Assortment and Reciprocity Mechanisms for Promotion of Cooperation in a Model of Multilevel Selection

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Abstract

In the study of the evolution of cooperation, many mechanisms have been proposed to help overcome the self-interested cheating that is individually optimal in the Prisoners’ Dilemma game. These mechanisms include assortative or networked social interactions, other-regarding preferences considering the payoffs of others, reciprocity rules to establish cooperation as a social norm, and multilevel selection involving simultaneous competition between individuals favoring cheaters and competition between groups favoring cooperators. In this paper, we build on recent work studying PDE replicator equations for multilevel selection to understand how within-group mechanisms of assortment, other-regarding preferences, and both direct and indirect reciprocity can help to facilitate cooperation in concert with evolutionary competition between groups. We consider a group-structured population in which interactions between individuals consist of Prisoners’ Dilemma games and study the dynamics of multilevel competition determined by the payoffs individuals receive when interacting according to these within-group mechanisms. We find that the presence of each of these mechanisms acts synergistically with multilevel selection for the promotion of cooperation, decreasing the strength of between-group competition required to sustain long-time cooperation and increasing the collective payoff achieved by the population. However, we find that only other-regarding preferences allow for the achievement of socially optimal collective payoffs for Prisoners’ Dilemma games in which average payoff is maximized by an intermediate mix of cooperators and defectors. For the other three mechanisms, the multilevel dynamics remain susceptible to a shadow of lower-level selection, as the collective outcome fails to exceed the payoff of the all-cooperator group.

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1 Introduction

In many biological systems, natural selection operates simultaneously across multiple levels of organization, with tensions arising between evolutionary incentives at different levels. Such conflicts readily arise in a wide variety of settings, including the formation of protocells and the origins of life (Hogeweg and Takeuchi 2003; Szathmáry and Demeter 1987; Szathmáry and Smith 1995), collective behavior in animal groups (Boza and Számadó 2010), the evolution of aggressive or cooperative behavior of ant queens (Shaffer et al. 2016), host-microbe mutualisms in the microbiome (Van Vliet and Doebeli 2019), and competition between pathogen strains under both immunological dynamics and epidemiological dynamics (Gilchrist et al. 2004; Levin and Pimentel 1981; Blackstone et al. 2020). Across these various systems, a common theme that arises is an evolutionary tug-of-war between individual-level competition favoring cheaters and higher-level competition favoring groups of cooperators. The evolution of cooperation provides a useful case study for questions of multilevel selection, and evolutionary game theory provides an instructive analytical framework for analyzing the tension between the interests of a group and the interests of the individuals comprising the group (Traulsen et al. 2005; Traulsen and Nowak 2006; Traulsen et al. 2008; Simon 2010; Markvoort et al. 2014; Böttcher and Nagler 2016; Killingback et al. 2006).

In the literature on the evolution of cooperation, there has been an emphasis on the role of mechanisms that can help to facilitate the possibility of promoting cooperation when cheating behaviors dominate under individual-level selection in a well-mixed population. Examples of commonly studied mechanisms include assortative interactions (Grafen 1979; Eshel and Cavalli-Sforza 1982), other-regarding preference (Maynard Smith 1982), the punishment of defectors via both reciprocal altruism (direct reciprocity) (Trivers 1971) and social reputations (indirect reciprocity) (Nowak and Sigmund 2005; Ohtsuki and Iwasa 2006), and embedding evolutionary game dynamics in space or on social networks (Durrett and Levin 1994; Killingback and Doebeli 1996; Ohtsuki et al. 2006; Ohtsuki and Nowak 2006). These mechanisms have been shown to facilitate cooperation in infinite populations via individual-level selection using a replicator equation approach, showing that the mechanisms can either promote long-time equilibrium coexistence of cooperators and defectors or the stabilization of the all-cooperator equilibrium for populations featuring a sufficient initial cohort of cooperators. These within-group mechanisms have often been compared with multilevel selection as alternative approaches for showing how to promote collectively beneficial cooperation over the individual temptation to defect (Nowak 2006; Taylor and Nowak 2007). However, the models of multilevel selection considered in these comparisons rely on stochastic framework modeling individual-level and group-level events in a finite population (Traulsen et al. 2005; Traulsen and Nowak 2006; Traulsen et al. 2008), differing from the replicator equation approach for studying the mechanisms that operate via individual-level selection.
However, recent work on multilevel selection has introduced and analyzed PDE analogues of replicator equations to study evolutionary dynamics operating at two competing levels. This framework provides a new opportunity for comparing and studying the combined effects of within-group mechanisms of assortment and reciprocity with multilevel selection in the promotion of cooperation in evolutionary games. Luo (2014) first introduced a stochastic description for a two-level birth–death process in a group-structured population with two types of individuals, one with an advantage under individual-level reproduction and the other conferring an advantage to its group in group-level reproduction. Considering the limit of infinite group size and infinitely many groups, Luo and coauthors derived a hyperbolic PDE describing the evolutionary competition at both levels, and characterized the long-time behavior of the PDE to determine the long-time support for cooperative behaviors (Luo 2014; van Veelen et al. 2014; Luo and Mattingly 2017). This model was further generalized to study multilevel competition when individual-level and group-level reproduction rates depend on the payoffs from two-strategy social dilemmas (Cooney 2019, 2020), and to model a broad class of models with continuously differentiable reproduction rates (Cooney and Mori 2021). This PDE framework provides an analytically tractable approach to study the conflicts between these levels of selection, and can be extended to include more realistic aspects of between-group competition by incorporating models of group-level fission events (Simon 2010; Simon and Nielsen 2012; Simon et al. 2013; Simon and Pilosov 2016; Puhalskii et al. 2017).

For these PDE models of multilevel selection, there exists a threshold relative strength of selection at the two levels such that cooperation can survive in the long-time population when between-group competition is sufficiently strong (Luo and Mattingly 2017; Cooney 2019, 2020; Cooney and Mori 2021). In such cases, the long-time population can sustain a range of levels of cooperation in the population at a density steady state, which results from the balancing of within-group competition favoring defectors and between-group favoring groups with cooperators. A striking behavior seen in these models is that within-group competition casts a long shadow on the multilevel dynamics: for games in which groups are best off with a mix of cooperators and defectors, no level of between-group competition strength can result in collective payoffs exceeding that of the all-cooperator group (Cooney 2019, 2020; Cooney and Mori 2021). For such games, the level of cooperation achieved by the multilevel dynamics will always be less than the composition which maximizes the average payoff of group members, even in the limit of infinitely strong between-group competition. Given the limitations on the ability to promote optimal collective benefits via multilevel selection, from the possibility of insufficient strength of between-group competition to promote cooperation to the shadow of lower-level selection, it is natural to ask whether the addition of within-group mechanisms can further facilitate the evolution of cooperation in concert with multilevel selection.

In this paper, we study the role of the within-group mechanisms of assortment, other-regarding preferences, and both direct and indirect reciprocity on the dynamics of the evolution of cooperation via multilevel selection. We do this by incorporating models for these mechanisms into the PDE replicator equation for multilevel selection, exploring how the modified payoffs generated by each mechanism impact the individual-level incentive to defect and the group-level incentive to cooperate in our
model of multilevel selection. For each mechanism we consider, we find that the presence of the mechanism decreases the threshold strength of between-group competition needed to sustain long-time cooperation relative to the case of multilevel selection based upon well-mixed within-group interactions, and similarly we find that each mechanism increases the long-time average payoff achieved for a given strength of between-group competition. We see a difference, however, when comparing how the mechanisms impact the collective outcome in the limit of strong between-group competition. Under the mechanisms of assortment, direct reciprocity, and indirect reciprocity, the multilevel dynamics will always produce as much cooperation as possible in the limit of strong between-group competition, even for games in which an intermediate level of cooperation is optimal for the group. By contrast, the model of other-regarding preference always produces the socially optimal level of cooperation for the limit in which individuals care equally about their own payoff and the payoff of their opponents. While all four mechanisms help facilitate the evolution of cooperation via multilevel selection, our model of other-regarding preference is the only mechanism we consider that helps to erase the shadow of lower-level selection.

The decrease we see in the threshold relative selection strength required to sustain long-time cooperation highlights the synergistic effects between incorporating competition between groups and within-group population structure on the outcome of evolutionary dynamics across scales. In particular, we find that there are parameter regimes in which neither our within-group mechanism nor multilevel selection cannot produce any cooperation on their own, while the combination of the two mechanisms can allow for long-time cooperation. Multilevel selection has also been attributed as a means by which within-group mechanisms can evolve (Boyd et al. 2003; Santos et al. 2007; Janssen et al. 2014), as competition between groups can select for groups that have established mechanisms that are conducive to supporting cooperative traits or behaviors. As a result, these synergistic effects between multilevel competition and within-group mechanisms can be seen playing an important role in the evolution of cooperative groups and the emergence of new evolutionary individuals operating at a higher level of selection (Szathmáry and Smith 1995; Michod 1996, 1997; Nowak 2006). From a biological perspective, we can view this exploration of within-group modifications as serving as an initial step toward trying to use PDE models of multilevel selection to understand major evolutionary transitions (Szathmáry and Smith 1995). A first attempt at exploring such an evolutionary transition has been made for the case of protocell evolution and the origin of chromosomes (Gabriel 1960; Smith and Szathmáry 1993; Szathmáry and Smith 1993), in which a PDE model shows how modification of gene-level and cell-level replication rates can help to overcome the shadow of lower-level selection (Cooney et al. 2021). We hope this approach for studying PDE models of multilevel selection with modified within-group interactions can be further applied as a tractable way to illustrate how evolutionary transitions can arise in a range of biological and cultural systems.

In this paper, our focus was on four within-group mechanisms that had been presented in comparison to multilevel selection and that have the added convenience that the modified multilevel dynamics under these mechanisms can be recast in terms of multilevel selection under a game with a transformed payoff matrix (Nowak 2006; Taylor and Nowak 2007). However, the generality of the results for PDE models
of multilevel selection allows for the exploration of much greater possible class of
within-group mechanisms, which may motivate potential future work on how multi-
level selection can work in concert with mechanisms including homophily between
players (Pacheco et al. 2006b), altruistic punishment and the punishment of socially
inefficient actions (Boyd et al. 2003; Boyd and Richerson 1992), social norms (Oht-
suki and Iwasa 2006), ostracism of defectors (Tavoni et al. 2012; Tilman et al. 2017),
or prosocial preferences for fairness (Rabin 1993). In a complementary paper, an
analysis of a PDE model for multilevel selection is completed for the case in which
game-theoretic interactions take place on \( k \)-regular graphs, using a pair-approximation
to account for the role of graphs structure on individual-level and group-level replica-
tion rates (Cooney et al. 2022). Finally, an interesting direction for future work would
be to explore the dynamics of multilevel selection for scenarios in which individuals
payoffs depend not on the payoffs from two-player games, but arise from the collective
behavior of group members through population games arising from public goods with
nonlinear benefits (Archetti and Scheuring 2012; Archetti 2018; Pacheco et al. 2009,
2011) or from the equilibrium outcome of an infectious disease with a mix of social
interaction strategies (Ashby and Farine 2022; Cooney et al. 2022).

The remainder of the paper is structured as follows. In Sect. 2, we present the original
model for the multilevel replicator dynamics, and describe existing results for PDE
models of multilevel selection that we will apply when analyzing the effects of each
of our within-group mechanisms. In Sect. 3, we present our results for the multilevel
dynamics incorporating the within-group mechanism of like-with-like assortment and,
in Sect. 4, we present results for the multilevel model incorporating other-regarding
preferences. In Sect. 5, we present our analysis of the multilevel dynamics for the
models of reciprocity, covering indirect reciprocity in Sect. 5.1 and direct reciprocity
in Sect. 5.2. We conclude in Sect. 6 with a recap of the behaviors found for multilevel
selection across our range of mechanisms, and discuss implications for further work
on the impact of changing within-group interactions on the evolution of cooperation
via multilevel selection. Finally, in Appendix A, we provide an example of combing
multiple within-group mechanisms in our multilevel framework, studying how
assortment and direct reciprocity can work together to further increase the level of
cooperation that can be achieved under multilevel selection.

2 PDE Model for Multilevel Selection in Evolutionary Games

In this section, we provide the necessary background on the PDE replicator equation
for describing multilevel selection when within-group and between-group competition
depends on payoffs obtained by playing two-player, two-strategy social dilemmas. In
Sect. 2.1, we present the payoff functions for these games and show how to use
these payoffs to formulate our baseline PDE model. In Sect. 2.2, we present existing
results for the long-time behavior for our baseline PDE model, which we will apply
in subsequent sections to explore the impact of within-group mechanisms on the
dynamics of multilevel selection.
2.1 PDE Replicator Equation for Two-Strategy Social Dilemmas

Here, we will illustrate the baseline model for deterministic multilevel selection for evolutionary games with well-mixed strategic interactions, as introduced in previous work (Cooney 2019). We consider two-strategy games, in which individuals can either choose to Cooperate (C) or Defect (D), and individuals receive payoff from pairwise interaction given by the following payoff matrix

\[
\begin{pmatrix}
C & D \\
C & R & S \\
D & T & P \\
\end{pmatrix}
\]

where the payoffs parameters are, respectively, named Reward, Sucker, Temptation, and Punishment. We can classify different two-player, two-strategy by the different possible rankings of the entries of the payoff matrix of Eq. (1). Following the approach taken by Allen and Nowak (2015), we will characterize our games of interest in terms of the following possible conditions on the collective benefits of cooperation and individual benefits of defection:

(i) \(R > P\): mutual cooperation is preferred to mutual defection
(ii) \(T > R\): the temptation to defect against a cooperator exceeds the reward for mutual cooperation
(iii) \(P > S\): the punishment for mutant defection is preferred to cooperating with a defector
(iv) \(T > S\): a defector earns a higher payoff than a cooperator in a cooperator–defector interaction.

We will call a game a social dilemma if its payoff matrix satisfies condition (i) and at least one of conditions (ii)–(iv) (Allen and Nowak 2015; Cooney et al. 2016; Cooney 2020). Notably, we see that condition (i) guarantees that a group composed entirely of cooperators achieves a higher average payoff than a group composed entirely of defectors.

The most stringent form of a social dilemma under this classification is when all four conditions hold, which is the case for the Prisoners’ Dilemma (PD). Combining conditions (i)–(iv), we see that PD games are characterized by the following ranking of payoffs:

\[
PD : T > R > P > S.
\] (2)

For the PD, defection is a dominant strategy, as a player receives a greater payoff by defecting regardless of the strategy employed by one’s opponent. A population playing the PD game is expected to see long-time extinction of cooperation under individual-level selection.

The next class of games of interest is anti-coordination games, in which a player receives a higher payoff when they play the opposite strategy from that of their opponent. There are three social dilemmas that fall into this category: the Hawk–Dove (HD) game, as well as two other games that we will call anti-coordination game 1
(AC1) and anti-coordination game (AC2). These three games are characterized by the following rankings of payoffs:

$$\text{HD : } T > R > S > P$$  \hspace{1cm} (3a)

$$\text{AC1 : } T > S > R > P$$  \hspace{1cm} (3b)

$$\text{AC2 : } S > T > R > P.$$  \hspace{1cm} (3c)

When such games are played by a population, individual-level selection promotes long-time coexistence of cooperators and defectors.

A third class of games we consider are coordination games, in which a player does best by using the same strategy as their opponent. There are three social dilemmas that fall into this category: the Stag-Hunt game (SH), as well as two games that we will call coordination game 1 (CG1) and coordination game 2 (CG2). These three games are characterized by the following rankings of payoffs:

$$\text{SH : } R > T > P > S$$  \hspace{1cm} (4a)

$$\text{CG1 : } R > P > S > T$$  \hspace{1cm} (4b)

$$\text{CG2 : } R > P > T > S.$$  \hspace{1cm} (4c)

When these coordination games are played by populations, individual-level selection supports bistability of the all-cooperator and all-defector compositions.

The final social dilemma we consider is the Prisoners’ Delight (PDel), in which cooperation is a dominant strategy because cooperating yields a higher payoff than defecting regardless of the action used by one’s opponent. The PDel is characterized by the following ranking of payoffs:

$$\text{PDel : } R > T > S > P.$$  \hspace{1cm} (5)

A population of individuals playing the PDel game is expected to see long-time extinction of defectors under individual-level selection.

The eight payoff rankings introduced above are the only ones consistent with our definition of a social dilemma. In this paper, we will primarily focus on interactions between individuals that consist of PD games, but our incorporation of mechanisms of assortment, other-regarding preferences, and reciprocity will produce scenarios such that the effective payoffs that shape the birth rates of cooperators and defectors that correspond to these eight games.

In a group composed of fraction $x$ cooperators and $1 - x$ defectors, the expected payoffs received by cooperators and defectors in well-mixed interactions are

$$\pi_C(x) = xR + (1 - x)S$$  \hspace{1cm} (6a)

$$\pi_D(x) = xT + (1 - x)P$$  \hspace{1cm} (6b)

and the average payoff of individuals in a group with $x$ fraction cooperators is

$$G(x) = x\pi_C(x) + (1 - x)\pi_D(x) = P + (S + T - 2P)x + (R - S - T + P)x^2.$$  \hspace{1cm} (7)
Using the framework of Luo and Mattingly (2017) for nested birth–death processes, we can describe the dynamics of multilevel selection in a group-structured population in which within-group competition follows individual payoff and between-group competition depends on the average payoff of group members. In a group composed of a fractions $x$ cooperators and $1 - x$ defectors, we assume that cooperators and defectors reproduce at rate $1 + w_I \pi_C(x)$ and $1 + w_I \pi_D(x)$, respectively, and the offspring individuals replace a randomly chosen member of the group. To model between-group competition, we assume that groups featuring a fraction $x$ of cooperators produce copies of themselves at rate $\Lambda \left(1 + w_G G(x)\right)$, replacing a randomly chosen group in the population. Here, the parameters $w_I$ and $w_G$ describe the respective importance of individual-level and group-level payoff on the rate of reproduction events, and $\Lambda$ describes the relative rate of within-group and between-group selection events.

In the limit in which there are infinitely many groups and each group has infinite size, we can describe the composition of strategies in our group-structured population by the probability density $f(t, x)$, characterizing the density of $x$-cooperator groups at time $t$. It has been shown in prior work that, in this limit, the dynamics of the two-level birth–death process described above can will evolve according to the following partial differential equation for the density $f(t, x)$:

$$\partial f(t, x) \partial t = -\frac{\partial}{\partial x} \left(x(1 - x)(\pi_C(x) - \pi_D(x)) f(t, x)\right)$$

$$+ \lambda f(t, x) \left[G(x) - \int_0^1 G(y) f(t, y) dy\right].$$

(8)

where the parameter $\lambda := \frac{\Lambda w_G}{w_I}$ measures the relative strength of within-group and between-group competition. The dynamics of multilevel selection provided by Eq. (8) must be supplied with an initial density $f(0, x) := f_0(x)$ describing the composition of strategies within groups when $t = 0$.

Equation (8) is a first-order hyperbolic PDE, whose time-dependent solutions can be analyzed using the method of characteristics (Strauss 2007; Evans and Society 1998). The advection term describes the effect of within-group competition. The characteristic curves are determined by the following ODE

$$\frac{dx(t)}{dt} = x(1 - x) (\pi_C(x) - \pi_D(x))$$

$$x(0) = x_0,$$

(9)

which is the replicator equation describing individual-level selection within groups (Taylor and Jonker 1978; Hofbauer and Sigmund 1998; Sandholm 2010; Cressman and Tao 2014). The non-local nonlinear term $\lambda f(t, x) \left[G(x) - \int_0^1 G(y) f(t, y) dy\right]$ describes the impact of between-group competition, and resembles an integro-differential replicator equation for group selection. Taking the two terms together,
we can think of Eq. (8) as the replicator equation describing the simultaneous effect of selection operating at two levels.

We can also use the expressions for \( \pi_C(x) \), \( \pi_D(x) \), and \( G(x) \) from Eqs. (6) and (7) to understand how the entries of the payoff matrix of Eq. (1) impact the dynamics of multilevel selection. Using the shorthand notation, \( \alpha = R - S - T + P \), \( \beta = S - P \), and \( \gamma = S + T - 2P \), the multilevel dynamics can be rewritten as

\[
\frac{\partial f(t, x)}{\partial t} = -\frac{\partial}{\partial x} \left[ x(1-x)(\beta + \alpha x) f(t, x) \right] + \lambda f(t, x) \left[ \gamma x + \alpha x^2 - \left( \gamma M_1 f(t) + \alpha M_2 f(t) \right) \right],
\]

where \( M_j f(t) := \int_0^1 x^j f(t, y) dy \) denotes the moments of the density \( f(t, x) \). In this notation, the average payoff of group members takes the form

\[
G(x) = P + \gamma x + \alpha x^2.
\]

Average payoff \( G(x) \) is maximized by the fraction \( x^\ast \) of cooperators given by

\[
x^\ast = \begin{cases} 
\gamma - 2\alpha : \gamma + 2\alpha < 0 \\ 
1 : \gamma + 2\alpha \geq 0
\end{cases}
\]

\[
= \begin{cases} 
\frac{S + T - 2P}{2(S + T - R - P)} : 2R < S + T \\ 
1 : 2R \geq S + T
\end{cases}
\]

(\text{Cooney 2019, 2020}), so the collective outcome of a group can be most favored by a mix of cooperators and defectors when the interaction between a cooperator and defector produces a better contribution to average payoff \((S + T)\) than produced by an interaction between two cooperators \((2R)\). For such payoff matrices, the average payoffs of groups \( G(x) \) can be improved by keeping a fraction of defectors in the group to allow for the cooperator–defector interactions that promote a higher payoff to the pair of individuals than that received by pairs of cooperators (which is the only kind of interaction that takes place in an all-cooperator group). In addition to the two-player, two-strategy symmetric games that can support maximal average group payoff at an intermediate level of cooperation, the collective incentive to maintain a mix of cooperating and defecting individuals arises in models for collective action with saturating benefits (Archetti 2018; Boza and Számadó 2010) and in empirical systems where there is a tradeoff between the collective benefit of diffusible public goods and the metabolic costs incurred by providing such goods for the group (MacLean et al. 2010).

Using this parametrization, the within-group dynamics take the form

\[
\frac{dx(t)}{dt} = x(1-x)(\beta + \alpha x),
\]

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whose equilibria are the all-defector group \( x = 0 \), the all-cooperator group \( x = 1 \), and a third equilibrium \( x_{eq} \) given by

\[
x_{eq} = \frac{\beta}{-\alpha} = \frac{S - P}{S - P + T - R}.
\]

The equilibrium \( x_{eq} \) is only biologically feasible for the HD, SH, coordination, and anti-coordination games. For two-strategy social dilemmas, there are four generic behaviors of interest for the within-group dynamics. For the PD game, the full-defector equilibrium is globally stable under the within-group replicator dynamics, while the PDel game features global stability of the all-cooperator equilibrium. For the HD and anti-coordination games (AC1,AC2), the interior equilibrium \( x_{eq} \) is globally stable, resulting in long-time coexistence of cooperators and defectors. For the SH game and the coordination games (CG1,CG2), the all-cooperator and all-defector equilibria are both locally stable, with basins of attraction that are separated by the equilibrium \( x_{eq} \).

**Remark 1** For PD games, we can use the payoff ranking from Eq. (2) to see that \( \beta = S - P < 0 \). However, the parameters \( \alpha \) and \( \gamma \) can take either sign within the class of PD games. From Eq. (2), we do have the constraint that \( \gamma + \alpha = (S + T - 2P) + (R - S - T + P) = R - P > 0 \), which means that at least one of \( \alpha \) or \( \gamma \) must be positive for any PD game. When, in subsequent sections, we consider the impact of various mechanisms on the payoffs received from PD games, we will therefore need to consider underlying PD games with payoff matrices satisfying either \( \gamma, \alpha > 0 \), \( \gamma < 0 \) and \( \alpha > 0 \), or \( \gamma > 0 \) and \( \alpha < 0 \). For the first two cases, the average payoff \( G(x) \) under well-mixed interactions is always maximized by the all-cooperator composition, while an intermediate level of cooperation can maximize \( G(x) \) for the third case (in which \( \alpha < 0 \)) under the additional assumption that \( \gamma + 2\alpha < 0 \) (as described in Equation (12)).

### 2.2 Existing Results on the Long-Time Behavior of PDE Models for Multilevel Selection

In this section, we will highlight existing results for the long-time behavior for solutions to the multilevel dynamics of Eq. (8), explaining how the long-time distribution of cooperation depends on the payoff matrix of the underlying game, the relative strength of between-group competition \( \lambda \), and the initial distribution of strategies \( f_0(x) \). We first present the results for the range of possible two-player, two-strategy social dilemmas presented above, and then, in Sect. 2.2.1 show how these results may be applied to analyze the mechanisms of assortment and reciprocity that we consider in this paper.

In prior work on PDE models of multilevel selection, it has been shown that the long-time behavior of \( f(t,x) \) depends on a property of the tail of the initial strategy distribution known as the Hölder exponent near \( x = 1 \) (Luo and Mattingly 2017; Cooney 2019, 2020; Cooney and Mori 2021). This quantity measures how the probability contained in the interval \([1 - y, 1]\) behaves as \( y \rightarrow 0 \), and has the following formal definition.
Definition 1 A probability distribution with density $f(t, x)$ has a Hölder exponent $\theta_t$ with associated Hölder constant $C_{\theta_t}$ near $x = 1$ if the density has the following limiting behavior

$$\lim_{x \to 0} \frac{\int_{1-x}^1 f(t, y) dy}{x^{\Theta}} = \begin{cases} 0 & : \Theta < \theta_t \\ C_{\theta_t} & : \Theta = \theta_t \\ \infty & : \Theta > \theta_t \end{cases}$$

(15)

By plugging into Eq. (15), we see that the family of densities $f^\theta(x) = \theta(1 - x)^{\theta - 1}$ provide examples of probability densities with Hölder exponent $\theta$ near $x = 1$, each with associated Hölder constant $C_{\theta_t} = 1$. As a result, we can think of the Hölder exponent $\theta$ for a density as describing like which power $(1 - x)^{\theta - 1}$ does probability of the density $f(t, x)$ vanishes near $x = 1$. For increasing Hölder exponent $\theta$ of our initial density $f_0(x)$, the initial population will feature a decreasing portion of groups with compositions close to the all-cooperator equilibrium.

The Hölder exponent near $x = 1$ has been shown to be preserved by the multilevel dynamics of Eq. (8) (Cooney 2020). In addition, there is at most one steady-state density for the multilevel dynamics with a given Hölder exponent $\theta$ (Cooney 2020; Cooney and Mori 2021), highlighting the key role played by the Hölder exponent of the initial population in characterizing the possible long-time behavior of solutions to Eq. (8). For the PD game, the unique steady-state density with Hölder exponent $\theta > 0$ near $x = 1$ takes the following form

$$f^\lambda_\theta(x) = Z_f^{-1} x^{\beta - 1}[\lambda(\gamma + \alpha - (|\beta| - |\alpha|)\beta)]^{-1}(1 - x)^{\theta - 1}(\gamma - \alpha x)^{-\frac{\lambda}{|\beta|}(\gamma + |\beta|)} - \frac{\lambda}{|\beta|}\theta^{1 - 1}$

(16)

where $Z_f^{-1}$ is a normalizing constant. This density will only be integrable near $x = 0$ if the exponent of $x$ exceeds $-1$, which occurs when that the between-group selection strength satisfies

$$\lambda > \lambda_0^{PD} := -\frac{(\beta + \alpha) \theta}{\gamma + \alpha} = \frac{(\pi_D(1) - \pi_C(1)) \theta}{G(1) - G(0)}$$

(17)

This threshold selection strength illustrates how the survival of long-time cooperation requires success of many-cooperator groups in the tug-of-war between the individual incentive to defect in compositions near the all-cooperator equilibrium $\pi_D(1) - \pi_C(1)$ and the collective incentive to achieve full cooperation rather than full defection $G(1) - G(0)$.

For HD games, the steady-state density with Hölder exponent $\theta > 0$ near $x = 1$ takes the form

$$g^\lambda_\theta(x) = \begin{cases} 0 & : x < \frac{\beta}{|\beta|} \\ Z_g^{-1} x^{\beta - 1}[\lambda(\gamma - |\beta|) + (|\beta| - |\alpha|)\beta]^{-1}(1 - x)^{\beta - 1}(|\alpha|x - \beta)^{\beta - 1} \lambda[|\beta| - |\alpha| - |\alpha|\beta]^{-1} & : x \geq \frac{\beta}{|\beta|} \end{cases}$$

(18)
supporting levels of cooperation between the within-group equilibrium \( x_{eq} = \frac{\beta}{\alpha} \) and the all-cooperator group \( x = 1 \). This density will be integrable near \( x = x_{eq} = \frac{\beta}{\alpha} \) when the exponent of \( |x - \beta| \) exceeds \(-1\), which occurs provided that between-group selection strength satisfies

\[
\lambda > \lambda^*_H := \frac{-\alpha \theta}{\gamma + \alpha - \beta} = \frac{(\pi_D(1) - \pi_C(1)) \theta}{G(1) - G(x_{eq})}.
\]  

(19)

For PD games when \( \lambda < \lambda^*_P \), HD games when \( \lambda < \lambda^*_H \), and all of the other games mentioned above, the only other possible steady-state solutions to Eq. (8) are delta-functions concentrated at equilibria of the within-group dynamics.

In recent work, the long-time behavior of solutions to the multilevel dynamics has been characterized for a class of models including the games with the payoff rankings presented above (Cooney 2020; Cooney and Mori 2021). In Theorem 1, we summarize results for convergence to steady state across the range of two-player, two-strategy social dilemmas given an initial population with density \( f(x, t) \).

In particular, for a limit function \( f(\infty, x) \), we say that \( f(t, x) \rightarrow f(\infty, x) \) (\( f(t, x) \) converges weakly to \( f(\infty, x) \)) if, for all continuous functions \( v(x) \),

\[
\int_0^1 v(x) f(t, x) dx \rightarrow \int_0^1 v(x) f(\infty, x) dx.
\]

**Theorem 1** Suppose the initial population is a probability density \( f(0, x) = f_\theta(x) \) with Hölder constant \( \theta > 0 \) and finite Hölder constant \( C_\theta > 0 \) near \( x = 1 \).

- For PD games, the population converges to a delta-function concentrated at the all-defector equilibrium \( f(t, x) \rightarrow g(\delta(x)) \) as \( t \rightarrow \infty \) if \( \lambda \leq \lambda^*_P \) (Cooney and Mori 2021, Theorem 1.8 and Proposition 5.3). If \( \lambda > \lambda^*_P \), the population converges to the unique density steady state with Hölder exponent \( \theta > 0 \) near \( x = 1 \):

  \( f(t, x) \rightarrow f^\delta_\theta(x) \) where \( f^\delta_\theta(x) \) is given by Eq. (16) (Cooney and Mori 2021, Theorem 1.2).

- For HD games, the population converges to a delta-function concentrated at the within-group HD equilibrium \( f(t, x) \rightarrow g(\delta(x - x_{eq})) \) as \( t \rightarrow \infty \) if \( \lambda \leq \lambda^*_H \) (Cooney and Mori 2021, Theorem C.2). If \( \lambda > \lambda^*_H \), the population converges to the unique density steady state with Hölder exponent \( \theta > 0 \) near \( x = 1 \):

  \( f(t, x) \rightarrow g^\delta_\theta(x) \) where \( g^\delta_\theta(x) \) is given by Eq. (18) (Cooney and Mori 2021, Theorem C.4).

- For all games in which the all-cooperator equilibrium is locally stable (PD, SH, CG1, CG2), the population converges to a delta-function at the all-cooperator equilibrium, \( f(t, x) \rightarrow g(\delta(x - 1)) \) as \( t \rightarrow \infty \), whenever there is any between-group competition (i.e., \( \lambda > 0 \)) (Cooney 2020, Proposition 8).

- For the anti-coordination games (AC1,AC2), the population converges to the within-group equilibrium, \( f(t, x) \rightarrow g(\delta(x - x_{eq})) \) as \( t \rightarrow \infty \), for any level of between-group competition \( \lambda \geq 0 \) (Cooney 2020, Proposition 9).

While the HD and anti-coordination games (AC1,AC2) both feature within-group dynamics with a globally stable within-group equilibrium \( x_{eq} \), the two types of games differ in the landscape they generate for between-group competition. For the HD game, the all-cooperator equilibrium features a higher average payoff from group
members than that of the within-group equilibrium \( x_{eq} \) \( (G(1) > G(x_{eq})) \), while the opposite is true for the anti-coordination games \( (G(1) < G(x_{eq})) \). As a result, both within-group and between-group competition promotes movement toward the within-group equilibrium for the anti-coordination games (AC1,AC2), yielding long-time concentration upon a delta-function the within-group equilibrium \( \delta(x - x_{eq}) \) for any strength of between-group competition.

For the case of PD and HD games, we can also characterize useful properties of the steady-state densities to quantify the collective outcome from maintaining cooperation in the long-time limit. For the PD steady states, we can calculate that the average payoff of the population at density steady state is given by

\[
\langle G(\cdot) \rangle_{f_\lambda} := \int_0^1 G(x) f_\lambda^x (x) dx = P + \gamma + \alpha + \frac{(\beta + \alpha) \theta}{\lambda} = G(1) - \frac{(\pi_D(1) - \pi_C(1)) \theta}{\lambda} \tag{20}
\]

for \( \lambda \geq \lambda_{PD}^* \) (Cooney 2020). In addition, we can use Eq. (17) to write the average payoff of the population at the density steady state using the threshold selection intensity \( \lambda_{PD}^* \), which gives us

\[
\langle G(\cdot) \rangle_{f_\lambda} = \left( \frac{\lambda_{PD}^*}{\lambda} \right) G(0) + \left( 1 - \frac{\lambda_{PD}^*}{\lambda} \right) G(1) \tag{21}
\]

(Cooney 2020; Cooney and Mori 2021). Therefore, the average payoff of the population at steady-state interpolates between \( G(0) \) at \( \lambda = \lambda_{PD}^* \) and \( G(1) \) as \( \lambda \to \infty \). Notably, this means that the average payoff of the population is limited by the average payoff of full-cooperator group \( G(1) \), even for cases of the PD game in which the average payoff of group members \( G(x) \) is maximized by an intermediate fraction of cooperators and defectors. An analogous behavior is seen for HD games when \( \lambda \geq \lambda_{HD}^* \), where the average payoff at steady state satisfies

\[
\langle G(\cdot) \rangle_{g_\lambda} = \left( \frac{\lambda_{HD}^*}{\lambda} \right) G(x_{eq}) + \left( 1 - \frac{\lambda_{HD}^*}{\lambda} \right) G(1) \tag{22}
\]

(Cooney 2020). From these expressions for the collective payoff at steady state, we see a signature of a shadow of lower-level selection: the presence of even a slight individual-level advantage for defection prevents the long-time achievement of intermediate collective payoff optima under the multilevel dynamics of Eq. (8).

We can also explore this shadow of lower-level selection by computing the modal fraction of cooperation in a given steady-state density. We will now summarize results from Cooney (2020) on the modal composition at steady state for both the PD and HD games. For both games, we can compute that, when \( \lambda \) is large enough such that the multilevel dynamics converge to a bounded density state, the modal level of cooperation
in the long-time population is given by the following expression:

\[
\hat{x}_\lambda = \frac{\lambda \gamma - 2(\alpha - \beta) - \sqrt{(\lambda \gamma - 2(\alpha - \beta))^2 + 4(\lambda(\gamma + \alpha) + (\beta + \alpha)\theta + \beta)(3 + \lambda)\alpha}}{-2(3 + \lambda)\alpha}
\]

(23)

(Cooney 2020). For the PD case, we further note that \( f(t, x) \) converges to \( \delta(x) \) when \( \lambda \leq \lambda_{PD}^* \) and that the steady-state density of Eq. (16) blows up near 0 when \( \lambda_{PD}^* < \lambda < \lambda_{PD}^* + |\beta|/(\gamma + \alpha) \). This tells us that the modal outcome at steady state for the PD game satisfies the following piecewise characterization

\[
\hat{x}_\lambda = \begin{cases} 
0 & : \lambda \leq \lambda_{PD}^* + |\beta|/(\gamma + \alpha) \\
\hat{x}_\lambda^+ & : \lambda > \lambda_{PD}^* + |\beta|/(\gamma + \alpha)
\end{cases}
\]

(24)

Using an analogous approach, we can find that the modal composition at steady state for the multilevel HD dynamics is given by

\[
\hat{x}_\lambda = \begin{cases} 
x_{eq} & : \lambda \leq \lambda_{HD}^* + \beta/\gamma + \alpha - \beta \\
\hat{x}_\lambda^+ & : \lambda > \lambda_{HD}^* + \beta/\gamma + \alpha - \beta
\end{cases}
\]

(25)

In the limit of infinite strength of between-group competition, we can further use Eq. (23) to compute that the modal composition at steady state satisfies

\[
\hat{x}_\infty := \lim_{\lambda \to \infty} \hat{x}_\lambda = \left\{ \begin{array}{ll}
\gamma + \alpha \\
\gamma + 2\alpha
\end{array} \right\}_{\alpha} : \begin{array}{ll}
\gamma + 2\alpha < 0 \\
\gamma + 2\alpha \geq 0
\end{array}
\]

(26)

For the case of PD and HD games for which there is an intermediate collective payoff optimum \( x^* = \frac{\gamma}{-2\alpha} < 1 \) (and correspondingly \( \gamma + 2\alpha < 0 \)), this means that \( \hat{x}_\infty = \lim_{\lambda \to \infty} \hat{x}_\lambda = \frac{\gamma + \alpha}{-\alpha} < \frac{\gamma}{-2\alpha} = x^* \) (Cooney 2020). As a result, the population will concentrate upon a composition feature less cooperation than is socially optimal even when we our relative emphasis \( \lambda \) on between-group composition tends to infinity (Cooney and Mori 2021). For the alternate case in which \( G(x) \) is maximized by the all-cooperator outcome \( x^* = 1 \), we instead have that the modal composition satisfies \( \hat{x}_\infty = 1 = x^* \), and the population concentrates upon the socially optimal all-cooperator composition in the limit as \( \lambda \to \infty \) (Cooney 2020; Cooney and Mori 2021).

In the remainder of our paper, we will use these expressions for the average payoff and modal composition of cooperation at steady state to quantify the impact of within-group mechanisms on supporting long-time cooperation. We will place emphasis on how these mechanisms impact the ability to facilitate cooperation at lower relative strengths of between-group selection \( \lambda \), and we will explore the behavior of the model
in the limit as \( \lambda \to \infty \) to see how the mechanisms interact with the shadow of lower-level selection. In Sect. 2.2.1, we will illustrate how we incorporate the changes in individual payoff to incorporate these mechanisms within our model of multilevel selection.

### 2.2.1 Transformed Payoff Matrices and Multilevel Dynamics

Here we present an approach we can use to incorporate the mechanisms of like-with-like assortment, other-regarding preferences, and reciprocity into our model of multilevel selection. For each of these mechanisms, we can describe the impact of these mechanisms by a one-parameter family of payoff functions \( \pi_C^\xi(x) \) for \( \pi_D^\xi(x) \), where the parameter \( \xi \) will depend on our model of the mechanism. We will associate each mechanism with a modified family of payoff matrices that depend on our structure parameter \( \xi \).

\[
\begin{pmatrix}
C & D \\
D & \begin{pmatrix}
R_\xi & S_\xi \\
T_\xi & P_\xi
\end{pmatrix}
\end{pmatrix}
\]  

(27)

and we can use the transformed payoff matrix to calculate the effective payoffs \( \pi_C^\xi(x) = R_\xi x + S_\xi (1 - x) \) and \( \pi_D^\xi(x) = T_\xi x + P_\xi (1 - x) \) for each mechanism (Nowak 2006; Taylor and Nowak 2007; Kaznatcheev 2018). By further calculating the average payoff for group members \( G_\xi(x) = x\pi_C^\xi(x) + (1 - x)\pi_D^\xi(x) \), we can then incorporate each within-group mechanism into the dynamics of multilevel selection by considering solutions to the following PDE:

\[
\frac{\partial f(t, x)}{\partial t} = -\frac{\partial}{\partial x} \left[ x(1 - x) \left( \pi_C^\xi(x) - \pi_D^\xi(x) \right) f(t, x) \right] + \lambda f(t, x) \left[ G_\xi(x) - \int_0^1 G_\xi(y) f(t, y) dy \right].
\]  

(28)

To explore the impact of each mechanism on the dynamics of multilevel selection, we will use both the modified payoff functions \( \pi_C^\xi(x) \), \( \pi_D^\xi(x) \), \( G_\xi(x) \) and the modified payoff parameters \( \alpha_\xi = R_\xi - S_\xi - T_\xi + P_\xi \), \( \beta_\xi = S_\xi - P_\xi \), and \( \gamma_\xi = S_\xi + T_\xi - 2P_\xi \) to characterize the long-time support of cooperation. In particular, we will calculate the threshold selection strength \( \lambda^\xi_\star \), the average payoff at steady state \( \langle G_\xi(\cdot) \rangle_{f_\lambda^\xi} \), and the modal composition of cooperation at steady state \( \hat{x}_{\lambda^\xi} \), based on the formulas from Eqs. (17), (20), and (24), respectively.

### 3 Within-Group Assortment

In this section, we will consider the effect of within-group assortment on the dynamics of our PDE model of multilevel selection. We consider game-theoretic interactions within groups which follow an \( r \)-assortment process as introduced by Grafen (1979).
and studied in various deterministic and stochastic settings (van Veelen et al. 2017; Allen and Nowak 2015; Cooney et al. 2016; Coder Gylling and Brännström 2018; Iyer and Killingback 2020). In particular, we assume a form of like-with-like assortment in which, with probability \( r \), individuals play the game with an individual with the same strategy, while, with probability \( 1 - r \), individuals play the game with a randomly chosen member of their group. In an infinitely large group with a fraction \( x \) of cooperators, the expected payoff of a cooperator \( \pi^r_C(x) \) and of a defector \( \pi^r_D(x) \) under this assortment process is

\[
\begin{align*}
\pi^r_C(x) &= rR + (1 - r)(xR + (1 - x)S) \\
\pi^r_D(x) &= rP + (1 - r)(xT + (1 - x)P).
\end{align*}
\]

We can also understand the role of the assortment process by describing the expected payoff with the following transformed payoff matrix for well-mixed interactions (Van Veelen 2011; Nowak 2006)

\[
\begin{pmatrix}
C & D \\
D & (1 - r)T + rP
\end{pmatrix}
\begin{pmatrix}
1 - rS + rR \\
(1 - r)S + rR
\end{pmatrix}.
\]

Using the shorthand \( \alpha = R - S - T + P, \beta = S - P, \) and \( \gamma = S + T - 2P \), we see from Eq. (29) that the difference in effective payoffs between cooperators and defectors is given by

\[
\pi^r_C(x) - \pi^r_D(x) = r(\gamma + \alpha) + (1 - r)(\beta + \alpha x).
\]

Using Eqs. (9) and (31), we see that the within-group dynamics have equilibria at 0, 1, and a third point \( x^r_{eq} \) satisfying \( \pi^r_C(x^r_{eq}) = \pi^r_D(x^r_{eq}) \), which is given by

\[
x^r_{eq} = -\frac{\beta}{\alpha} + \left(\frac{r}{1 - r}\right)\left(\frac{\gamma + \alpha}{-\alpha}\right).
\]

The all-defector equilibrium is unstable when \( \pi^r_C(0) > \pi^r_D(0) \), which, for an underlying PD game, occurs for \( r \) exceeding the threshold value \( r^*_W \) given by

\[
r^*_W = \frac{-\beta}{-\beta + \gamma + \alpha} \in (0, 1)
\]

Similarly, we define \( r^a_W \) as the minimum level of \( r \) above which \( \pi^r_C(1) > \pi^r_D(1) \), which is given by

\[
r^a_W = \frac{-(\alpha + \beta)}{\gamma - \beta},
\]

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and therefore the all-cooperator equilibrium is stable under the within-group dynamics when $r > r^a_W$. From Eqs. (33) and (34), we see that $r^s_W < r^a_W$ when $\alpha < 0$ and $r^a_W > r^s_W$ when $\alpha > 0$. This means that, as $r$ increases, the within-group dynamics will feature a stable intermediate equilibrium $x_{\text{eq}}^r$ for $r^s_W < r < r^a_W$ (resembling the within-group Hawk–Dove dynamics) when $\alpha < 0$ and will feature bistability of the all-cooperator and all-defector equilibria (resembling the within-group Stag-Hunt dynamics) when $r^a_W < r < r^s_W$ when $\alpha > 0$.

Using Eq. (29), we see that the average payoff for a group with interactions following this $r$-assortment process is given by

$$G_r(x) = x\pi^C(x) + (1 - x)\pi^D(x)$$
$$= r[P + (R - P)x] + (1 - r)\left[P + (S + T - 2P)x + (R - S - T + P)x^2\right]$$
$$= r[P + (\gamma + \alpha)x] + (1 - r)\left[P + \gamma x + \alpha x^2\right].$$

(35)

(36)

We see that the group payoff function interpolates between the group payoff function for well-mixed interactions $G_0(x) = P + \gamma x + \alpha x^2 = G(x)$ when $r = 0$ and an affine function of cooperator composition $G_1(x) = P + (\gamma + \alpha)x$ favoring as much cooperation as possible when $r = 1$.

Noting that $G'_r(x) = r(\gamma + \alpha) + (1 - r)(\gamma + 2\alpha x)$, we see that for PD games with average payoff $G(x)$ most favoring a mix of cooperators and defectors, average group payoff is maximized by the fraction of cooperators $x^*_r$ given by

$$x^*_r = \begin{cases} 
\frac{\gamma}{2\alpha} + \frac{r}{1 - r}\left(\frac{\gamma + \alpha}{-2\alpha}\right): r < r_B, \\
\frac{\gamma + \alpha}{-2\alpha}: r \geq r_B
\end{cases}$$

(37)

where the critical assortment parameter above which between-group competition most favors full-cooperator groups is

$$r_B = \frac{\gamma + 2\alpha}{\alpha}.$$  

(38)

From our characterization of the within-group dynamics in Eq. (31) and group payoff function (36), we can now look to characterize how assortative interactions with assortment probability $r$ impacts the dynamics of multilevel selection. In Fig. 1, we present two bifurcation diagrams illustrating the within-group equilibria and the collective optimum for cases of PD games in which group-level payoff is maximized by an intermediate level of cooperation under well-mixed interactions. From Eqs. (33), (34), and (38), we see that, when $\alpha < 0$, we do not have a definitive ordering on $r^a_W$ and $r_B$, so, in Figure (31), we depict the two possible rankings of these threshold quantities: $r_B < r^s_W < r^a_W$ (left) and $r^a_W < r_B < r^s_W$ (right). In the former case, the average group-level payoff $G_r(x)$ transitions to most favoring full cooperation at an assortment probability for which the individual-level dynamics feature global stability.
Fig. 1 Bifurcation diagram for within-group replicator dynamics and group type with maximal average payoff our in model for other-regarding preferences. Game-theoretic parameters are given by $\gamma = 1.5$, $\alpha = -1$, and either $\beta = -1$ (left) or $\beta = -1/4$ (right), displaying cases in which either $r_B < r^*_W$ (left) or $r^*_W < r_B$ (right). The green lines refer to the group composition which maximizes average payoff of group members $\bar{x}_F$. Solid blue lines refer to stable equilibria of the within-group dynamics, while dashed blue lines describe unstable equilibria. The gray dot-dashed lines refer to the levels of the assortment probability above which the all-defector equilibrium becomes locally unstable $r^*_W$, above which the all-cooperator equilibrium becomes locally stable $r^*_W$, and above which the average payoff of group members is maximized by the all-cooperator group $r_B$ (Color Figure Online).

Table 1 Long-time behavior of within-group and multilevel dynamics for Prisoners’ Dilemma games for various values of assortment probability $r$.

| Payoff parameters | Assortment probability ($r$) | Within-group | Steady state for multilevel dynamics |
|-------------------|------------------------------|--------------|-------------------------------------|
| $\alpha < 0$      | $r < r^*_W$                  | 0 stable     | $\lambda \leq \lambda^*_r$: delta supported at $x = 0$ |
|                   | $r^*_W < r < r^*_W$         | $x^{eq}_r$ stable | $\lambda > \lambda^*_r$: density supported on $[0,1]$ |
|                   | $r > r^*_W$                  | 1 stable     | $\lambda \leq \lambda^{**}_r$: delta concentrated at $x = x^{eq}_r$ |
| $\alpha > 0$      | $r < r^*_W$                  | 0 stable     | $\lambda \leq \lambda^*_r$: delta supported at $x = 0$ |
|                   | $r^*_W < r < r^*_W$         | $x^{eq}_r$ stable | $\lambda > \lambda^*_r$: density supported on $[0,1]$ |
|                   | $r > r^*_W$                  | 1 stable     | Delta concentrated at $x = 1$ |

The threshold $\lambda^*_r$ denotes the threshold strength of between-group competition $\lambda$ required to sustain cooperation at steady state when the multilevel dynamics with assortment are in the PD regime (corresponding to Eq. (17) for $\lambda^*_P$). The threshold $\lambda^{**}_r$ corresponds to the analogous threshold when the effective payoffs of Eq. (30) correspond to a PD game, and it can be calculated using Eq. (19) for $\lambda^{**}_H$.

of the all-defector equilibrium, while, in the latter case, we the within-group dynamics begin to feature a stable within-group equilibrium at an assortment probability for which group payoff is maximized by an intermediate mix of cooperators and defectors.

In Table 1, we characterize the long-time behavior of the multilevel dynamics for the different possible cases of the assortment probability $r$ and the payoff parameters $\gamma$ and $\alpha$ for the PD game. In addition to the case of $\alpha < 0$ illustrated in Fig. 1, we also present the long-time behavior when $\alpha > 0$ and the within-group dynamics feature bistability of the all-cooperator and all-defector equilibria when $r^*_W < r < r^*_W$. 

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The characterization of the long-time behavior for the different ranges of $\gamma$ and $\alpha$ is based on the characterizing the effective social dilemma given by the transformed payoff matrix of Eq. (30), and then applying the result of Theorem 1 that holds for the transformed game.

Next, we can explore how the presence of assortment impacts the support for cooperation and the collective payoff achieved under the multilevel dynamics. When the assortment probability is sufficiently weak (when $r < r^s_W$ for $\alpha < 0$ and when $r < r^a_W$ for $\alpha > 0$), we can use the results for the multilevel PD dynamics to characterize the long-time outcome in terms of a tug-of-war between the collective incentive to cooperate $G_r(1) - G_r(0)$ and the individual incentive to defect in a many-cooperator group $\pi_D^r(1) - \pi_C^r(1)$. Using Eq. (31), we see that

$$\pi_D^r(1) - \pi_C^r(1) = -r(\gamma - \beta) - (\beta + \alpha) = -r(T - P) + (T - R),$$

so the individual incentive to defect is a decreasing function of $r$. From Eq. (36), we see that group payoff function satisfies

$$G_r(1) - G_r(0) = \gamma + \alpha \quad \text{and} \quad G_r(1) = P + \gamma + \alpha = R = G(1),$$

so the collective incentive to achieve full cooperation over full defection is unchanged by introducing assortative interactions.

Plugging these formulas for $\pi_D^r(1) - \pi_C^r(1)$ and $G_r(1) - G_r(0)$ into Eq. 20, we can find that the average payoff at steady state in the PD regime is

$$\langle G_r(\cdot) \rangle_{f^\lambda_\theta} = P + \gamma + \alpha + \frac{(\alpha + \beta + r(\gamma - \beta)) \theta}{\lambda},$$

so we can note that $\gamma - \beta = T - P > 0$ to deduce that the average payoff at steady state is increasing as assortment increases. Using Eq. (17), we can similarly find the threshold selection strength needed to achieve cooperation is given by

$$\lambda^*_r = \frac{[-(\beta + \alpha) + (\beta - \gamma) r] \theta}{\gamma + \alpha},$$

so the threshold to achieve cooperation decreases with increasing assortment probability $r$. As a result, we see that increasing the assortment probability both facilitates easier achievement of cooperation via multilevel selection as well as a greater long-time collective average payoff under the multilevel dynamics. However, noting from Eq. (40) that $\lim_{\lambda \to \infty} \langle G_r(\cdot) \rangle_{f^\lambda_\theta} = P + \gamma + \alpha = G(1) = R$, we find that assortment has no effect on the collective outcome achieved in the limit of infinite between-group selection strength. While adding assortment to the game-theoretic interactions does help for finite relative selection strength $\lambda$, we still see that best possible outcome of multilevel dynamics is still limited by the payoff of the all-cooperator group. Therefore, adding assortment to the multilevel dynamics cannot erase the shadow of lower-level selection, and an optimal intermediate mix of cooperation and defection still cannot be achieved under the multilevel dynamics with within-group assortment.
Fig. 2  Steady-state densities for \( \lambda = 10, \gamma = 1.5, \alpha = \beta = -1, \theta = 2 \) and various values of the assortment parameter \( r \). The vertical dotted line corresponds to the equilibrium for within-group dynamics for the value of \( r = 0.7 \), and is displayed in the same color as the corresponding steady-state density for that assortment probability (Color Figure Online)

We can also examine how the assortment probability \( r \) impacts the steady-state densities achieved via multilevel selection. In Fig. 2, we display density steady states for the multilevel dynamics for various assortment probabilities \( r \) and a fixed initial condition and relative selection strength \( \lambda \). We see the densities support increasing levels of steady-state cooperation as \( r \) increases, and that for the largest value of \( r \) depicted, the within-group dynamics now favor a stable mix of cooperation depicted with a vertical dashed line with the same color as the corresponding density.

We can also consider the composition of group with greatest abundance at steady state, using Eq. (24) for the case of \( r < r^a_W \) and the fact that the population concentrates upon full cooperation for \( r > r^a_W \). In Fig. 3, we show a comparison between the group type with maximal average payoff \( x^*_r \) (given by Eq. (37)) and the group type that is most abundant at steady state, plotted as a function of the assortment probability \( r \).

In the case of a fixed, finite \( \lambda \) (Fig. 3, left), we see that the modal group type reaches full cooperation as \( r = r^a_W \) and the within-group dynamics themselves favor full cooperation. In the case of infinite \( \lambda \) (Fig. 3, right), we see that the modal group type at steady-state features fewer cooperators than in the optimal group \( x^*_r \) when \( r < r_B \), and then the optimal group and modal group as \( \lambda \to \infty \) coincide at full cooperation when \( r > r_B \). As a result, we see that incorporating additional within-group assortment helps to increase steady-state cooperation for fixed \( \lambda \) and to facilitate the achievement of all-cooperative outcomes in the limit of strong between-group competition.

4 Other-Regarding Preference

In this section, we will consider a model of multilevel selection in which individual-level replication rates depend not only on the payoffs received by a focal individual, but
Fig. 3 Group composition with maximal payoff $x^*$ (blue) and group type that is most abundant at steady state for relative strength of between-group selection $\lambda = 8$ (left) and in the limit as $\lambda \to \infty$ (right), plotted for various values of the assortment parameter $r$. Parameters for game are $\gamma = \frac{3}{2}$, $\alpha = \beta = -1$ for both panels, and the initial condition is chosen to satisfy $\theta = 2$ for the left panel. In both panels, left vertical dashed line corresponds to $r_W^c$ and right vertical dashed line corresponds to $r_W^a$ (Color Figure Online).

Weighing both the payoff of an individual and their opponent serves as a model of other-regarding preferences, as individuals take into account the effect of their cooperation or defection on others when evaluating their payoff for a given interaction. This mechanism of other-regarding preference was originally introduced by Maynard Smith (1982) to be as one representation of the effect of genetic relatedness on cooperation in evolutionary games (Maynard Smith 1982; Taylor and Nowak 2007; Szabo and Szolnoki 2012; Peña et al. 2015), capturing the idea that individuals care not only about their own payoff but could also care about the payoff of relatives. However, the form of this model could also be used to describe a variety of prosocial or moral preferences regarding how to weigh ones own payoff and the payoffs of peers, so, for example, this approach could be used to study the role of norms for fairness or empathy in promoting evolution of cooperation among populations of non-relatives as well.

For our model of other-regarding preferences, we will assume that players interact with others according to the payoff matrix of Eq. (1). From each interaction, the effective payoff obtained by a focal individual will be computed by placing weight $\frac{1}{1+F}$ on the individual’s payoff and weight $\frac{F}{1+F}$ on the payoff of their opponent. The parameter $F$ measures the relative emphasis on one’s own payoff and on the payoff of an opponent, and is sometimes referred to as the degree of fraternity for an interaction (Szabo and Szolnoki 2012). For $F = 0$, individual-level success is determined only the payoff of the focal individual, while, for $F = 1$, individual success places equal weight on the payoff of the individual and their opponent.

Using this rule for weighing the payoffs of an individual and their opponent, we see from the payoff matrix of Eq. (1) that, under the effective payoffs of cooperators and defectors in an $x$-cooperator group are given by

$$
\pi^F_C(x) = x \left[ \frac{R}{1+F} + \frac{FR}{1+F} \right] + (1-x) \left[ \frac{S}{1+F} + \frac{FT}{1+F} \right]
$$
\[
= Rx + \left( \frac{S + FT}{1 + F} \right) (1 - x) \tag{41a}
\]

\[
\pi^F_D(x) = x \left[ \frac{T}{1 + F} + \frac{FS}{1 + F} \right] + (1 - x) \left[ \frac{P}{1 + F} + \frac{FP}{1 + F} \right]
\]

\[
= \left( \frac{T + FS}{1 + F} \right) x + P(1 - x) \tag{41b}
\]

These effective payoffs can also be represented in terms of the following transformed payoff matrix:

\[
\begin{pmatrix}
C & D \\
C & \frac{R}{1 + F} \\
D & \frac{T + FS}{1 + F} \\
D & \frac{P}{1 + F}
\end{pmatrix}.
\tag{42}
\]

Using our shorthand \(\alpha = R - S - T + P\), \(\beta = S - P\), and \(\gamma = S + T - 2P\), we can from Eq. (41) that the difference between the effective payoffs of cooperators and defectors in an \(x\)-cooperator group are given by

\[
\pi^F_C(x) - \pi^F_D(x) = x \left[ R - \frac{S + FT}{1 + F} - \frac{T + FS}{1 + F} + P \right] + \frac{S + FT}{1 + F} - P
\]

\[
= \beta + \left( \frac{F}{1 + F} \right) (\gamma - 2\beta) + \alpha x. \tag{43}
\]

The full-defection equilibrium becomes unstable when \(\pi^F_C(0) > \pi^F_D(0)\), which occurs for

\[
F > F^s_W := \frac{-\beta}{\gamma - \beta}. \tag{44}
\]

We see that \(F^s_W < 1\) provided that \(\gamma > 0\), while the all-defector equilibrium will remain stable for all \(F\) for underlying PD games in which \(\gamma < 0\). This stands in contrast to the \(r\)-assortment model, in which the all-defector equilibrium is always destabilized for sufficiently strong assortment probability.

The full-cooperator equilibrium becomes stable when \(\pi^F_C(1) > \pi^F_D(1)\), which occurs for

\[
F > F^a_W := \frac{-(\beta + \alpha)}{\gamma + \alpha - \beta}. \tag{45}
\]

From Eqs. (44) and (45), we see that \(F^s_W < F^a_W\) for \(\alpha < 0\), while \(F^s_W > F^a_W\) for \(\alpha > 0\).
For a range of fraternity parameters $F$, there also exists an interior equilibrium $x_{eq}^F$ at which $\pi_C^F(x_{eq}^F) = \pi_D^F(x_{eq}^F)$, which is given by

$$x_{eq}^F = \frac{\beta}{-\alpha} + \left(\frac{F}{1 + F}\right) \left(\frac{\gamma - 2\beta}{-\alpha}\right).$$

(46)

This equilibrium is stable when it exists when $\alpha < 0$, while it unstable and separates the basins of attraction for full defection and full cooperation when $\alpha > 0$.

When $F = 1$, the payoff difference of Eq. (41) takes the form

$$\pi_1^C(x) - \pi_1^D(x) = \frac{\gamma}{2} + \alpha x,$$

(47)

and so we see that, in this case, within-group dynamics can support global stability of full cooperation (when $\gamma > 0$ and $\gamma + 2\alpha > 0$), bistability of full cooperation and full defection (for PD games with $\gamma < 0$, whose payoff parameters must correspondingly satisfy $\alpha > 0$ and $\gamma + 2\alpha > 0$), or stability of an interior equilibrium (when $\gamma > 0$ and $\gamma + 2\alpha < 0$). This stands in contrast to the case of the $r$-assortment model, which only allows for the possibility of global stability of full cooperation under individual-level selection when $r = 1$.

In addition, we see from taking the limit as $F \to 1$ in Eq. (46) that, in this case, the interior equilibrium takes the form

$$x_{eq}^F \bigg|_{F=1} = \frac{\gamma}{-2\alpha} = x^*,$$

(48)

which is the intermediate level of cooperation $x^*$ that maximizes average payoff for a group playing a PD game when $\gamma + 2\alpha < 0$. Consequently, when individuals care just as much about their own payoff as the payoff for their opponent, within-group selection can promote the level of cooperation that maximizes the average payoff of the population for the underlying PD game.

Next, we consider the role of average group payoff in this model with other-regarding preferences. We compute that the average payoff of group members for an $x$-cooperator group is given by

$$G_F(x) = x\pi_C^F(x) + (1 - x)\pi_D^F(x) = x \left[ Rx + \left(\frac{S + FT}{1 + F}\right) (1 - x) \right]$$

$$+ (1 - x) \left[ \left(\frac{T + FS}{1 + F}\right) x + P (1 - x) \right]$$

$$= P + (S + T - 2P) x + (R - S - T + P)x^2. \tag{49}$$

Therefore, the collective average payoff is unchanged as $F$ ranges between 0 and 1. In particular, this means that if the baseline game has a group payoff function $G(x)$ that
with an intermediate optimum, then \( G_F(x) \) also has collective payoff maximized by the same intermediate level of cooperation.

Because the group-reproduction function \( G_F(x) \) does not depend on \( F \), we further see in the case that \( G_F(x) \) is maximized by an interior level of cooperation that \( G (x_{eq}^F) \) will exceed \( G(1) \) when \( x_{eq}^F \in \left( \frac{\gamma + \alpha}{-\alpha}, 1 \right) \). In this case, \( x_{eq}^F \) is globally stable under the within-group dynamics, while the condition \( G_F(x_{eq}^F) > G_F(1) \) reflects multilevel dynamics consistent with the anti-coordination games (AC1, AC2) rather than a Hawk–Dove game. The condition \( G_F(x_{eq}^F) > G_F(1) \) is satisfied when \( \gamma + 2\alpha < 0 \) and \( F \) exceeds the following threshold level

\[
F > F_{\text{AC}}^w := \frac{\gamma + \alpha - \beta}{-(\beta + \alpha)} = \frac{1}{F_{\text{W}}}.
\]  

(50)

Notably, only one of the thresholds \( F_{\text{AC}}^w \) or \( F_{\text{AC}}^a \) can be achieved by a feasible weight \( F \leq 1 \) placed on one’s opponent’s payoff. We can deduce from Eqs. (45) and (50) that \( F_{\text{AC}}^a < 1 \) when \( G_F(x) = G(x) \) is maximized by full cooperation (\( \gamma + 2\alpha > 0 \)), while \( F_{\text{AC}}^w < 1 \) when \( G_F(x) \) has an interior optimum (\( \gamma + 2\alpha < 0 \)).

Now that we have characterized the within-group and between-group replication rates for our model with other-regarding preferences, we illustrate several possible bifurcation diagrams for our model in Fig. 4 as we vary the fraternity parameter \( F \). In particular, we illustrate a case in which the full-cooperator equilibrium \( x = 1 \) maximizes average group payoff \( G_F(x) \) (Fig. 4, left), and we see that the within-group dynamics eventually favor full cooperation for \( F \) sufficiently close to 1. We also illustrate a case in which average payoff is maximized by an intermediate fraction of cooperators (4, right), and we see that, as \( F \to 1 \), the equilibrium \( x_{eq}^F \) converges to the intermediate social optimum. In Table 2, we characterize the long-time behavior of the individual-level and multilevel selection for the different possible combinations of the payoff parameters \( \gamma \) and \( \alpha \) and the fraternity parameter \( F \). This highlights the broader class of dynamical behaviors that are possible for the model with other-regarding preferences, as compared to the \( r \)-assortment model and the models of reciprocity that we will present in Sect. 5.

Under this model for other-regarding preferences, the individual-level advantage of defecting in a many-cooperator group is given by

\[
\pi_F^D(1) - \pi_F^C(1) = -(\beta + \alpha) - \left( \frac{F}{1 + F} \right) (\gamma - 2\beta),
\]  

(51)

which is a decreasing function of the weight \( F \) placed on other-regarding payoff (as \( \gamma - 2\beta = T - S > 0 \) for any PD game). The collective incentive to cooperate is given by \( G_F(1) - G_F(0) = G(1) - G(0) = \gamma + \alpha \), which is constant in \( F \). When \( F < \min \left( F_{\text{W}}^a, F_{\text{W}}^w \right) \) and the effective game under other-regarding preference corresponds to a PD game, we can use these formulas and Eq. (17) to see that cooperation can be achieved via multilevel selection when the relative strength of between-group selection
Fig. 4 Bifurcation diagram for within-group replicator dynamics and group type with maximal average payoff in assortment model. The green lines refer to the group composition which maximizes average payoff of group members $x^*_F$. Solid blue lines refer to stable equilibria of the within-group dynamics, while dashed blue lines describe unstable equilibria. The gray dot-dashed lines refer to the fraternity parameter above which the all-defector equilibrium becomes locally unstable $F^*_W$, above which the all-cooperator equilibrium becomes locally stable $F^a_W$, and above which the effective payoff reflects an anti-coordination game $F^AC_W$ (Color Figure Online)

Table 2 Long-time behavior of within-group and multilevel dynamics for Prisoners’ Dilemma games with other-regarding preferences.

| Payoff parameters | Other-regarding preference ($F$) | Within-group Steady state for multilevel dynamics |
|-------------------|---------------------------------|-----------------------------------------------|
| $\gamma > 0$, $\alpha < 0$, $\gamma + 2\alpha < 0$ | $F < F^s_W$ | 0 stable | $\lambda \leq \lambda^*_F$: delta supported at $x = 0$ | $\lambda > \lambda^*_F$: density supported on $[0, 1]$ |
|                   | $F^s_W < F < F^AC_W$ | $x^F_{eq}$ stable | $\lambda \leq \lambda^{**}_F$: delta concentrated at $x = x^F_{eq}$ | $\lambda > \lambda^{**}_F$: density supported on $[x^F_{eq}, 1]$ |
|                   | $F > F^AC_W$ | $x^F_{eq}$ stable | Delta concentrated at $x = x^F_{eq}$ |
| $\gamma > 0$, $\alpha < 0$, $\gamma + 2\alpha > 0$ | $F < F^s_W$ | 0 stable | $\lambda \leq \lambda^*_F$: delta supported at $x = 0$ | $\lambda > \lambda^*_F$: density supported on $[0, 1]$ |
|                   | $F^s_W < F < F^a_W$ | $x^F_{eq}$ stable | $\lambda \leq \lambda^{**}_F$: delta concentrated at $x = x^F_{eq}$ | $\lambda > \lambda^{**}_F$: density supported on $[x^F_{eq}, 1]$ |
|                   | $F > F^a_W$ | 1 stable | Delta concentrated at $x = 1$ |
| $\gamma, \alpha > 0$ | $F < F^a_W$ | 0 stable | $\lambda \leq \lambda^*_F$: delta supported at $x = 0$ | $\lambda > \lambda^*_F$: density supported on $[0, 1]$ |
|                   | $F^a_W < F < F^a_W$ | 0, 1 bistable | Delta concentrated at $x = 1$ |
|                   | $F > F^a_W$ | 1 stable | Delta concentrated at $x = 1$ |
| $\gamma < 0$, $\alpha > 0$ | $F < F^a_W$ | 0 stable | $\lambda \leq \lambda^*_F$: delta supported at $x = 0$ | $\lambda > \lambda^*_F$: density supported on $[0, 1]$ |
|                   | $F > F^a_W$ | 0, 1 bistable | Delta concentrated at $x = 1$ |

The threshold $\lambda^*_F$ denotes the threshold strength of between-group competition $\lambda$ required to sustain cooperation at steady state when the multilevel dynamics with other-regarding preferences are in the PD regime (corresponding to Eq. (17) for $\lambda^*_PD$). The threshold $\lambda^{**}_F$ corresponds to the analogous threshold when the effective payoffs of Eq. (30) correspond to an HD game, and it can be calculated using Eq. (19) for $\lambda^{**}_{HD}$.
satisfies
\[
\lambda > \lambda_F^* := \frac{-\left[\beta + \alpha + \left(\frac{F}{1+F}\right) (\gamma - 2\beta)\right]}{\gamma + \alpha} .
\] (52)

In addition, we can use Eq. (20) to see that, for this range of \( F \), the average payoff at steady state is given by
\[
\langle G_F(\cdot) \rangle_{\tilde{f}_\theta^F} = P + \gamma + \alpha + \frac{\left[\beta + \alpha + \left(\frac{F}{1+F}\right) (\gamma - 2\beta)\right]}{\lambda} \left(\gamma + \alpha\right) .
\] (53)

Therefore, we see that, for \( F < \min \left(F^*_W, F^*_W^a\right), \lambda^*_F \) is decreasing in \( F \) and \( \langle G_F(\cdot) \rangle_{\tilde{f}_\theta^F} \) is increasing in \( F \), so increasing the weight individuals place on the payoff of their opponents makes it easier to achieve cooperation via multilevel selection and to achieve a higher collective payoff at steady state.

In Fig. 5, we display how changing the fraternity parameter \( F \) impacts the steady-state densities \( f^\lambda_F(x) \) achieved as the long-time behavior for a given initial density, fixed relative selection strength \( \lambda \), and a pair of PD games with \( \gamma > 0 \) and \( \alpha < 0 \). The expression for these densities is derived using the effective payoff matrix of Eq. (42), as well as the formulas from Eqs. (16) and (18) for the cases in which \( F < F^*_W \) and in which \( F^*_W < F < \min \left(F^*_W, F^*_W^a, F^*_W^{AC}\right) \), respectively. In Fig. 5(left), we illustrate a case in which full cooperation is collectively optimal \((\gamma + 2\alpha > 0)\), showing that increasing levels of weight \( F \) placed on other-regarding preference allows steady-state outcomes approaching the full-cooperation outcome as \( F \to F^*_W \). In Fig. 5(right), we depict a case in which average group payoff is maximized by 75 percent cooperation, and see that the steady states appear to concentrate upon a concentration of 50 percent cooperation as \( F \to F^*_W^{AC} \). For this choice of parameters, the steady-state population is approaching the composition with the same collective payoff as the full-cooperator group, consistent with the fact the multilevel dynamics will concentrate upon a delta-function \( \delta \left(x - x_{eq}^F\right) \) when \( F > F^*_W^{AC} \) and the effective payoff matrix resembles an anti-coordination game.

In Fig. 6, we present the modal fraction of cooperators \( \tilde{\gamma}_F^\lambda \) achieved at steady state across the range of possible fraternity parameters \( F \in [0, 1] \), given a fixed initial density, relative strength of between-group competition \( \lambda \), and underlying PD game for which average group payoff is maximized by a composition with 75 percent cooperators. This modal outcome is calculated from Eq. (24) when the long-time dynamics result in a bounded steady-state density, and coincide with the within-group equilibrium \( x_{eq}^F \) for values of \( F \) in which the long-time behavior concentrates upon the delta-function \( \delta \left(x - x_{eq}^F\right) \). We see that the modal cooperation is increasing in the fraternity parameter \( F \), and that this modal value approaches the socially optimal level \( x_F^* = \frac{\gamma}{2\alpha} = x^* \) as \( F \to 1 \). Because the group payoff function \( G_F(x) = G(x) \) is unchanged by incorporating other-regarding preferences, the corresponding concentration of the steady-state population upon the socially optimal level of cooperation \( x_F^* \) means that collective payoff population will eventually exceed \( G(1) \) and achieve.
Fig. 5 Steady-state densities for various weights of opponent payoff $F$ and fixed relative between-group selection strength $\lambda = 5$. The parameters to generate these steady states are $\gamma = 2.5$ (left) and $\gamma = 1.5$ (right), with $\beta = \alpha = -1$ and $\theta = 2$ for both panels. The black dashed line in the right panel corresponds to the composition $x^*_F = \frac{\gamma}{-2\alpha}$ that optimizes group payoff (Color Figure Online).

Fig. 6 Comparison of modal level of cooperation achieved at steady state with the composition of cooperators maximizing average payoff, plotted as a function of the fraternity parameter $F$. The solid blue line represents the maximal group payoff $x^*_F = \frac{\gamma}{2\alpha}$, the solid green line represents the modal composition at steady state $x^\lambda_F$, the dashed black line represents the interior within-group equilibrium $x^{Feq}$ when it exists, and the vertical dashed gray lines describe the fraternity levels $F^*_W$ and $F^{AC}_W$ at which the effective payoffs transition to an HD game and to an AC game, respectively (Color Figure Online).

the optimal value $G(x^*) = G\left(\frac{\gamma}{-2\alpha}\right)$. In this sense, we can see the other-regarding preference as a mechanism that helps to overcome the shadow of lower-level selection.

Intuitively, we see that this ability for within-group competition to achieve a social optimum stems from the fact that for $F = 1$, the payoffs received by individuals in an interaction are equal to half of the payoff contributed to the average payoff of group members generated by this interaction. As a result, this equal weighting of payoffs perfectly aligns the individual-level and group-level interests derived from the effective payoffs from the game-theoretic interactions, and synchronizes the dynamics of selection at the two levels upon favoring the outcome $x^* = \frac{\gamma}{-2\alpha}$ when $F = 1$. This
stands in contrast to the mechanism of the $r$-assortment process, which serves to cluster cooperators with cooperators and defectors with defectors, facilitating increased cooperation but with no effort to promote interact the cooperator–defector interactions that can generate optimal group benefit when $S + T > 2R$ (and correspondingly $\gamma + 2\alpha < 0$).

### 5 Reciprocity Mechanisms

Now we turn to analyzing interactions with reciprocity mechanisms, in which cooperators can punish defectors and can help to stabilize populations with an established social norm of cooperation. In Sect. 5.1, we consider a model of Nowak and Sigmund (2005) for social interactions with indirect reciprocity in which cooperators sometimes detect that their opponent is a defector and punish them for their defector status. In Sect. 5.2, we consider a model of direct reciprocity via repeated games, exploring multilevel competition between individuals who always defect and those who conditionally cooperation following the tit-for-tat or grim trigger strategies.

#### 5.1 Simplified Model for Indirect Reciprocity

In this section, we consider the simplified model of indirect reciprocity introduced by Nowak and Sigmund (1998), which modifies our baseline model of game-theoretic interactions by allowing for the possibility for cooperative individuals to punish defection. In particular, we retain the assumption that defectors will always defect, and that cooperators will always cooperate in interactions with other cooperators. The main feature of this model is our assumption about the behavior of cooperators when paired with a defector: with probability $q$, they recognize the defector and punish them with defection, while, with probability $1 - q$, they do not recognize the defector and choose to cooperate. If the payoffs from these interactions follow the payoff matrix of Eq. (1), then the interaction rules for this model of reciprocity result in the following effective payoffs for cooperators and defectors in an $x$-cooperator group

$$
\pi^q_C(x) = xR + (1 - x)(qP + (1 - q)S) = (1 - q)\pi_C(x) + qP + q(\gamma + \alpha)x
$$

$$
\pi^q_D(x) = x(qP + (1 - q)T) + (1 - x)P = (1 - q)\pi_D(x) + qP.
$$

For this process, it can also be helpful to view the detection probability $q$ and the expected payoffs in terms of a transformed payoff matrix

$$
\begin{pmatrix}
C \\
D
\end{pmatrix}
\begin{pmatrix}
C \\
R \\
\gamma + \alpha
\end{pmatrix}
\begin{pmatrix}
D \\
(1 - q)S + qP \\
P
\end{pmatrix}
$$

(55)
(Taylor and Nowak 2007). From Eq. (54), we see that the difference in payoffs between a cooperator and defector in the same group is given by

$$\pi^q_C(x) - \pi^q_D(x) = (1 - q) \beta + (\alpha + q \gamma) x. \quad (56)$$

By plugging in $x = 0$, we see from Eq. (56) that $(\pi_C(0) - \pi_D(0) = (1 - q)\beta < 0)$, so the all-defector equilibrium will be locally asymptotically stable for any $q < 1$. In addition, we see that, for any PD game, the all-cooperator equilibrium will become locally asymptotically stable when $\pi^q_C(1) > \pi^q_D(1)$, which occurs for defector detection probability satisfying

$$q > q_{WG} := \frac{-(\beta + \alpha)}{\gamma - \beta}. \quad (57)$$

This means that, for $q \in (q_{WG}, 1)$, the all-cooperator and all-defector equilibria will be bistable under the within-group dynamics, separated by the unstable intermediate equilibrium given by

$$x^q_{eq} = -\frac{(1 - q)\beta}{\alpha + q \gamma}. \quad (58)$$

Average payoff in a group with fraction $x$ cooperators is given by

$$G_q(x) = x \left[ (1 - q)\pi_C(x) + q P + q (\gamma + \alpha) x \right] + (1 - x) \left[ (1 - q)\pi_D(x) + q P \right] = P + (1 - q)\gamma x + (q \gamma + \alpha) x^2. \quad (59)$$

For PD games with intermediate group payoff maxima $x^* = \frac{\gamma}{2\alpha} < 1$, we see that there is a threshold level of detection probability $q_{BG}$ given by

$$q_{BG} = \frac{-2\alpha}{\gamma} - 1 \quad (60)$$

such that the level of cooperation $x^*_q$ maximizing collective payoff $G_q(x)$ under indirect reciprocity has the piecewise characterization

$$x^*_q = \begin{cases} \frac{(1 - q)\gamma}{-2(\alpha + q \gamma)} : q < q_{BG} \\ 1 : q \geq q_{BG} \end{cases}. \quad (61)$$

We note that

$$q_{WG} - q_{BG} = \frac{(\gamma + \alpha)(\gamma - 2\beta)}{\gamma(\gamma - \beta)} < 0$$

for all PD games, so full cooperation will always be most favored by between-group competition for values of the punishment probability $q$ for which the all-cooperator
equilibrium is locally stable under within-group competition. As a result, the effective payoff matrix of Eq. (55) will correspond to an SH game for \( q > q_{WG} \), so, for such values of \( q \), the population will concentrate upon a delta-function at full cooperation in the presence of any between-group competition (i.e., when \( \lambda > 0 \)).

From the above properties of individual and collective payoff functions \( \pi^q_C(x) \), \( \pi^q_D(x) \), and \( G_q(x) \), we are able to illustrate in Fig. 7 the generic bifurcation for the two-level q-process dynamics for an underlying PD game with intermediate group optimum. In particular, we see as \( q \) increases that optimal group composition \( x^*_q \) increases to 1 as \( q \) increases to \( q_{BG} \), while within-group dynamics still favor full defection in this regime and the multilevel dynamics still resemble the PD. Then, as \( q \) increases past \( q_{WG} \), the unstable equilibrium \( x^q_{eq} \) appears, allowing for the bistability of full cooperation and full defection under the within-group dynamics. Finally, full cooperation becomes globally stable within groups when \( q = 1 \) and cooperators punish defectors whenever they interact. In Table 3, we further characterize the behavior of our model of indirect reciprocity under individual-level and multilevel selection, seeing that the effective payoff matrix of Eq. (55) corresponds to a PD game for \( q < q_{WG} \) and an SH game for \( q > q_{WG} \).

Using these formulas, we see that \( G(1) - G(0) = \gamma + \alpha \) and that \( \pi^q_D(1) - \pi^q_C(1) = - (\beta + \alpha) - q (\gamma - \beta) \). When \( q < q_{WG} \) and the multilevel dynamics are in the PD regime, we then see from Eq. (17) that the threshold level of relative selection strength needed to achieve cooperation is

\[
\lambda^*_q = \frac{\theta}{\gamma + \alpha} (- (\beta + \alpha) - q (\gamma - \beta)),
\]
Table 3 Long-time behavior of within-group and multilevel dynamics for Prisoners’ Dilemma games with indirect reciprocity for various values of defector detection probability $q$.

| Detection probability ($q$) | Within-group dynamics | Steady state for multilevel dynamics |
|-----------------------------|------------------------|-------------------------------------|
| $q < q_{WG}$               | 0 stable               | $\lambda \leq \lambda_q^*$: delta supported at $x = 0$ |
| $q_{WG} < q < 1$            | 0, 1 bistable          | $\lambda > \lambda_q^*$: density supported on [0, 1] |

The threshold $\lambda_q^*$ denotes the threshold strength of between-group competition $\lambda$ required to sustain cooperation at steady state when the multilevel dynamics with indirect reciprocity are in the PD regime (corresponding to Eq. (17) for $\lambda_{PD}^*$)

which is decreasing in $q$. Further, we see that

$$\lim_{q \to q_{WG}} \lambda_q^* = \frac{\theta}{\gamma + \alpha} \left[ -\left( \frac{\beta + \alpha}{\gamma - \beta} \right) (\gamma - \beta) \right] = 0,$$

so the relative strength of between-group competition $\lambda_q^*$ needed to achieve any cooperation decreases to 0 in the limit as $q \to q_{WG}$. This coincides with $q$ achieving the punishment probability at which within-group selection is sufficient to sustain the stability of cooperation on its own.

We can also use Eq. (20) to see that the average payoff at the steady-state density is

$$\langle G^q (\cdot) \rangle_{f_\lambda^q} = P + \gamma + \alpha + \frac{(\alpha + \beta + q (\gamma - \beta)) \theta}{\lambda},$$

so the average payoff at steady state is increasing as the probability of detecting defectors. Further, we see that as $q \to q_{WG} = -\frac{\alpha + \beta}{\gamma - \beta}$ that $\langle G^q (\cdot) \rangle_{f_\lambda^q (\alpha)} = P + \gamma + \alpha = G(1)$, in agreement with the observation that the multilevel dynamics are in the SH regime when $q > q_{WG}$ and the population should concentrate at the full-cooperator equilibrium.

In Fig. 8, we illustrate the impact of introducing indirect reciprocity and increasing the defector detection probability $q$ on the steady-state densities of the multilevel dynamics for a fixed initial condition and relative strength of selection $\lambda$. The leftmost and lightest-colored curve corresponds to within-group PD interactions without detection and punishment of defectors ($q = 0$), for which our value of $\lambda$ is only slightly over the threshold level $\lambda_{PD}^*$ needed to produce a steady-state density supporting some cooperation. As we increase the parameter $q$, the steady-state densities with darker-colored curves show increased support for cooperation, with almost all groups consisting mostly of cooperators by the time $q = 0.625$. This is consistent with our result that the steady-state densities should concentrate upon a delta-function at full cooperation when $q \to q_{WG}$, where $q_{WG} = 0.8$ for our choice of parameters.
Fig. 8 Steady-state densities for $\lambda = 10, \gamma = 1.5, \theta = 2, \alpha = \beta = -1$ and various values of the defector detection probability $q$. For this choice of parameters, $q_{WG} = \frac{4}{5}$ and $q_{BG} = \frac{1}{3}$ (Color Figure Online)

5.2 Multilevel Selection in a Repeated Game

In this section, we will consider our multilevel dynamics when game-theoretic interactions correspond to a repeated Prisoners’ Dilemma. Individuals will be paired up for social interactions and initially play a PD game with the payoff matrix from Eq. (1). After each game is played, individuals continue their interaction by playing an additional game with probably $\delta$, and terminate their interaction with probability $1 - \delta$. As a result, a pair of individuals will a sequence of PD games against each other, and the expected length of their interaction is $\frac{1}{1-\delta}$ games. We consider two strategies: always defect (All-D), in which individuals defect in each round, and tit-for-tat (TFT), in which individuals cooperate in the round of an interaction and then copy the action of their opponent in each subsequent round. For consistency with our terminology from previous sections, we will often denote the TFT strategy by $C$ and the All-D strategy by $D$ when describing the individual-level and group-level replication rates.

We now formulate the expected payoffs received by individuals following the TFT and All-D strategies. When two TFT players meet, they both start with cooperation and respond in each subsequent round by cooperation, receiving a reward $R$ for cooperation in each round and accruing an expected payoff of $R \left( \frac{1}{1-\delta} \right)$. When two All-D players meet, they will both defect and receive a punishment $P$ in each round, accruing an expected payoff of $P \left( \frac{1}{1-\delta} \right)$. Finally, when a TFT and All-D player meet, the TFT player cooperates in the first round, receiving payoff $S$, then defects and receives payoff $P$ in all subsequent rounds, resulting in an expected payoff of $S + P \left( \frac{\delta}{1-\delta} \right)$. Correspondingly, an all-D player will receive an expected payoff of $T + P \left( \frac{\delta}{1-\delta} \right)$ when paired with a TFT player.

We then assume that individuals will play the repeated PD against all of the members of their group. In a group composed of fraction $x$ TFT players and $1 - x$ fraction All-D
players, we assume that individuals will play the expected payoff achieved by TFT players and All-D players is given by

$$\pi^C_\delta(x) = x \frac{1}{1-\delta} R + (1-x) \left( S + \frac{\delta}{1-\delta} P \right) = \pi_C(x) + \frac{\delta}{1-\delta} (x R + (1-x) P)$$

(63a)

$$\pi^D_\delta(x) = x \left( T + \frac{1}{1-\delta} P \right) + (1-x) \frac{1}{1-\delta} P = \pi_D(x) + \frac{\delta}{1-\delta} P.$$ 

(63b)

We can also describe this payoff achieved

TFT
\[
\begin{pmatrix}
R \\
\frac{1}{1-\delta} S + \frac{\delta}{1-\delta} P
\end{pmatrix}
\]

All-D
\[
\begin{pmatrix}
\frac{1}{1-\delta} P - \delta \\
\frac{1}{1-\delta}
\end{pmatrix}
\]

(64)

Therefore, the payoff difference between TFT players and All-D players in an $x$-cooperator group is

$$\pi^C_\delta(x) - \pi^D_\delta(x) = \pi_C(x) - \pi_D(x) + \frac{\delta}{1-\delta} (R - P) x$$

$$= \beta + \left[ \left( \frac{1}{1-\delta} \right) \alpha + \left( \frac{\delta}{1-\delta} \right) \gamma \right] x.$$ 

(65)

By plugging in $x = 0$, we see that $\pi^C_\delta(0) - \pi^D_\delta(0) = \beta < 0$ for any PD game and for any $\delta < 0$, so the all-defector equilibrium is always stable under the within-group dynamics. For the all-cooperator equilibrium, we find that

$$\pi^D_\delta(1) - \pi^C_\delta(1) = -\beta - \left[ \left( \frac{1}{1-\delta} \right) \alpha + \left( \frac{\delta}{1-\delta} \right) \gamma \right],$$

(66)

so the all-cooperator equilibrium becomes locally stable when the continuation probability $\delta$ satisfies

$$\delta > \delta_W := \frac{-(\alpha + \beta)}{\gamma - \beta}.$$ 

(67)

We can also use Eq. (63) to see that the average payoff of group members is given by

$$G_\delta(x) = P + \gamma x + \left( \alpha + \frac{\delta}{1-\delta} (\gamma + \alpha) \right) x^2.$$ 

(68)

and that the average payoff in a full-cooperator group is

$$G_\delta(1) = P + \gamma + \alpha + \left( \frac{\delta}{1-\delta} \right) (\gamma + \alpha) = \left( \frac{1}{1-\delta} \right) P + (\gamma + \alpha).$$ 

(69)
Using the quantities calculated above for individual and collective payoff functions \( \pi^C_\delta(x), \pi^D_\delta(x), \) and \( G_\delta(x) \), we see the bifurcation picture and general possibilities for long-time behavior in our model for multilevel selection with direct reciprocity are analogous to that of the indirect reciprocity model presented in Fig. 7 and Table 3.

When \( 0 \leq \delta < \delta_W \), the multilevel dynamics are in the PD regime, so we expect to see density steady states in the form of Eq. (16) when the relative of between-group selection \( \lambda \) is sufficiently large. In particular, we can use Eq. (17) to see that the threshold to establish cooperation through multilevel selection is given by

\[
\lambda^*_\delta = \frac{\theta}{\gamma + \alpha} \left[ \beta + \left( \frac{1}{1 - \delta} \right) \alpha + \left( \frac{\delta}{1 - \delta} \right) \gamma \right],
\]

(70)

which is a decreasing function of the continuation probability \( \delta \). Similarly, we can apply our formulas for direct reciprocity to Eq. (20) to see that, when \( 0 \leq \delta < \delta_W \), the average payoff at the steady-state density

\[
\langle G^\delta(\cdot) \rangle_{f(x)} = \frac{P + \gamma + \alpha}{1 - \delta} + \frac{1}{\lambda} \left[ \beta + \left( \frac{1}{1 - \delta} \right) \alpha + \left( \frac{\delta}{1 - \delta} \right) \gamma \right],
\]

(71)

which is increasing in \( \delta \). Furthermore, in the limit as \( \lambda \to \infty \), the long-time average payoff achieved by the population is given by

\[
\lim_{\lambda \to \infty} \langle G^\delta(\cdot) \rangle_{f^\lambda} = \frac{P + \gamma + \alpha}{1 - \delta},
\]

(72)

which, for \( \delta > 0 \), exceeds the collective payoff achieved by an all-cooperator group under the original game of Eq. (1) under well-mixed one-shot interactions.

In Fig. 9, we illustrate the average payoff of the population at steady state for various values of relative selection strength \( \lambda \) and continuation probability \( \delta \). Unlike the previously studied mechanisms, we see that higher values of average payoff are achieved for larger continuation probabilities than for the average payoff achieved in the limit of strong between-group competition \( (\lambda \to \infty) \) under the multilevel dynamics for the case of well-mixed, one-shot interactions. We also illustrate the threshold level of relative selection strength \( \lambda^*_\delta \) needed to sustain cooperation at steady state by the downward-sloping dashed line.

As we see that allowing repeated interactions improves the maximal possible payoff achieved by groups, it is potentially unfair to measure payoff for an entire repeated game in terms of the payoff matrix of the one-shot stage game. Alternatively, we can consider the possibility of measuring the payoff of the repeated game in the units of the stage game, using the notion of discounted average payoff (Fudenberg and Tirole 1991). Under this approach, we multiply individual payoffs by \( 1 - \delta \) to balance the denominator \( \frac{1}{1 - \delta} \) arising from the receipt of expected payoffs over the potentially infinite horizon of the game. Therefore, the discounted average payoffs \( \tilde{\pi}_C(x) := (1 - \delta)\pi_C(x) \) and \( \tilde{\pi}_D(x) := (1 - \delta)\pi_D(x) \) for the TFT and All-D strategies are given by

\[
\pi^\delta_C(x) = (1 - \delta)\pi_C(x) + \delta (\gamma + \alpha) x + \delta P
\]

(73a)
From these expressions, we see that the discounted average payoffs under direct reciprocity take the same form as the payoffs \( \pi^D_\delta(x) \) and \( \pi^q_D(x) \) from Eq. (54) from our model of indirect reciprocity, except with the continuation probability \( \delta \) taking the place of the defector detection probability \( q \). Intuitively, we can understand this equivalence between the payoffs from our models of indirect reciprocity and of direct reciprocity with discounted average payoffs because interactions between a defector and a cooperator/TFT player generates two punishment payoffs with a given probability (respectively, \( q \) and \( \delta \)) and generates an S payoff and a T payoff with the complementary probability. Under discounted average payoff, we then expect the dynamics of multilevel selection with direct reciprocity to agree with the results from Sect. 5.1 under indirect reciprocity.

6 Discussion

In this paper, we considered the dynamics of a PDE model for multilevel selection arising from evolutionary game theory, exploring the effects of modifying within-group competition through the mechanisms of assortment, other-regarding preferences, and both direct and indirect reciprocity. We found that all four of these mechanisms helped to promote cooperation via multilevel selection, improving the outcome from
multilevel competition relative to the case of well-mixed within-group interactions. Applying recent results for the long-time behavior for this class of PDE models, we were able to characterize the effects of the within-group mechanisms on both the threshold relative strength of between-group selection needed to sustain cooperation at steady state and on the average payoff achieved in a population at steady state. For each mechanism, we find that there is a regime in which the mechanism is sufficiently weak that it cannot help promote any long-time cooperation under individual-level selection, but that the mechanism can help to facilitate the survival of cooperation in concert with multilevel selection.

We illustrate this synergistic effect in Fig. 10, showing, in the case of the assortment model, that there is a broad region of the parameter space of between-group selection strength $\lambda$ and the assortment probability $r$ such that cooperation can be achieved through a combination of assortment and multilevel selection, while defection would dominate in the absence of either of the two mechanisms. A similar figure can be produced to illustrate the synergy of within-group population structure and between-group competition for the promotion of cooperation, highlighting how population structure can help to decrease the individual-level incentive to defect and thereby facilitate the collective achievement of greater levels of cooperation. In Appendix A, we highlight further synergies between multilevel selection and within-group mechanisms when we allow within-group interactions to both follow assortative matching rules and the repeated playing of games. We find that multilevel selection, assortment, and reciprocity can work together to allow achievement of long-time cooperation for values of the between-group selection strength $\lambda$, assortment probability $r$, and continuation probability $\delta$ at which no cooperation could be achieved by any mechanism along or by any combination of two of the three mechanisms.

While we have seen that each of the mechanisms we consider helps to facilitate long-time cooperation and increase the average payoff at steady state for finite strengths of between-group selection, we see that the mechanism differed in their ability to improve the maximal collective outcome achievable under the dynamics of multilevel selection. For our models of assortment and indirect reciprocity, the collective outcome achieved in the limit of infinite strength of between-group competition ($\lambda \to \infty$) was still the payoff of the all-cooperator group ($G(1)$), even under fully assortative interactions ($r = 1$) or when cooperators always punished defectors ($q = 1$). As a result, these two within-group mechanisms were not able to erase the shadow cast by lower-level selection, as, for PD games in which an intermediate level of cooperation maximized collective payoff under well-mixed interactions, no level of assortment or reciprocity could allow the achievement of the socially optimal payoff.

For our model of direct reciprocity, the maximal achievable average payoff was $G_\delta(1) = (1 - \delta)^{-1} G(1)$, so the presence of repeated interactions did result in improved collective outcomes, with the caveat that repeated interactions naturally increases the total available payoff from interactions between individuals. Finally, for our model with other-regarding preferences, we saw that, when individual-level reproduction rates place sufficient weight on the payoffs of one’s opponents we were able to see that the dynamics of individual-level and multilevel selection can promote collective outcomes that can outperform the all-cooperator group. Furthermore, the socially optimal collective outcome is always achieved in the limit when individual payoffs
Fig. 10 Illustration of regions of parameter space of between-group selection strength $\lambda$ and assortment probability $r$ in which cooperation can be supported under individual-level selection with assortative interactions, under multilevel selection, or with a combination of the two mechanisms. Given a fixed initial distribution of strategies, we can divide the parameter space into the following four regions: in which cooperation survives under multilevel selection with well-mixed interactions (Region I), in which cooperation can only survive under the combination of assortment and multilevel selection (Region II, highlighted in green), in which defection dominates the population even in the presence of assortment and multilevel selection (Region III), and in which cooperation can survive by individual-level selection alone in the presence of assortative interactions (Region IV). Game-theoretic parameters are given by $\alpha = \beta = -1$ and $\gamma = 1.5$, and then initial condition has Hölder exponent $\theta = 2$ near the all-cooperator equilibrium (Color Figure Online)

place equal weight on one’s own own payoff and the payoffs of one’s opponents, achieving perfect alignment of individual and collective evolutionary interests.

From a modeling perspective, the difference between the maximal collective outcomes depends on the ways in which each mechanism alters the individual-level and group-level evolutionary incentives. Each of these mechanisms decreases the individual-level incentive to defect in a group with many cooperators, which is why we see the decrease in threshold between-group selection strength and the increase in average payoff at steady state when there is a marginal increase in the strength of each of our mechanisms (corresponding to increasing the parameters $r$, $F$, $q$, or $\delta$ in each of our models). However, our mechanisms differ in how they serve to either promote cooperation or help increase average payoff of the group. Our model of assortment clusters cooperators with cooperators and defectors with defectors, serving to increase the individual-level incentive to cooperate even when an intermediate level of cooperation may produce the best average outcome in a group. Similarly, both the models of direct and indirect reciprocity considered in this paper serve to decrease the individual incentive to defect, and results in punishing defectors even when some presence of defectors would actually benefit the group. By contrast, the mechanism of other-regarding preference serves to incentivize individuals to care about the impacts of their actions on their opponents, connecting the individual benefit derived from a game-theoretic interaction with the contribution that this interaction makes toward the average payoff of the group. As other-regarding preference is the only mechanism we
consider that emphasizes improving average payoff rather than increasing cooperation per se, it makes sense that this is the only mechanism that can allow achievement of collective outcomes exceeding the all-cooperator payoff when the underlying game most favors a mix of cooperators and defectors under between-group replication.

From a mathematical perspective, the analysis of the models in this paper highlights two different key routes for mechanisms to improve the best possible collective outcome achievable under the long-time dynamics of multilevel selection. The first option is for a mechanism to increase the collective reproduction rate $G(1)$ of the all-cooperator group, which occurs in our model of direct reciprocity. The second option is for a mechanism to change the within-group dynamics such that a new equilibrium $x_{eq}$ can feature a greater collective reproduction rate $G(x_{eq})$ than that of the all-cooperator group. This can occur either through a bifurcation creating a stable within-group equilibrium, as seen in our model of other-regarding preferences, or by the creating of a new unstable equilibrium, as seen in a recent paper on a PDE model for protocell evolution through the introduction of a third strategy (Cooney et al. 2021). The identification of these two routes to improving the best possible collective payoff can be applied in future work to understand how a range of within-group mechanisms can work in concert with multilevel selection to help promote cooperative behaviors, from homophilous processes like active linking (Pacheco et al. 2006b) and assortative matching (Bergstrom 2003, 1995, 2013) to reciprocity mechanisms like social norms (Axelrod 1986; Nowak and Sigmund 2005; Ohtsuki and Iwasa 2006; Pacheco et al. 2006a) and the social ostracism of defectors (Tavoni et al. 2012; Tilman et al. 2017).

The different behaviors displayed by the mechanisms we considered in this paper also raise questions regarding the ways in which within-group mechanisms work in concert with multilevel selection in the underlying stochastic processes from which our PDE model was derived. In particular, the model of other-regarding preference resulted in convergence to a delta-function at interior levels of cooperation when such mixes of cooperation and defection were socially optimal and sufficient weight was placed on the payoff of opponents. For multilevel selection in groups of finite size, one may expect fixation upon an all-cooperator or all-defector composition, so it may be interesting to explore how such behavior pushing toward intermediate compositions may impact fixation probabilities of cooperation under multilevel selection with other-regarding preference. Furthermore, many PDE models multilevel selection featuring finite size effects, migration, and or mutation (Ogura and Shimakura 1987a, b; Fontanari and Serva 2013, 2014b, a; Velleret 2019), and therefore it may be interesting how such biological factors may interact differently with mechanisms including assortment, reciprocity, and other-regarding preference. Finally, considering factors like non-constant group size and more realistic group-level events (Markvoort et al. 2014; Traulsen and Nowak 2006; Simon 2010) or mechanisms of multilevel selection with assortative group formation (Jensen and Rigos 2018; Bergstrom 2002; Wilson 1975) may have interesting interactions with the within-group mechanisms and the possibility of long-time support for cooperation via multilevel selection.

In prior work by Nowak and coauthors comparing the achievement of cooperation under multilevel selection, assortment, and reciprocity, these mechanisms were presented alongside models in which game-theoretic interactions took place on $k$-regular graphs. Introduced by Ohtuski and coauthors, these models for evolutionary games on
graphs showed how a group of individuals having game-theoretic interactions and competing for replication with neighbors on a graph could achieve cooperation for games in which defection dominated under well-mixed interactions (Ohtsuki et al. 2006; Ohtsuki and Nowak 2006). Ohtsuki and Nowak (2006) used a pair-approximation to derive a replicator equation for individual-level selection on \( k \)-regular graphs for a variety of update rules, and characterize the resulting dynamics in terms of a transformed payoff matrix. Unlike the transformed payoff matrices for the models discussed in this paper, the Ohtsuki–Nowak payoff transformation does not actually describe the payoffs achieved by cooperators and defectors with interactions taking place on a graph, and therefore this payoff matrix cannot be used to formulate the function \( G(x) \) describing the average payoffs of group members in an \( x \)-cooperator group. To study multilevel selection for the case in which within-group interactions and replication competition take place on a \( k \)-regular graph, we will need to return to the pair-approximation to derive an appropriate description of between-group competition and the resulting PDE model for multilevel competition. The details of this analysis are carried out in a complementary paper, and it is shown how the number of graph neighbors \( k \) and the update rule for individual-level selection (death–birth, birth–death, or imitation) impact the level of cooperation achieved via multilevel selection (Cooney and Mori 2021).

Multilevel selection has also been suggested to work in concert with the mechanisms of strong reciprocity via altruistic punishment (Gintis 2000; Boyd et al. 2003; Janssen et al. 2014), institutional incentives for the management of common-pool resources (Waring et al. 2017), and social norms for evaluating and incentivizing individuals based on social reputations (Santos et al. 2007; Scheuring 2010). Simulation studies of cultural group selection have shown that the presence of altruistic punishers can result in greater levels of long-time cooperation than would be achieved under multilevel competition between defectors and non-punishing cooperators alone. Because the approach taken in this paper can be extended to study a broad family of within-group and between-group replication rates for multilevel competition between pairs of types (Cooney and Mori 2021), a potential direction for future research could be to formulate and analyze analytically tractable versions of these models from cultural group selection for the evolution of altruistic punishment or the evolution of social norms. Such an approach would provide a useful baseline for further study in the dynamics of multilevel selection in cultural evolution, and to understand how the ability for social and cultural institutions to facilitate long-time cooperation may depend on the impact they have on the individual incentive to defect and the collective incentive to feature full cooperation over full defection. Furthermore, because many of these existing models study the multilevel competition with three players (defectors, cooperators, and either conditional cooperators or altruistic punishers), these mechanisms also motivate further numerical and analytical investigations for PDE models of multilevel selection with three types of individuals. By considering the different ways in which modifying interactions between individuals can impact the dynamics of PDE models of multilevel selection, we can both learn more about these mechanisms and identify new mathematical approaches for studying the class of non-local, hyperbolic PDEs that arise as replicator equations for selection at multiple levels.
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Data Availability  Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

Code Availability  All codes needed to perform the numerical simulations and to produce the figures of the paper have been archived on GitHub (https://github.com/dbcooney/Multilevel-Mechanism-Paper-Code) and licensed for reuse, with appropriate attribution/citation, under a BSD 3-Clause Revised License.

A Modeling Multilevel Selection with Within-Group Assortment and Repeated Interactions

In this section, we consider the combination of the effects of the mechanisms of within-group assortment and direct reciprocity on the evolution of cooperation via multilevel selection. The combination of these two within-group mechanisms allows us to consider the biological scenario in which individuals play repeated games among relatives. Mathematically, this combined model will assume that game-theoretic interactions consist of repeated games with continuation probability $\delta$ and that the individual-level payoffs are calculated using discounted average payoff. Individuals can either always defect in each round of interaction, or they can play a Tit-for-Tat (TFT) strategy in the repeated game. We then assume that the choice of partners for game-theoretic interactions follows an assortative rule in which individuals are paired with an individual following the same strategy with probability $r$ and are paired with a randomly chosen partner with probability $1 - r$. The choice of discounted average payoff is used to remove the possibility that including repeated interactions increases the total pool of possible payoff achieved during a pairwise interaction between players, so that our analysis of multilevel selection under the combined mechanisms of assortment and direct reciprocity mainly focuses on the impacts of changing interaction partners and punishing defectors on promoting cooperation via multilevel selection.

For notational convenience, we will refer to TFT players as cooperators and use $\pi_C(x)$ to represent the payoff received by TFT players in a group feature fractions $x$ TFT players and $1 - x$ defectors. If interactions with individuals follow an assortative process and the resulting game-theoretic interactions are repeated games with discounted average payoff, we can use Eq. (73) to see that the expected payoffs of cooperators and defectors under this combined within-group mechanism are given by

$$
\pi^{r,\delta}_C(x) = rR + (1 - r)\pi^{\delta}_C(x) = rP + (1 - r)(1 - \delta)\pi_C(x)
$$

$$
+ (1 - r)\delta \left[ P + (\gamma + \alpha)x \right]
$$

(A.1a)

$$
\pi^{r,\delta}_D(x) = rR + (1 - r)\pi^{\delta}_D(x) = rP + (1 - r)(1 - \delta)\pi_D(x) + (1 - r)\delta P.
$$

(A.1b)

We can use these payoffs and the definition of our parameters $\alpha = R - S - T + P$, $\beta = S - P$, and $\gamma = S + T - 2P$ to see that the combined impact of assortment and
direct reciprocity results in the following effective payoff matrix

\[
\begin{pmatrix}
C & R \\
D & (1 - r)(1 - \delta)T + [r + (1 - r)\delta]P
\end{pmatrix}
\begin{pmatrix}
(1 - r)(1 - \delta)S + rR + (1 - r)\delta P \\
PP
\end{pmatrix},
\]

(A.2)

From this effective payoff matrix, we see how the within-group dynamics are modified through both assortative mixing and punishment of defectors in repeated interactions, showing how increase in the parameters \(r\) and \(\delta\) both result in helping to favor the shared incentive of the two players to achieve mutual cooperation over mutual defection.

Using the fact that \(\pi_C(x) - \pi_D(x) = \beta + \alpha x\), we can then compute that the payoff difference between cooperator / TFT players and defectors is given by

\[
\pi^{r, \delta}_C(x) - \pi^{r, \delta}_D(x) = (1 - r)(1 - \delta)(\pi_C(x) - \pi_D(x)) + [r + (1 - r)\delta x] (\gamma + \alpha) = (1 - r)(1 - \delta)(\beta + \alpha x) + [r + (1 - r)\delta x] (\gamma + \alpha).
\]

This expression tells us that increasing either the assortment probability \(r\) or continuation probability \(\delta\) both decreases the impact of the intrinsic incentive to defect in the one-shot PD game \((\pi_D(x) - \pi_C(x))\) and increases the incentive to cooperate through placing weight on the incentive to cooperate under assortative or repeated interactions \((\gamma + \alpha = R - P)\).

We see that the all-defector equilibrium is destabilized under the within-group dynamics when

\[
\pi^{r, \delta}_C(0) - \pi^{r, \delta}_D(0) = (1 - r)(1 - \delta)\beta + r(\gamma + \alpha) > 0.
\]

Given \(\delta > 0\), we see that this condition is satisfied provided that assortment probability exceeds the following threshold value

\[
r > r^{s}_W(\delta) := \frac{-(1 - \delta)\beta}{\gamma + \alpha - (1 - \delta)\beta} = 1 - \frac{\gamma + \alpha}{\gamma + \alpha - \beta(1 - \delta)} \in (0, 1),
\]

(A.5)

where we deduced that \(r^{s}_W(\delta) \in (0, 1)\) using the fact that \(\gamma + \alpha = R - P > 0\) and \(\beta = S - P < 0\) for the PD game. We note that \(r^{s}_W(\delta)\) is a decreasing function of the continuation probability \(\delta\), and therefore adding repeated interactions and direct reciprocity can work in concert with assortment to help promote cooperation through within-group selection.

We can similarly find that the all-cooperator equilibrium will become stable when \(\pi^{r, \delta}_C(1) > \pi^{r, \delta}_D(1)\), which, for given value of \(\delta\), occurs when the assortment probability satisfies

\[
r > r^{a}_W(\delta) := \frac{-(\beta + \alpha) - \delta(\gamma - \beta)}{(1 - \delta)(\gamma - \beta)} = 1 - \frac{\gamma + \alpha}{(1 - \delta)(\gamma - \beta)} \in (0, 1)
\]

(A.6)
This threshold is also decreasing in the continuation probability $\delta$, as we can compute that

$$\frac{\partial}{\partial \delta} \left( r_W^a(\delta) \right) = \frac{-(\gamma + \alpha)}{(1 - \delta)^2(\gamma - \beta)} < 0,$$  \hspace{1cm} (A.7)

with $\gamma + \alpha > 0$ and $\gamma - \beta = T - P > 0$ for the PD game. Furthermore, we can use Eqs. (A.5) and (A.6) to compute that

$$r_W^d(\delta) - r_W^s(\delta) = (\gamma + \alpha) \left[ \frac{1}{\gamma + \alpha - \beta(1 - \delta)} - \frac{1}{(1 - \delta)(\gamma - \beta)} \right]$$

$$= \frac{-(\gamma + \alpha)}{(1 - \delta)(\gamma - \beta)} \left[ \delta \gamma + \alpha \right].$$  \hspace{1cm} (A.8)

We see from Eq. (A.8) that $r_W^a(\delta) < r_W^s(\delta)$ when either $\alpha > 0$ (in agreement with the result derived in Sect. 3 for assortment in the absence of direct reciprocity) or $\alpha < 0$ and $\delta > \frac{-\alpha}{\beta}$ (where $\frac{-\alpha}{\beta} < \frac{-(\beta + \alpha)}{\gamma - \beta}$ for PD games). This later case means that there are PD games for which assortment alone will always destabilize the all-defector equilibrium before stabilizing the all-cooperator equilibrium, but the combination of assortment and direct reciprocity can result in the bistability of the all-cooperator and all-defector equilibria. In such a case, the multilevel dynamics will resemble that of an SH game when $r_W^a(\delta) < r < r_W^s(\delta)$, and will result in the long-time concentration of the population upon a delta-function at the all-cooperator equilibrium in the presence of any between-group competition (i.e., when $\lambda > 0$).

When, instead, we have that $\alpha < 0$ and $\delta < \frac{-\alpha}{\beta}$, we have that $r_W^s(\delta) < r_W^a(\delta)$, so there exists a range of assortment probabilities for which a stable interior mix of cooperators and defectors will be achieved under individual-level selection acting on its own. In the presence of multilevel selection, the combination of assortment and direct reciprocity will result in dynamics resembling an HD game when $r_W^s(\delta) < r < r_W^a(\delta)$. In this case, there exists a unique equilibrium $x^r_{\text{eq}} \in (0, 1)$ that is the globally stable attractor for the within-group evolutionary dynamics.

Next, we study the average payoff in an $x$-cooperator group under our model combining assortment and direct reciprocity. We can use the expressions in Eq. (A.1) to see that the average payoff $G_{r, \delta}(x)$ is given by

$$G_{r, \delta}(x) = x \left[ rR + (1 - r)(1 - \delta)\pi_C(x) + (1 - r)\delta (P + (\gamma + \alpha)x) \right]$$

$$+ (1 - x) \left[ rP + (1 - r)(1 - \delta)\pi_D(x) + (1 - r)\delta P \right]$$

$$= (1 - r)(1 - \delta)G(x) + (1 - r)\delta P + rP + r(\gamma + \alpha)x$$

$$+ \left[ (1 - r)(\gamma + \alpha) \right] x^2$$

$$= P + \left[ r(\gamma + \alpha) + (1 - r)(1 - \delta)\gamma \right] x$$

$$+ \left[ \delta(1 - r)(\gamma + \alpha) + (1 - r)(1 - \delta)\alpha \right] x^2.$$  \hspace{1cm} (A.9)
From Eq. (A.9), we see that the difference between the average payoff of the full-cooperator and full-defector groups is given by

\[ G_{r,\delta}(1) - G_{r,\delta}(0) = \left[ r(\gamma + \alpha) + (1 - r)(1 - \delta)\gamma \right] \\
+ \left[ \delta(1 - r)(\gamma + \alpha) + (1 - r)(1 - \delta)\alpha \right] \\
= \gamma + \alpha \\
= G(1) - G(0), \tag{A.10} \]

so the collective incentive to achieve full cooperation over full defection is unchanged due to combined effects of the mechanisms of assortment and direct reciprocity.

Using Eq. (A.3), we can also see that individual incentive to defect in a full-cooperator group is given by

\[ \pi^{r,\delta}_{D}(1) - \pi^{r,\delta}_{C}(1) = - \{(1 - r)(1 - \delta)(\beta + \alpha) + [r + (1 - r)\delta](\gamma + \alpha)\} \cdot \tag{A.11} \]

We compute the following partial derivatives,

\[ \frac{\partial}{\partial r} \left( \pi^{r,\delta}_{D}(1) - \pi^{r,\delta}_{C}(1) \right) = -(1 - \delta)(\gamma - \beta) = -(1 - \delta)(T - P) < 0 \tag{A.12a} \]

\[ \frac{\partial}{\partial \delta} \left( \pi^{r,\delta}_{D}(1) - \pi^{r,\delta}_{C}(1) \right) = -(1 - r)(\gamma - \beta) = -(1 - r)(T - P) < 0, \tag{A.12b} \]

so the individual incentive to defect is decreasing in both the assortment probability \( r \) and the continuation probability \( \delta \).

Combining our expressions for the individual-level and group-level incentives with Eq. (17), we can see to see that, when \( r < \min\{r^s_{W}(\delta), r^a_{W}(\delta)\} \) and \( \lambda > \lambda^*_{r,\delta} \), the threshold relative selection strength to sustain long-time cooperation is given by

\[ \lambda^*_{r,\theta} = \frac{\left[ \pi^{r,\delta}_{D}(1) - \pi^{r,\delta}_{C}(1) \right] \theta}{G_{r,\delta}(1) - G_{r,\delta}(0)} \\
= - \{(1 - r)(1 - \delta)(\beta + \alpha) + [r + (1 - r)\delta](\gamma + \alpha)\} \theta \tag{A.13} \]

Using Eq. (20), we see that, for \( r < \min\{r^s_{W}(\delta), r^a_{W}(\delta)\} \) and \( \lambda > \lambda^*_{r,\delta} \), the average payoff at steady state is given by

\[ \langle G(\cdot) \rangle_{f} = G_{r,\delta}(1) - \frac{\left[ \pi^{r,\delta}_{D}(1) - \pi^{r,\delta}_{C}(1) \right] \theta}{\lambda} \\
= P + \gamma + \alpha + \frac{(1 - r)(1 - \delta)(\beta + \alpha) + [r + (1 - r)\delta](\gamma + \alpha)}{\lambda} \tag{A.14} \]

Using the expressions above and the partial derivatives of Eq. (A.12), we can deduce that the threshold \( \lambda^*_{r,\delta} \) is a decreasing function of \( r \) and \( \delta \), while the average payoff at
Table 4  Long-time behavior of within-group and multilevel dynamics for Prisoners’ Dilemma games for various values of assortment probability $r$ and for continuation probabilities $\delta < \delta_W$ for repeated game-theoretic interactions.

| Assortment probability ($r$) | Within-group | Steady state for multilevel dynamics |
|------------------------------|--------------|-------------------------------------|
| $\alpha < 0$, $\delta < -\frac{\alpha}{\gamma}$ | $r < r^a_W(\delta)$ | $0$ stable |
|                              | $r^a_W(\delta) < r < r^d_W(\delta)$ | $x_{eq}$ stable |
|                              | $r > r^d_W(\delta)$ | $1$ stable |
| $\alpha > 0$                 | $r < r^a_W(\delta)$ | $0$ stable |
|                              | $r^a_W(\delta) < r < r^d_W(\delta)$ | $0, 1$ bistable |
|                              | $r > r^d_W(\delta)$ | $1$ stable |

The threshold $\lambda^*_{r,\delta}$ denotes the threshold strength of between-group competition $\lambda$ required to sustain cooperation at steady state when the multilevel dynamics under the combined effects assortment and direct reciprocity are in the PD regime (corresponding to Eq. (17) for $\lambda^{PD}_{r,\delta}$). The threshold $\lambda^{**}_{r,\delta}$ corresponds to the analogous threshold when the effective payoffs of Eq. (A.2) correspond to a PD game, and it can be calculated using Eq. (19) for $\lambda^{HD}_{r,\delta}$.

The density steady state $\langle G(\cdot) \rangle_{\theta}$ increases with both these parameters. This means that, as we increase either probability of assortment or the expected length of repeated interactions, we decrease the difficulty of sustaining cooperation via multilevel selection and increase the collective payoff that can be achieved in the long-run population.

In Table 4, we summarize the dynamics of multilevel selection when within-group dynamics follow our model combining assortment and direct reciprocity. Holding fixed the values of the continuation probability $\delta < \delta_W$ and the payoff parameters $\gamma$ and $\alpha$, we describe how changing the assortment probability $r$ impacts the possible long-time behaviors of the multilevel dynamics given an initial density with Hölder exponent $\theta > 0$ near $x = 1$. The main qualitative difference between the behavior of this combined model and our model of multilevel selection with assortative interactions in one-shot games is the type bifurcation in the within-group dynamics that occurs when $\alpha > 0$ and $\delta > -\frac{\alpha}{\gamma}$. In the presence of positive continuation probabilities $\delta$, increasing the assortment probability $r$ first moves the multilevel dynamics from resembling a PD game to that of an SH game, and then further transitioning to PDel dynamics. For the case of assortment in the absence of direct reciprocity, the multilevel dynamics always transition from the PD regime to the HD regime (featuring stable within-group equilibria) whenever the payoff condition $\alpha < 0$ is satisfied for the underlying PD game.
Finally, in Fig. 11, we summarize the synergies between multilevel selection, assortment, and direct reciprocity in the support of long-time cooperation in group-structured populations. We view $\delta > 0$ as fixed parameter, and consider how the strength of between-group selection $\lambda$ required to sustain long-time cooperation varies with the assortment probability $r$. Because the within-group dynamics are capable of producing cooperation on its own when $r \geq \min \{ r^w_s(\delta), r^a_w(\delta) \}$, we know that cooperation can be sustained for any level of between-group competition for such values of the assortment probability. To highlight this fact, we plot in Fig. 11 the threshold of the between-group selection strength $\lambda$ above which cooperation can be sustained in the long-time behavior of the multilevel dynamics, which is given by

$$\hat{\lambda}_{r,\delta} = \begin{cases} \lambda^*_r \colon r < \min \{ r^w_s(\delta), r^a_w(\delta) \} \\ 0 \colon r \geq \min \{ r^w_s(\delta), r^a_w(\delta) \} \end{cases}.$$  

(A.15)

We see from Fig. 11 that the threshold $\hat{\lambda}_{r,\delta}$ is non-increasing in $\delta$ and $r$, so adding greater assortment and continuation probability both decrease the level of between-group competition required to sustain cooperation via multilevel selection. Furthermore, the combination of between-group competition with relative strength $\lambda$, assortment with probability $r$, and direct reciprocity with continuation probability $\delta$ can all work together to promote cooperation in regimes for which cooperation could not be achieved by a single mechanism alone or through a combination of only two of the three mechanisms.
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