehmann, 2014) can differ. Hence, our results for spatially structured populations need not be identical to those reported in SP15.

We further note that our approach assumes that the population is always essentially monomorphic. An initial state of, say, $z = 1/3$ in our Fig. 2 means that all individuals in the population play the same mixed strategy $z = 1/3$. Evolution then proceeds by means of a trait substitution sequence (TSS), whereby a single mutant (which we also assume plays a slightly different mixed strategy $z+\delta$, where δ is small) will either become extinct or invade and replace the resident population (Champagnat, 2006). If the latter happens, the resident strategy is updated to $z + \delta$ and the process starts again, until a convergence stable state is reached. The TSS assumption, common in adaptive dynamics and related mathematical methods studying the evolution of continuous traits in spatially structured populations (Metz et al., 1992; Rousset, 2004) is then in stark contrast to the numerical simulations used in SP15 and related studies (Perc et al., 2013), where evolution starts from a polymorphic population where a large number of mutants appear en masse either randomly or clustered together according to a given "prepared initial state".

Our motivation for a different set of assumptions was both analytical tractability and wider applicability. An analytical solution of the model with discrete strategies (as in SP15) would require tracking higher-order genetic associations and effects of local competition (Roze and Rousset, 2008; Ohtsuki, 2010; Wu et al., 2013; Ohtsuki, 2014; Mullon and Lehmann, 2014), which can be a complicated task even in relatively simple models of spatial structure under weak selection. By contrast, assuming continuous strategies allowed us to identify convergence stable levels of prosocial rewarding in a wide array of spatially structured populations, each characterized by a particular value of scaled relatedness. This way, we made analytical progress going beyond the numerical results on a particular type of population structure (a square lattice with overlapping groups of size $n = 5$) studied in SP15. Furthermore, treating scaled relatedness as an exogenous parameter independent of specific demographic assumptions, allows making more general predictions on the evolution of a trait, as well as relating results from different types of models (**?**). On the other hand, understanding the effect of more specific

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

parameters (e.g., dispersal rate or degree of the network), can be achieved by determining how scaled relatedness can be expressed in terms of those parameters (as we have shown above).

An important drawback of our study is that our results are valid only to the first order of δ (the difference between the trait of mutants and the trait of residents). As a result, we cannot evaluate whether or not the singular strategies we identify as convergence stable are also "evolutionarily stable" or "locally uninvadable", i.e., if a population monomorphic for a singular value will resist invasion by mutants with traits close to the singular value (Eshel, 1983; Christiansen, 1991; Geritz et al., 1998; Mullon et al., 2016). This also means that our model does not allow one to check whether or not evolutionary branching (whereby a convergence stable but locally invadable population diversifies into differentiated coexisting morphs; Doebeli et al. 2004) might occur. We hasten to note that such drawback is not particular to our method (Rousset, 2004). Evolutionary stability in spatially structured populations is significantly more challenging to characterize than convergence stability (Day, 2001; Metz and Gyllenberg, 2001; Ajar, 2003; Wakano and Lehmann, 2014; Mullon et al., 2016) and is thus beyond the scope of the present paper.

A related issue has to do with our assumption that individuals play mixed strategies and hence that payoffs are linear in the focal's own strategy. For this kind of models, "a peculiar degeneracy raises its ugly head" (Dieckmann and Metz, 2006), namely that the second-order condition to evaluate evolutionary stability in a well-mixed population is null. In turn, this implies that strategy variants at a singular point that is convergence stable are strictly neutral. Such degeneracy is however restricted to well-mixed populations, and does not necessarily apply to spatially structured populations. Indeed, the condition for uninvadibility under weak selection in subdivided populations has been shown to depend also on mixed partial derivatives of the payoff function (Mullon et al., 2016), which in general are not zero. All in all, our view is that assuming individuals play mixed strategies of a matrix game is not that problematic: For well-mixed populations (where the degeneracy raises its head), the convergence stable mixed strategies can be reinterpreted as evolutionarily stable points of a replicator dynamics in discrete strategies; for spatially structured populations, there is simply no degeneracy. Future work should explore the conditions under which convergence stable mixed strategies of the model presented here and other matrix games are locally uninvadable.

Both our model and that of SP15 have not considered the presence of in-

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

dividuals who are able to benefit from reward funds without contributing to them. In other words, second-order defection is avoided by design. Allowing for second-order defection makes cooperation through pool rewarding vulnerable, even in the absence of antisocial rewarding (Sasaki and Unemi, 2011). Therefore, even though the conclusions of SP15 contradict the findings of dos Santos 2015, namely that antisocial rewarding deters cooperation except in certain conditions (e.g., better rewarding abilities for prosocials), SP15 did not investigate standard pool-rewarding (Sasaki and Unemi, 2011; Sasaki and Uchida, 2014; dos Santos, 2015). Hence, their claim that spatial structure prevents antisocial rewarding from deterring cooperation, while not always true as we have shown here, does not apply to the more general case of pool-reward funds where second-order defection is allowed. Exploring the effects of spatial structure in these more realistic cases remains an interesting line of research.

To conclude, we find that antisocial rewarding deters the evolution of cooperation from rare unless scaled relatedness is sufficiently high and rewards are relatively low, or ideally absent. We argue that additional countermeasures, such as exclusion and better rewarding abilities for prosocials (dos Santos, 2015), are still required to (i) prevent antisocial rewarding from deterring cooperation between unrelated social partners, and (ii) allow prosocial rewarding to invade either when relatedness is low or when rewards are too large.

Competing interests

The authors declare no competing interests.

Authors' contributions

M.D.S. and J.P. conceived and designed the study, performed the analysis, and wrote the manuscript. Both authors gave final approval for submission.

Acknowledgements

We thank Pat Barclay, Laurent Lehmann, and Stu West for comments.

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Funding statement

This work was supported by Swiss NSF Grant P2LAP3-158669 (to M.D.S.)

Appendix A Inclusive gain function

To derive the gain function $\mathcal{G}(z)$, we first calculate the direct and indirect gains from switching (Eq. (5) and (6)) associated to the payoffs of the game. We find that the gains from switching depend on the group size n in the following way.

1. For $n = 2$: $(\Delta_0, \Delta_1) = (r_1/2 - r_2, r_1/2 + r_2 - 2)$ and $(\Theta_0, \Theta_1) = (r_1/2 - r_2 + 1, r_1/2 + r_2 - 1)$.
2. For $n = 3$: $(\Delta_0, \Delta_1, \Delta_2) = (r_1/3 - r_2, r_1/3 - 1, r_1/3 + r_2 - 2)$ and $(\Theta_0, \Theta_1, \Theta_2) = (2r_1/3, 2r_1/3, 2r_1/3)$.
3. For $n = 4$: $(\Delta_0, \Delta_1, \Delta_2, \Delta_3) = (r_1/4 - r_2, r_1/4 - 1, r_1/4 - 1, r_1/4 + r_2 - 2)$ and $(\Theta_0, \Theta_1, \Theta_2, \Theta_3) = (3r_1/4, 3r_1/4 + r_2 - 1, 3r_1/4 - r_2 + 1, 3r_1/4)$.
4. For $n \geq 5$: $(\Delta_0, \Delta_1, \ldots, \Delta_{n-2}, \Delta_{n-1}) = (r_1/n - r_2, r_1/n - 1, \ldots, r_1/n - 1, r_1/n + r_2 - 2)$ and $(\Theta_0, \Theta_1, \Theta_2, \ldots, \Theta_{n-3}, \Theta_{n-2}, \Theta_{n-1}) = ((n-1)r_1/n, (n-1)r_1/n + r_2 - 1, (n-1)r_1/n, \ldots, (n-1)r_1/n, (n-1)r_1/n - r_2 + 1, (n-1)r_1/n)$.

Replacing the direct gains from switching Δ_k into the expression for the direct effect $-\mathcal{C}(z)$ (Eq. (4a)) and the indirect gains from switching Θ_k into the expression for the indirect effect $\mathcal{B}(z)$ (Eq. (4b)), and then both of these functions into the expression for the gain function $\mathcal{G}(z)$ (Eq. (**??**)), and simplifying, we obtain the formula given in Eq. (11), which is valid for all $n \geq 2$.

Appendix B Evolutionary dynamics for $\kappa = 0$

For $\kappa = 0$, the gain function $\mathcal{G}(z)$ reduces to $-\mathcal{C}(z)$. This function is increasing and its end-points are given by $-\mathcal{C}(0) = r_1/n - r_2$ and $-\mathcal{C}(1) = r_1/n + r_2 - 2$. Since $1 < r_1 < n$ and $r_2 > 1$, $-\mathcal{C}(0) < 0$ always hold, and $z = 0$ is always stable. If $r_1/n + r_2 \geq 2$, $-\mathcal{C}(z)$ is nonpositive for all z and $z = 0$ is the only stable equilibrium. If $r_1/n + r_2 < 2$, $-\mathcal{C}(1) > 0$ and $z = 1$ is also stable. In this case, and since $-\mathcal{C}(z)$ is increasing, $-\mathcal{C}(z)$ has a single

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

zero z^* in $(0,1)$ giving rise to an unstable equilibrium. Such zero is given by the unique solution to

$$\underbrace{z^{n-1} - (1-z)^{n-1}}_{p(z)} = \underbrace{\frac{n - r_1}{n(r_2 - 1)}}_{\alpha}.$$

Since $p(z)$ is increasing in z, $p(1/2) = 0$, and $\alpha > 0$ always holds, $z^* > 1/2$ holds true. Additionally, since α is decreasing in both r_1 and r_2, z^* is increasing in both r_1 and r_2.

Appendix C Evolutionary dynamics for $\kappa \neq 0$

Rearranging terms, the gain function $\mathcal{G}(z)$ given by Eq. (11) can be alternatively written as

$$\mathcal{G}(z) = \frac{r_1}{n}\left[1 + \kappa(n-1)\right] - 1 + (r_2 - 1)\mathcal{P}(z)$$

where

$$\mathcal{P}(z) = \sum_{k=0}^{n-1} \binom{n-1}{k} z^k (1-z)^{n-1-k} \zeta_k$$

is a polynomial in Bernstein form (Peña et al., 2014) of degree $n-1$ with coefficients given by

1. $(\zeta_0, \zeta_1) = (-(1+\kappa), 1+\kappa)$ if $n = 2$.
2. $(\zeta_0, \zeta_1, \zeta_2) = (-1, 0, 1)$ if $n = 3$.
3. $(\zeta_0, \zeta_1, \zeta_2, \zeta_3) = (-1, \kappa, -\kappa, 1)$ if $n = 4$.
4. $(\zeta_0, \zeta_1, \zeta_2, \ldots, \zeta_{n-3}, \zeta_{n-2}, \zeta_{n-1}) = (-1, \kappa, 0, \ldots, 0, -\kappa, 1)$ if $n \geq 5$.

The number of sign changes (and hence of singular points) of $\mathcal{G}(z)$ is bounded from above by the number of sign changes of $\mathcal{P}(z)$. Moreover, and by the variation-diminishing property of polynomials in Bernstein form (Peña et al., 2014), the number of sign changes of $\mathcal{P}(z)$ is equal to the number of sign changes of the sequence of coefficients $(\zeta_0, \ldots, \zeta_{n-1})$ minus an even integer. It then follows that the number of singular points is at most one if $n \leq 3$ or if scaled relatedness is nonpositive, $\kappa \leq 0$. In this case, the unique singular point z^* is convergence unstable. However, if $n \geq 4$ and $\kappa > 0$, there could be up to three singular points z_{L}, z_{M}, and z_{R} satisfying $0 < z_{\mathrm{L}} < z_{\mathrm{M}} < z_{\mathrm{R}} < 1$ such that z_{L} and z_{R} are convergence unstable and z_{M} is convergence stable.

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

References

Ajar, É. (2003): "Analysis of disruptive selection in subdivided populations," *BMC Evolutionary Biology*, 3, 22.

Allen, B., M. A. Nowak, and U. Dieckmann (2013): "Adaptive Dynamics with Interaction Structure." *The American Naturalist*, 181, E139–E163.

Axelrod, R. (1984): *The evolution of cooperation*, New York, NY: Basic Books.

Boyd, R. and P. Richerson (1992): "Punishment allows the evolution of cooperation (or anything else) in sizable groups," *Ethology and sociobiology*, 13, 171–195.

Champagnat, N. (2006): "A microscopic interpretation for adaptive dynamics trait substitution sequence models," *Stochastic Processes and their Applications*, 116, 1127 – 1160.

Christiansen, F. B. (1991): "On Conditions for Evolutionary Stability for a Continuously Varying Character," *The American Naturalist*, 138, 37–50.

Day, T. (2001): "Population structure inhibits evolutionary diversification under competition for resources," *Genetica*, 112, 71–86.

Débarre, F., C. Hauert, and M. Doebeli (2014): "Social evolution in structured populations," *Nature Communications*, 5, 4409.

Dieckmann, U. and J. A. Metz (2006): "Surprising evolutionary predictions from enhanced ecological realism," *Theoretical Population Biology*, 69, 263 – 281.

Diekmann, A. (1985): "Volunteer's Dilemma," *Journal of Conflict Resolution*, 29, 605–610.

Doebeli, M., C. Hauert, and T. Killingback (2004): "The Evolutionary Origin of Cooperators and Defectors," *Science*, 306, 859–862.

dos Santos, M. (2015): "The evolution of anti-social rewarding and its countermeasures in public goods games." *Proceedings of the Royal Society B: Biological Sciences*, 282, 20141994.

dos Santos, M., D. J. Rankin, and C. Wedekind (2011): "The evolution of punishment through reputation." *Proceedings of the Royal Society B: Biological Sciences*, 278, 371–377.

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Eshel, I. (1983): "Evolutionary and Continuous Stability," *Journal of Theoretical Biology*, 103, 99–111.

——— (1996): "On the changing concept of evolutionary population stability as a reflection of a changing point of view in the quantitative theory of evolution," *Journal of Mathematical Biology*, 34, 485–510.

Frank, S. A. (1998): *Foundations of social evolution*, Princeton, NJ: Princeton University Press.

Geritz, S. A. H., E. Kisdi, G. Meszéna, and J. A. J. Metz (1998): "Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree," *Evolutionary Ecology Research*, 12, 35–57.

Grafen, A. (1979): "The hawk-dove game played between relatives," *Animal behaviour*, 27, 905–907.

Griffin, A. S., S. A. West, and A. Buckling (2004): "Cooperation and competition in pathogenic bacteria," *Nature*, 430, 1024–1027.

Hardin, G. (1968): "The Tragedy of the Commons." *Science*, 162, 1243–1248.

Hauert, C. (2010): "Replicator dynamics of reward and reputation in public goods games," *Journal of Theoretical Biology*, 267, 22–28.

Hauert, C. and M. Doebeli (2004): "Spatial structure often inhibits the evolution of cooperation in the snowdrift game," *Nature*, 428, 643–646.

Hibbing, M. E., C. Fuqua, M. R. Parsek, and S. B. Peterson (2010): "Bacterial competition: surviving and thriving in the microbial jungle," *Nature Reviews Microbiology*, 8, 15–25.

Hilbe, C. and K. Sigmund (2010): "Incentives and opportunism: from the carrot to the stick." *Proceedings of the Royal Society B: Biological Sciences*, 277, 2427–2433.

Hilbe, C. and A. Traulsen (2012): "Emergence of responsible sanctions without second order free riders, antisocial punishment or spite." *Scientific Reports*, 2, 458.

Hohnadel, D. and J. M. Meyer (1988): "Specificity of pyoverdine-mediated iron uptake among fluorescent Pseudomonas strains," *Journal of bacteriology*, 170, 4865–4873.

Hughes, D. P. and P. d'Ettorre (2008): *Sociobiology of communication: an interdisciplinary perspective*, Oxford: Oxford University Press.

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Kerr, B., P. Godfrey-Smith, and M. W. Feldman (2004): "What is altruism?" *Trends in Ecology & Evolution*, 19, 135–140.

Khan, A., R. Geetha, A. Akolkar, A. Pandya, G. Archana, and A. J. Desai (2006): "Differential cross-utilization of heterologous siderophores by nodule bacteria of Cajanus cajan and its possible role in growth under iron-limited conditions," *Applied Soil Ecology*, 34, 19–26.

Lehmann, L. and L. Keller (2006): "The evolution of cooperation and altruism–a general framework and a classification of models," *Journal of Evolutionary Biology*, 19, 1365–1376.

Lehmann, L., L. Keller, and D. J. T. Sumpter (2007): "The evolution of helping and harming on graphs: The return of the inclusive fitness effect," *Journal of Evolutionary Biology*, 20, 2284–2295.

Lehmann, L. and F. Rousset (2010): "How life history and demography promote or inhibit the evolution of helping behaviours," *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2599–2617.

——— (2014): "The genetical theory of social behaviour," *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 369.

Matessi, C. and S. Karlin (1984): "On the evolution of altruism by kin selection," *Proceedings of the National Academy of Sciences*, 81, 1754–1758.

Metz, J., R. Nisbet, and S. Geritz (1992): "How should we define fitness for general ecological scenarios?" *Trends in Ecology & Evolution*, 7, 198 – 202.

Metz, J. A. J. and M. Gyllenberg (2001): "How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionarily stable dispersal strategies," *Proceedings of the Royal Society of London B: Biological Sciences*, 268, 499–508.

Mullon, C., L. Keller, and L. Lehmann (2016): "Evolutionary Stability of Jointly Evolving Traits in Subdivided Populations," *The American Naturalist*, 188, 175–195.

Mullon, C. and L. Lehmann (2014): "The robustness of the weak selection approximation for the evolution of altruism against strong selection," *Journal of Evolutionary Biology*, 27, 2272–2282.

Ohtsuki, H. (2010): "Evolutionary games in Wright's island model: Kin selection meets evolutionary game theory," *Evolution*, 64, 3344–3353.

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

——— (2014): "Evolutionary dynamics of n-player games played by relatives," *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369.

Ohtsuki, H., C. Hauert, E. Lieberman, and M. A. Nowak (2006): "A simple rule for the evolution of cooperation on graphs," *Nature*, 441, 502–505.

Oliver, P. (1980): "Rewards and Punishments as Selective Incentives for Collective Action: Theoretical Investigations," *American Journal of Sociology*, 85, 1356–1375.

Ostrom, E. (1990): *Governing the commons: the evolution of institutions for collective action*, Cambridge: Cambridge University Press.

Peña, J., L. Lehmann, and G. Nöldeke (2014): "Gains from switching and evolutionary stability in multi-player matrix games," *Journal of Theoretical Biology*, 346, 23–33.

Peña, J., G. Nöldeke, and L. Lehmann (2015): "Evolutionary dynamics of collective action in spatially structured populations," *Journal of Theoretical Biology*, 382, 122–136.

Peña, J., B. Wu, J. Arranz, and A. Traulsen (2016a): "Evolutionary Games of Multiplayer Cooperation on Graphs," *PLOS Computational Biology*, 12, 1–15.

Peña, J., B. Wu, and A. Traulsen (2016b): "Ordering structured populations in multiplayer cooperation games," *Journal of the Royal Society Interface*, 13, 20150881.

Perc, M., J. Gómez-Gardeñes, A. Szolnoki, L. Floría, and Y. Moreno (2013): "Evolutionary dynamics of group interactions on structured populations: a review," *Journal of the Royal Society Interface*, 10, 20120997.

Queller, D. C. (1994): "Genetic relatedness in viscous populations," *Evolutionary Ecology*, 8, 70–73.

Rousset and Billiard (2000): "A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal," *Journal of Evolutionary Biology*, 13, 814–825.

Rousset, F. (2004): "Genetic Structure and Selection in Subdivided Populations," *Monographs in Population Biology*, 40, 264.

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Roze, D. and F. Rousset (2008): "Multilocus models in the infinite island model of population structure," *Theoretical Population Biology*, 73, 529 – 542.

Sasaki, T. and S. Uchida (2014): "Rewards and the evolution of cooperation in public good games," *Biology Letters*, 10, 20130903.

Sasaki, T., S. Uchida, and X. Chen (2015): "Voluntary rewards mediate the evolution of pool punishment for maintaining public goods in large populations," *Scientific Reports*, 5, 8917.

Sasaki, T. and T. Unemi (2011): "Replicator dynamics in public goods games with reward funds," *Journal of Theoretical Biology*, 287, 109–114.

Sigmund, K. (2007): "Punish or perish? Retaliation and collaboration among humans." *Trends in Ecology & Evolution*, 22, 593–600.

——— (2010): *The Calculus of Selfishness*, Princeton University Press.

Sugden, R. (1986): *The economics of rights, co-operation and welfare*, Oxford and New York: Blackwell.

Szolnoki, A. and M. Perc (2015): "Antisocial pool rewarding does not deter public cooperation," *Proceedings of the Royal Society B: Biological Sciences*, 282, 20151975.

Taylor, P. D. (1989): "Evolutionary stability in one-parameter models under weak selection," *Theoretical Population Biology*, 36, 125 – 143.

Uyenoyama, M. and M. W. Feldman (1980): "Theories of kin and group selection: A population genetics approach." *Theoretical Population Biology*, 17, 380–414.

Van Cleve, J. (2015): "Social evolution and genetic interactions in the short and long term," *Theoretical Population Biology*, 103, 2 – 26.

Van Cleve, J. and L. Lehmann (2013): "Stochastic stability and the evolution of coordination in spatially structured populations," *Theoretical Population Biology*, 89, 75 – 87.

Wakano, J. Y. and L. Lehmann (2014): "Evolutionary branching in deme-structured populations," *Journal of Theoretical Biology*, 351, 83 – 95.

West, S. A., A. S. Griffin, and A. Gardner (2007): "Evolutionary explanations for cooperation." *Current biology*, 17, R661–72.

bioRxiv preprint doi: https://doi.org/10.1101/092932; this version posted March 9, 2017. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Wild, G. and A. Traulsen (2007): "The different limits of weak selection and the evolutionary dynamics of finite populations," *Journal of Theoretical Biology*, 247, 382–390.

Wright, S. (1931): "Evolution in Mendelian populations," *Genetics*, 16, 97–159.

Wu, B., A. Traulsen, and C. S. Gokhale (2013): "Dynamic properties of evolutionary multi-player games in finite populations," *Games*, 4, 182–199.