

Research



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Exit rights open complex pathways to cooperation

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We study the evolutionary dynamics of the Prisoner's Dilemma game in which cooperators and defectors interact with another actor type called exiters. Rather than being exploited by defectors, exiters exit the game in favour of a small pay-off. We find that this simple extension of the game allows cooperation to flourish in well-mixed populations when iterations or reputation are added. In networked populations, however, the exit option is less conducive to cooperation. Instead, it enables the coexistence of cooperators, defectors, and exiters through cyclic dominance. Other outcomes are also possible as the exit pay-off increases or the network structure changes, including network-wide oscillations in actor abundances that may cause the extinction of exiters and the domination of defectors, although game parameters should favour exiting. The complex dynamics that emerges in the wake of a simple option to exit the game implies that nuances matter even if our analyses are restricted to incentives for rational behaviour.

1. Introduction

In economic game theory, the conditions and consequences of quitting a game [1], and voluntary participation in general, are fundamental topics [2]. In the theory of the evolution of cooperation, however, they are rarer guests [3,4]. Because evolutionary game theory traditionally concerns competition between species, it is not surprising that the primary focus is on involuntary interactions [5,6]. Nevertheless, there is an increasing interest in modelling the interface between cooperation and social behaviour in human populations. We will also take this route and extend the canonical model of cooperation between selfish individuals—the Prisoner's Dilemma [2,7,8]—with an option of exiting the game. To more realistically incorporate sociality, our players, or actors, will interact over model social networks [8–10].

There are historical examples where the option to exit a game could have had a dramatic impact on the outcome. In the final years of the 1950s, China carried out far-reaching collectivization of its society. Everyone in the countryside had to belong to a 'people's commune' where people shared everything—farming tools, seeding crops, draft animals, kitchens and healthcare. Even private cooking was banned and replaced by communal canteens. Between 1958 and 1962, one of the worst famines in the history of humanity struck the country [11]. Ever since then, scholars have debated the connections between these social changes and the famine [12].

One intriguing theory was proposed in 1990 by the economist Justin Yifu Lin of Peking University [13]. He pointed out that with the establishment of the people's

communes, leaving a collective was no longer an option. He reasoned that this revocation of the right to exit took away a disincentive to free ride, as now farmers could no longer avoid negative feedback loops of perfidy. Just how important this mechanism was in the onset of famine has been debated. For example, Dong & Dow [14] and MacLeod [15] contend that Lin was wrong to use various economic arguments, while Orbell *et al.* [16] and Orbell & Dawes [17] lend support to the general idea of exit options promoting cooperation.

We will not dwell further on the question of how well Lin's hypothesis explains the connection between the collectivization and the famine. Instead, intrigued by this historical example, we will investigate in a more generic setting how much a simple right to exit can impact the evolution of cooperation. Our starting point is the Prisoner's Dilemma—a basic mathematical formulation of the situation in which cooperation would be most beneficial in the long run, but only considering the next interaction defection would be advantageous [2,5,8]. There are many mechanisms promoting cooperation in the Prisoner's Dilemma. Nowak [18] divides these mechanisms into five categories—kin and group selection, as well as direct, indirect and network reciprocity. Others try to identify common principles behind all these mechanisms [19–21].

People interact in social networks [8]. The structure of the networks can influence the game dynamics. Therefore, many authors have investigated games in which actors interact over model networks [9,10]. We will investigate the Prisoner's Dilemma with an exit option on the regular lattice, as well as three additional types of network models: (i) small-world networks that have many triangles and short path lengths characteristic of social networks [22], (ii) random regular graphs known to be very robust to perturbations, and (iii) scale-free networks that have fat-tailed degree distributions characteristic of socioeconomic systems [23].

Networked populations have received tremendous attention among evolutionary game theorists upon the discovery that the Prisoner's Dilemma in lattices may generate spatial chaos [24]. Exploring the role of network topology [25], and especially that of heterogeneous networks [26], has proven fruitful, leading up to a landmark result that, when social networks are scale-free, cooperation dominates throughout much of the phase space of the Prisoner's Dilemma and other common social-dilemma games [23,27]. Even in the multi-player generalization of the Prisoner's Dilemma called the Public Goods Game [28], cooperation has been shown to benefit if the game is played in heterogeneous networks [29]. Although networked populations promote cooperation without adding strategic complexity, there have been numerous studies that extend the Prisoner's Dilemma in networks with, for example, punishment [30], reward [31] and reputation [32]. Interestingly, empirical studies have failed to confirm some of these theoretical results. A scale-free topology, for example, was unable to promote cooperation among human actors above the levels established in a lattice [33]. Similarly, introducing peer punishment into simple networks of human actors left cooperation levels unchanged, all the while diminishing other benefits of network reciprocity [34]. Empirical studies have—unrelated to networks—been known to produce conflicting or surprising results. Peer punishment thus may [35] or may not [36] promote cooperation, whereas rewarding may do so, but in a convoluted manner of exploiting a known cognitive bias [37].

Empirical studies notwithstanding, networked populations remain a pillar of modern evolutionary game theory. We build

Table 1. Pay-off matrix for the weak Prisoner's Dilemma with an exit option.

	C	D	E
C	1	0	0
D	b	0	0
E	ϵ	ϵ	ϵ

The first row indicates that when a cooperator, C, meets another cooperator, defector D, or exiter E, they earn a pay-off equal to 1, 0, or 0, respectively. Analogously, when a defector meets a cooperator, defector, or exiter, they earn a pay-off equal to $b \in (1, 2)$, zero, or zero, respectively. Finally, exiters earn a pay-off equal to $\epsilon \in [0, 1)$, irrespective of whom they meet. In the most general variant of the Prisoner's Dilemma, a cooperator meeting another cooperator would earn the pay-off R , a cooperator meeting a defector would earn S , a defector meeting a cooperator would earn T , and a defector meeting another defector would earn P , where these pay-offs must satisfy $T > R > P > S$.

on this pillar by introducing a simple exit option that guarantees a small pay-off to an exiter irrespective of what other actors do. Such a small pay-off should intuitively be understood in the context of our motivational example on farming collectives, in which the farmer who exits their collective forgoes a larger potential benefit (i.e. the economies of scale) but still benefits from cultivating their own land. We begin our analysis with a well-mixed population in which both one-shot and iterated Prisoner's Dilemma games with an exit option are played. We thereafter progressively add more complexity by considering populations in a lattice formation, as well as homogeneous and heterogeneous networks. In doing so, we observe a multitude of dynamic phenomena ranging from cyclic dominance to global oscillations to hub-node stabilization.

2. Methods

The key elements of our modelling approach comprised (i) actions and pay-offs, (ii) population structure, (iii) action selection, and (iv) simulation settings. We proceed to briefly describe each of these elements.

2.1. Actions and pay-offs

For the sake of simplicity, we chose to base our model on the weak Prisoner's Dilemma [38]. In this game, cooperators encountering cooperators receive the pay-off equal to unity. Cooperators encountering defectors receive nothing. Conversely, defectors encountering cooperators receive the temptation pay-off $b > 1$. Defectors encountering defectors receive nothing. We added a third action to this set-up, dubbed exit, such that exiters typically receive a small-but-positive pay-off $\epsilon > 0$ irrespective of whom they encounter. Cooperators and defectors encountering exiters receive nothing. Additional limits imposed on the pay-offs were $b \leq 2$ and $\epsilon < 1$ in order to (i) make the cumulative value of mutual cooperation greater than or equal to that of defection and (ii) make exiting less valuable than cooperating, respectively. The described set-up is neatly summarized in table 1.

2.2. Population structure

We assumed two general types of populations: well-mixed and networked. In the former case, an actor can encounter any other actor. In the latter case, an actor encounters only their neighbours

as prescribed by the network. The basic network structure used in simulations was the regular lattice in two dimensions. Neighbourhood was von Neumann's, meaning that each actor has four neighbours: left, right, up, and down. Boundary conditions were periodic, meaning that, in a lattice of size $L \times L$, actors in the L th row (column) are linked to actors in the first row (column). We also generated regular small-world networks and random regular networks by rewiring the underlying lattice, where the probability of rewiring any particular link ranged from 1% (small-world) to 99% (random). To generate scale-free networks for simulation purposes, we used the Barabási–Albert algorithm [39]. All networks used in this study are visualized in electronic supplementary material, figure S1.

2.3. Action selection

In well-mixed populations, action selection followed the usual replicator dynamics. Actors in networked populations selected their actions through imitation. Specifically, denoting the pay-off earned by a focal actor i with Π_i and the pay-off of a randomly selected neighbour j with Π_j , the probability of the actor i imitating the neighbour j was given by the Fermi rule,

$$W_{i \leftarrow j} = \frac{1}{1 + \exp((\Pi_i - \Pi_j)/K)}, \quad (2.1)$$

where K measures the irrationality of selection. Note that, as $K \rightarrow 0$, the Fermi rule turns into the Heaviside step function such that $W_{i \leftarrow j} = 1$ if $\Pi_i < \Pi_j$, and $W_{i \leftarrow j} = 0$ if $\Pi_i > \Pi_j$, while $W_{i \leftarrow j} = 0.5$ if $\Pi_i = \Pi_j$ holds by definition. We set $K = 0.1$ throughout the study.

2.4. Simulation settings

We arranged simulations in a series of Monte Carlo time steps. In each time step, we randomly selected a focal actor who then played the game with all their neighbours. We thereafter randomly selected one of the focal actor's neighbours, and allowed this neighbour to play the game with all their neighbours as well. We finally compared the pay-offs of the focal actor and the selected neighbour to determine whether the focal actor imitates the neighbour or not.

We paid special attention in simulations to ensure that (i) transient dynamics had subsided and (ii) finite-size effects had been eliminated. We thus ran simulations for $\mathcal{O}(10^4)$ time steps, typically 50 000, while averaging actor abundances over the last $\mathcal{O}(10^3)$ time steps, typically 5000. Networks used in the study contained $\mathcal{O}(10^3)$ nodes, typically 5000.

3. Results

3.1. Well-mixed populations

We start our analysis from one of the simplest possible situations. Specifically, we consider a one-shot Prisoner's Dilemma with an exit option in a well-mixed population and, as mentioned, we simplify the exposition without much loss of generality by assuming the pay-off structure of the weak Prisoner's Dilemma (table 1). Under these conditions, only the monomorphic exiting equilibrium is stable, which is why the existence of the exit option is in no way helpful in establishing cooperation; see electronic supplementary material, remark 1. Actors simply choose to exit the game even if the pay-off obtained by doing so is arbitrarily small; it is better to have some return with certainty than to risk getting exploited by defectors.

The situation changes when we replace the single-shot game by an iterated game. Iterations, provided the game proceeds sufficiently many rounds, may favour cooperation; see electronic supplementary material, remark 2 and [7]. The exit option helps to eliminate defection irrespective of how small the exit

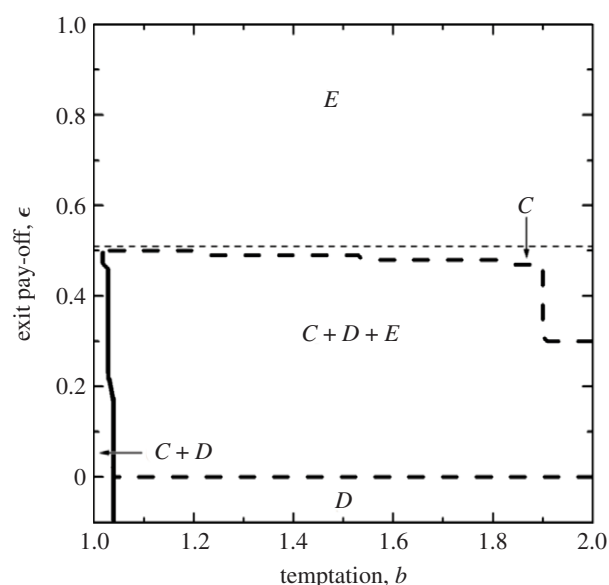


Figure 1. Cooperation is sustained, but rarely dominant, in networked populations with exit. We plot the full ϵ - b phase diagram as obtained by Monte Carlo simulations of the weak Prisoner's Dilemma comprising an exit option in a lattice. When the exit option is highly rewarding, $\epsilon \gtrsim 0.52$, exiters dominate. A less rewarding exit option, $\epsilon \lesssim 0.52$, leads to four different outcomes. If temptation is small, $b \lesssim 1.04$, network reciprocity *eo ipso* ensures that cooperators remain in the population indefinitely alongside defectors (the $C + D$ phase). Larger temptation values, $b \gtrsim 1.04$, lead to defector domination for $\epsilon \leq 0$ (the D phase), but otherwise sustain the coexistence of all three actor types (the $C + D + E$ phase) or lead to cooperator domination (the C phase). Note that purely cooperative outcomes emerge only over a small domain of the ϵ - b phase plane.

pay-off is. Put more technically, the equilibrium of full defection is unstable in this case and cannot be reached by means of evolutionary dynamics. Even if the population initially consisted of defectors alone, such a population would crumble under the slightest perturbation. The reason for this is that, provided the exit pay-off is positive, exiting always confers more benefit than defecting. Actors ultimately choose to cooperate because, without defection as a viable option, cooperation is more beneficial than exiting the game. If we extend the game by adding a variable representing actor reputation, the effect is the same; see electronic supplementary material, remark 3. Our model thus shows that, for well-mixed populations, the availability of the exit option supports cooperation, but only when accompanied by another mechanism, e.g. iterations (i.e. direct reciprocity) or reputation (i.e. indirect reciprocity), that makes cooperation feasible in the first place. These results open the question of what happens when the exit option is available in networked populations, in which the mechanism known as network reciprocity favours cooperation.

3.2. Regular lattice

To answer the question of how cooperation fares in networked populations with an exit option, we resorted to numerical Monte Carlo simulations; see Methods for details. We first performed simulations in lattices characterized by the von Neumann neighbourhood and the periodic boundary conditions. The game parameters were the pay-offs b , $1 < b \leq 2$, and ϵ , $-0.1 < \epsilon < 1$.

In figure 1, we show a phase diagram covering the full range of parameter values. We can see that adding an exit option can

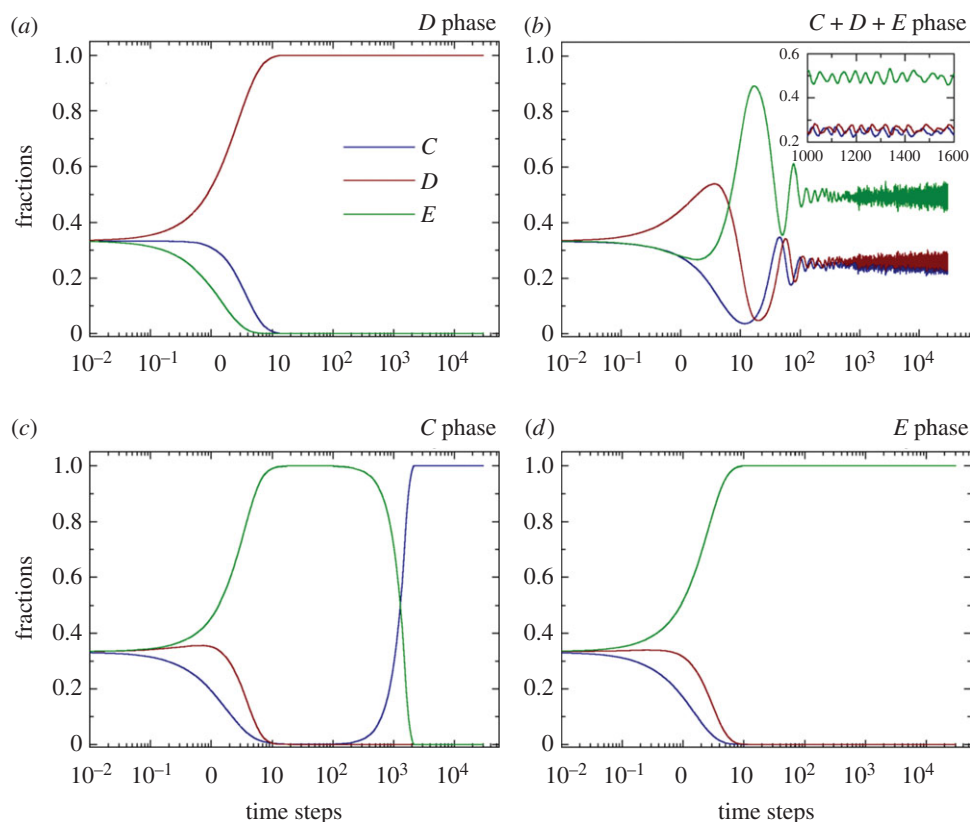


Figure 2. Time dependence of actor abundances reveals cyclic dominance or sole game winners. (a) In the *D* phase, defectors win by eliminating first exitters, then cooperators. (b) In the *C + D + E* phase, oscillating actor abundances are a signature of cyclic dominance. (c) In the *C* phase, the rise of exitters drives defectors to extinction, while rare cooperators survive and later prosper. There is, however, a narrow margin for this to happen. (d) In the *E* phase, the rise of exitters wipes out cooperators even before defectors. We show the results for over 10^4 time steps, which was sufficient for actor abundances to stabilize.

lead to complicated dynamics. First, when the exit pay-off is $\epsilon \gtrsim 0.52$, exitters outcompete other actor types (the *E* phase in figure 1). Conversely, when $\epsilon \lesssim 0.52$, there are four possible outcomes. Small temptation $b \lesssim 1.04$ allows network reciprocity alone to secure the coexistence of cooperators and defectors, while exitters get eliminated from the population (the *C + D* phase in figure 1). Larger temptation $b \gtrsim 1.04$ gives rise to either (i) defector domination for $\epsilon \leq 0$, (ii) the coexistence of all three actor types, or (iii) cooperator domination (respectively, the *D* phase, the *C + D + E* phase, and the *C* phase in figure 1). A chief distinction between well-mixed and networked populations emerging from these results is that the latter permit dimorphic and trimorphic equilibria in which the different types of actors coexist. The exit option thus seems unable to entirely displace defection in networked populations, which is in contrast to our findings in well-mixed populations with either iterations or reputation, as described above.

We can gain a better understanding of how the three types of actors affect one another by looking at the change in their abundances through time (figure 2). In the *D* phase (figure 2a), exitters are the first to give way to defectors, followed shortly thereafter by cooperators. In the *C + D + E* phase (figure 2b), it is cooperators who start giving way to defectors, but then—with fewer cooperators around—exitters temporarily outnumber defectors. Fewer defectors, in turn, allow cooperators to partly recover at the expense of exitters. This proceeds until recovering cooperators once more start giving way to defectors. We have thus described a phenomenon called cyclic dominance in which three actor types dominate one another in an intransitive manner. In our case, cooperators dominate exitters, who dominate defectors, who dominate cooperators. Cyclic dominance

has proven influential in ecological [40] and evolutionary game-theoretic [41] contexts, especially in voluntary dilemmas and extensions thereof [3,42,43].

The phenomenon of cyclic dominance disappears in the *C* phase (figure 2c) because, here, a substantial rise of exitters drives defectors to extinction. At the same time, a tiny fraction of cooperators survive and, in the absence of defectors, eventually take over the lattice. The rise of exitters in the *E* phase (figure 2d), however, is so forceful that they wipe out cooperators even before defectors, thus remaining the sole actor type in the lattice.

The relationships between actor types described here could be seen as power relations, in the sense of who dominates whom and under which conditions. In figure 3, we further analyse such relations by examining the equilibrium abundances of cooperators, defectors, and exitters along several transects of the phase space. These horizontal transects reveal power relations between the three actor types depending on the temptation pay-off, b . In the usual weak Prisoner's Dilemma without exit, this pay-off is equivalent to dilemma strength [44] and thus a crucial determinant of the game outcome. Here, we find that, when exiting is neutral or costly ($\epsilon \leq 0$), network reciprocity can support cooperation by itself for small values of temptation ($b \lesssim 1.04$), but, generally, defectors dominate (figure 3a). When, in contrast, exiting is marginally to moderately profitable ($0 < \epsilon \lesssim 0.52$), network reciprocity still supports cooperation for small values of temptation ($b \lesssim 1.04$), but otherwise the domination of defectors is replaced by the coexistence of all three actor types (figure 3b).

The coexisting state is unusual in that the abundance of exitters increases with temptation, first more at the expense of

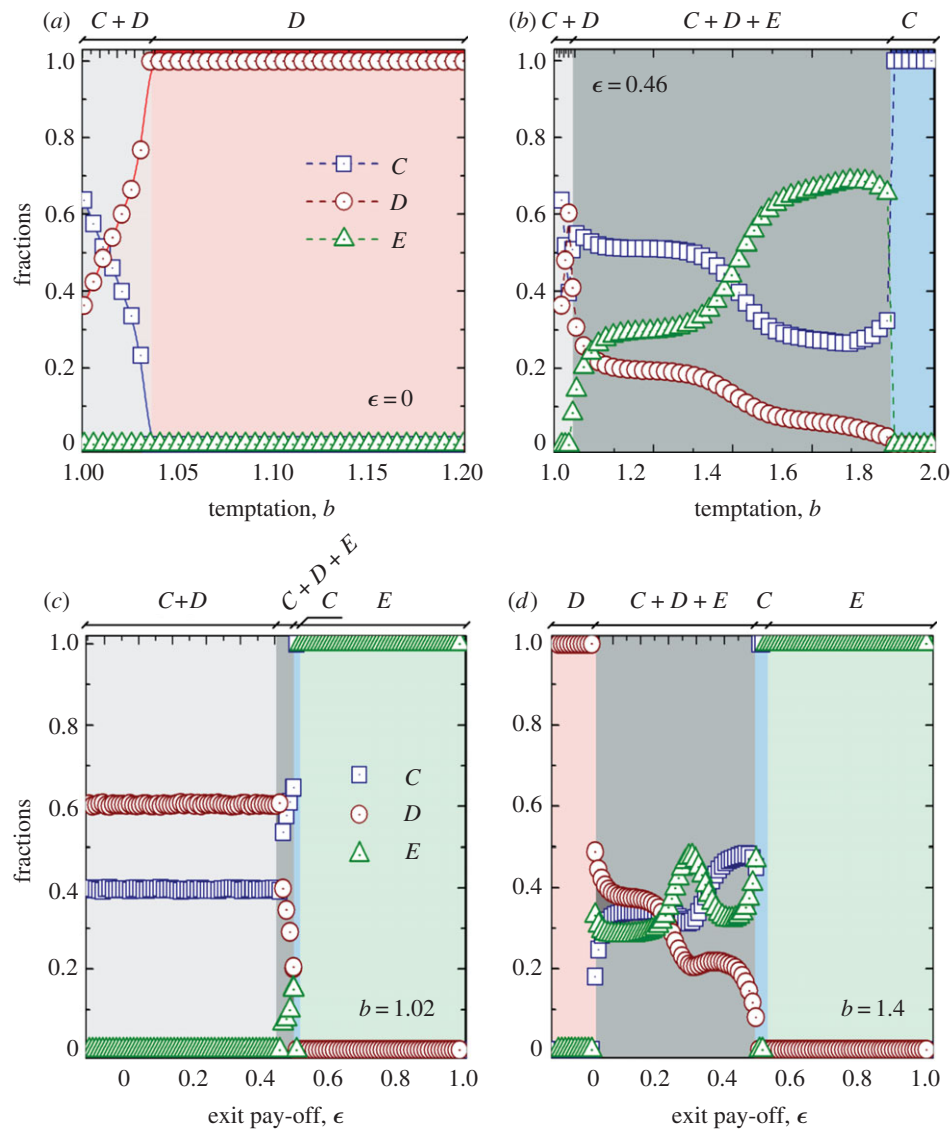


Figure 3. Power relations between cooperators, defectors, and exiters exhibit intricate patterns. (a) Along the horizontal transect of the ϵ - b phase plane at $\epsilon = 0$, network reciprocity alone is enough to secure the coexistence of cooperators and defectors for $b \lesssim 1.04$. Thereafter, defectors prevail. (b) Along the horizontal transect at $\epsilon = 0.46$, cooperators, defectors, and exiters coexist over the temptation range $1.04 \lesssim b \lesssim 1.90$ by way of cyclic dominance. For $b \gtrsim 1.90$, cooperators dominate. (c) Along the vertical transect of the ϵ - b phase plane at $b = 1.02$, network reciprocity secures the coexistence of cooperators and defectors up to a relatively large exit pay-off of $\epsilon \approx 0.45$. In the range $0.45 \lesssim \epsilon \lesssim 0.50$ all three actor types coexist, whereas in the range $0.50 \lesssim \epsilon \lesssim 0.52$ there is a narrow strip of cooperator dominance. Thereafter, exiters prevail. (d) Along the vertical transect at $b = 1.4$, defectors dominate for $\epsilon \leq 0$, the three actor types coexist for $0 < \epsilon \lesssim 0.49$, cooperators dominate over a narrow strip in the range $0.49 \lesssim \epsilon \lesssim 0.52$, and, finally, exiters dominate thereafter. Symbols (squares, circles, and triangles) indicate the average steady-state abundances of the three actor types.

defectors and later at the expense of cooperators. Temptation thus fails to entice defection but instead pushes actors to exit the game. This ultimately hurts defectors, who can even go extinct by temptation being too large ($b \gtrsim 1.90$) and exiting sufficiently profitable ($0.30 \lesssim \epsilon \lesssim 0.52$). Without defectors to exploit them, cooperators become free to dominate (figure 3b).

In a similar vein to horizontal transects, vertical transects of the ϵ - b phase plane also reveal power relations between the three actor types, but this time depending on the exit reward ϵ . For small temptation values, $b \lesssim 1.04$, network reciprocity is enough to ensure the coexistence of cooperators and defectors for a relatively wide range of exit reward values (figure 3c). After crossing $\epsilon \approx 0.45$, exiters are able to reduce the abundance of defectors, and after crossing $\epsilon \approx 0.50$, defectors are eliminated, thus allowing cooperators to flourish (figure 3c). Cooperator domination, however, is short-lived because already beyond $\epsilon \approx 0.52$ cooperators die out ahead of

defectors, so exiters ultimately prevail (figure 3c). For larger temptation ($1.04 \lesssim b \lesssim 1.90$), the described situation partly repeats, that is, for $\epsilon \approx 0.49$ there is again a narrow strip of cooperator domination, followed by a region of exiter domination (figure 3d). The situation changes below $\epsilon \approx 0.49$ because network reciprocity is replaced by cyclic dominance, which ensures the coexistence of all three actor types between $0 < \epsilon \lesssim 0.49$. Defectors prevail if $\epsilon \leq 0$ (figure 3d).

Cyclic dominance gives rise to non-trivial dependence of actor abundances on the exit pay-off. The average steady-state abundance of exiters thus first goes up at the expense of defectors from $\epsilon \approx 0.21$, then goes down in favour of cooperators from $\epsilon \approx 0.30$, only to go up one more time at the expense of defectors from $\epsilon \approx 0.44$ (figure 3d). These undulations in exiter prevalence show that, whenever exiting suppresses defection, cooperation will soon increase. The margin for cooperator domination is generally narrow and

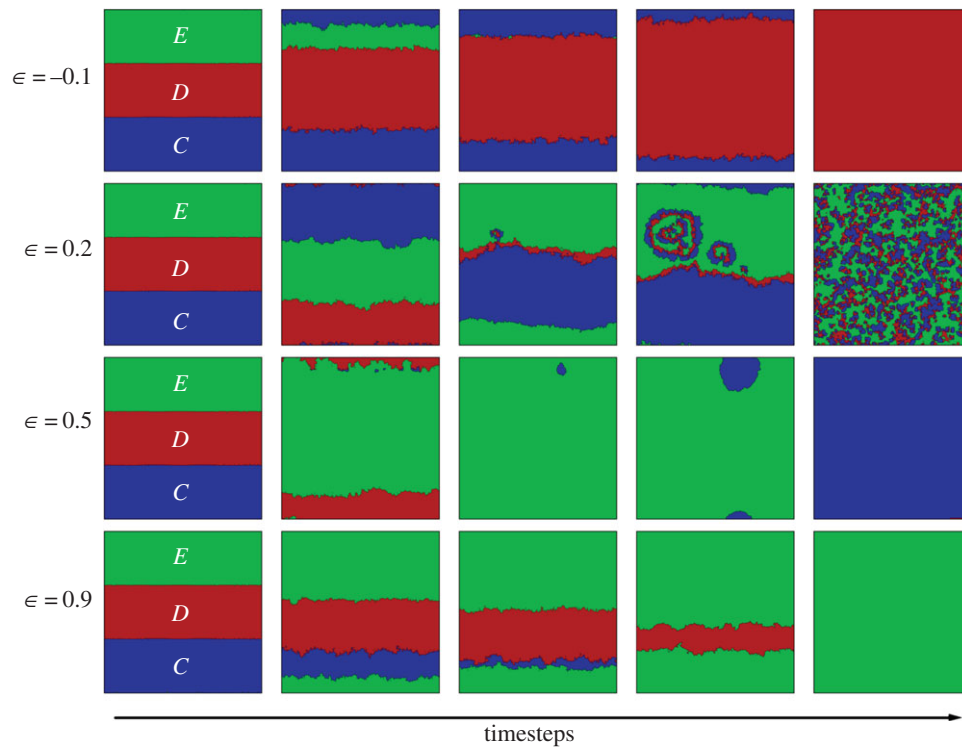


Figure 4. Snapshots of evolutionary dynamics expose in detail the interactions between actor types. When the exit pay-off is negative (top row), both cooperators and defectors oust exiters, who get eliminated first. Afterwards, defectors prevail. When the exit pay-off is small-but-positive (second row), cyclic dominance ensues, as recognizable by the eventual patchy distribution of actor types. A larger positive exit pay-off (third row) enables exiters to eliminate defectors, but in the struggle between remaining cooperators and exiters the former prevails. When the positive pay-off is even larger (bottom row), defectors and exiters oust cooperators. Defectors ultimately lose to exiters, who dominate alone. All simulations were run with temptation $b = 1.9$ for 30 000 time steps to generate the final snapshots (rightmost column). The intermediate snapshots (second to fourth columns) were taken at different time steps across rows to make the figure as illustrative as possible.

widens only for the largest temptation that we consider, $1.90 \lesssim b \leq 2$ (see the C-phase in figure 1).

In contrast to the time series in figure 2, which show the aggregate development of actor abundances along the temporal dimension, snapshots of evolutionary dynamics provide insights into the development of local actor abundances along both spatial and temporal dimensions (figure 4). Snapshots thus open up the opportunity to reexamine the described phenomena from a microscopic perspective. Fixing temptation to $b = 1.9$, we learn that non-positive exit pay-offs make exiters weaker than cooperators or defectors (top row in figure 4). Consequently, cooperators and defectors jointly eliminate exiters, after which cooperators succumb to defectors (top row in figure 4). This sequence of events no longer transpires when the exit pay-off turns positive. Then, instead, all three actor types get perpetually stuck in a loop of cyclic dominance (second row in figure 4). Making the exit pay-off even more positive allows small pockets of cooperators to survive until the elimination of defectors by exiters. Afterwards, cooperators dominate exiters (third row in figure 4). Finally, if the exit pay-off becomes too large, then even cooperators cannot stand up to exiters. Pressured from both defectors and exiters, cooperators get eliminated first, while defectors experience the same fate shortly thereafter, leaving exiters to dominate alone (bottom row in figure 4).

The above analysis of evolutionary snapshots demonstrates that network reciprocity combines with the exit option differently from iterations and reputation. The latter allow that an arbitrarily small-but-positive exit pay-off undermines defection (electronic supplementary material, figure

S2). By contrast, in combination with network reciprocity, cooperation primarily happens via the coexistence of all three actor types owing to cyclic dominance. How general are these observations? To answer this question, we proceed to examine whether and how the underlying network structure affects evolutionary dynamics.

3.3. Other networks

To understand the effects of network structure on evolutionary dynamics, we ran simulations along the vertical transects of the ϵ - b phase plane in three additional network types: regular small-world, random regular, and scale-free (figure 5). The results of these simulations are thus analogous—and best understood by comparing—to the results in figure 3*c,d*. In constructing regular small-world networks, we started with the regular lattice and used random rewiring with the probability of 3% to disconnect two neighbouring nodes and connect two nodes that had been distant before. This construction reduced the network diameter but left other properties, for example the density of squares, almost unchanged, which is why the simulation results for this network type and the regular lattice are similar (figure 5*a*). The only noteworthy difference is that, for small temptation values ($b = 1.02$), regular small-world networks support cyclic dominance more easily than the lattice (upper panel in figure 5*a*). For larger temptation values ($b = 1.4$), we observe the same evolutionary dynamics in both network types (lower panel in figure 5*a*).

In constructing random regular networks, we followed the same procedure as for regular small-world networks, but with

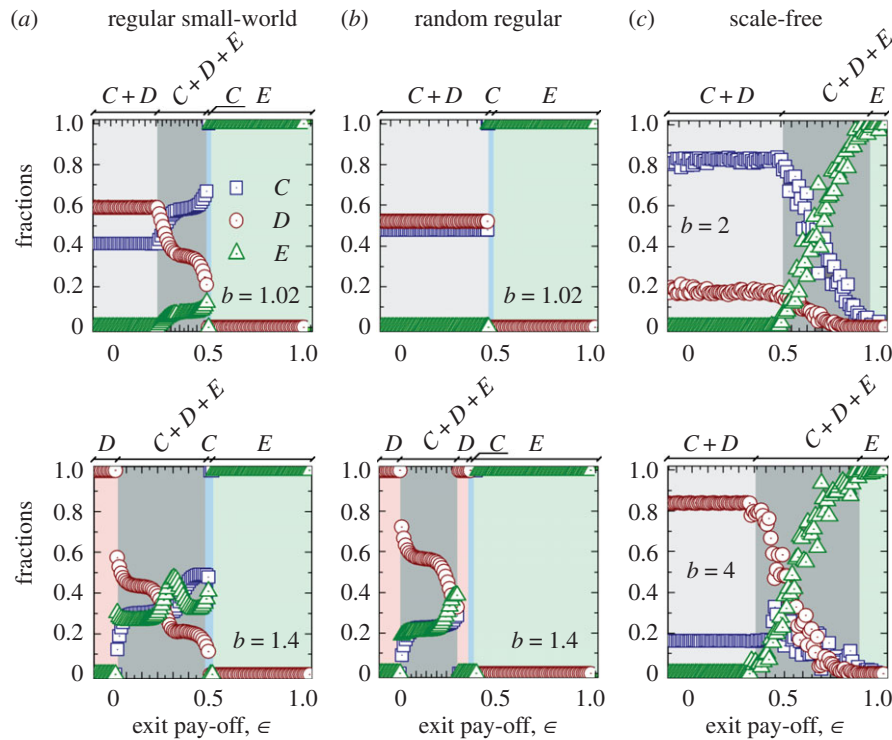


Figure 5. Network structure is an important determinant of evolutionary dynamics in the studied game. (a) Regular small-world networks have a smaller diameter, but otherwise remain similar to the regular lattice from which they were constructed. Consequently, the results here resemble those in figure 3c,d for both small temptation ($b = 1.02$) in the upper panel and larger temptation ($b = 1.4$) in the lower panel. (b) Random regular networks differ more extensively from the regular lattice than regular small-world networks. This affects evolutionary dynamics. For example, there is no cyclic dominance in the upper panel when temptation is small ($b = 1.02$). Cyclic dominance is seen again in the lower panel when temptation is larger ($b = 1.4$), but here the rise of exiters can trigger defector domination for exit pay-offs in the range $0.30 \lesssim \epsilon \lesssim 0.35$. (c) Scale-free networks, constructed using the Barabási–Albert algorithm [39], give rise to fundamentally different evolutionary dynamics from those of other network structures. These networks support a large cooperator abundance even at temptation $b = 2$, as seen in the upper panel. Some level of cooperation is possible even at temptation $b = 4$, as seen in the lower panel. The coexistence of all three actor types, which arises at relatively large values of the exit pay-off, is supported by a mechanism different from cyclic dominance. Finally, the sole domination of exiters is seen only at the near-maximum values of the exit pay-off. Symbols (squares, circles, and triangles) indicate the average steady-state abundances of the three actor types.

the rewiring probability as large as possible. This reduced not only the network diameter but also the density of squares [45], causing evolutionary dynamics to change in two important ways (figure 5b). For small temptation ($b = 1.02$), cyclic dominance vanishes (upper panel in figure 5b), whereas for larger temptation ($b = 1.4$) there is a region of cyclic dominance as before, but now this region is separated from the narrow strip of cooperator domination by a strip of defector domination (lower panel in figure 5b). How is it possible that defectors become dominant when the values of the exit pay-off already strongly favour exiters? We will resolve this mystery shortly, after looking at the evolutionary dynamics in scale-free networks.

Scale-free networks, constructed using the Barabási–Albert model [39], lead to evolutionary dynamics that are fundamentally different from other network types (figure 5c). Even if temptation is ramped up to $b = 2$, network reciprocity supports a large cooperator abundance up to the exit pay-off of $\epsilon \approx 0.48$ (upper panel in figure 5c). After that, the abundance of exiters increases linearly with the exit pay-off up to $\epsilon \approx 0.91$, when this actor type finally prevails. A similar picture holds even for temptation $b = 4$, except that the abundances of cooperators and defectors switch places (lower panel in figure 5c).

It is illustrative at this point to look at the time series of cooperator, defector, and exiter abundances when all three actor types coexist (figure 6). In the regular lattice, we find

that initial large oscillations subside rather quickly, after which there are only small oscillations around the average abundances that are characteristic of cyclic dominance (figure 6a). The situation is similar in regular small-world networks, although the amplitude of oscillations around the average abundances is larger than before (figure 6b). The similarity between the time series in these two cases seems to arise from almost the same density of squares in regular small-world networks as in the regular lattice. It would appear that squares keep oscillations local, and thereby small in amplitude (electronic supplementary material, figure S3A). This is perhaps expected for the regular lattice that lacks long-distance links, but less so for regular small-world networks that are much more compact.

Consistent with the above ideas, we further observe that, as the density of squares approaches zero in random regular networks, oscillations become network-wide and develop very large amplitudes (figure 6c; see also electronic supplementary material, figure S3). There are even instances in which amplitudes are large enough to exterminate exiters, which is the reason why defector domination appears in the lower panel of figure 5b when the exit pay-off should strongly support exiters. We also find that the nature of actor coexistence in scale-free networks is entirely different from that of other network structures. Hub nodes tend to cooperate, while small-degree nodes tend to switch between defection and exiting, which ultimately creates noisy rather than oscillating time

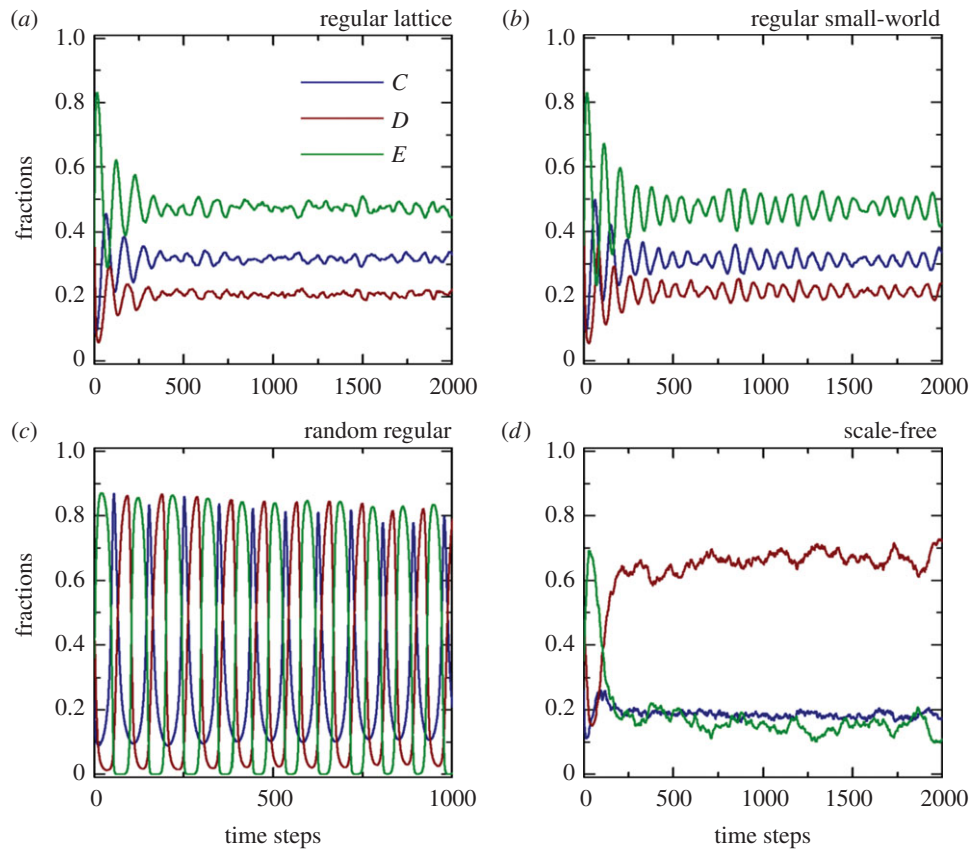


Figure 6. Nature of cooperator, defector, and exiter coexistence changes with network structure. (a) In the regular lattice, initial large oscillations in average actor abundances quickly dampen and give way to much smaller oscillations that are a signature of cyclic dominance. (b) Regular small-world networks have a smaller diameter than the regular lattice, but a similar density of squares, which somewhat increases the amplitude of oscillations. (c) Random regular networks have not only a smaller diameter than the regular lattice but also a much smaller density of squares. This is sufficient to trigger global-scale oscillations that may be large enough to eliminate exiters in some instances. (d) In scale-free networks, hub nodes are predominantly cooperative, while small-degree nodes switch between defection and exiting. Temptation is $b = 1.4$ and the exit pay-off is $\epsilon = 0.3$, except in the scale-free network where $b = 4$ and $\epsilon = 0.5$.

series of actor abundances (figure 6d). We visualize the described coexistence patterns by animated movies that are available at doi.org/10.17605/OSF.IO/GRHSB.

4. Discussion

We have shown that adding an exceedingly simple exit option to a weak variant of the Prisoner's Dilemma is enough to generate complicated dynamics. In particular, we have seen that, in well-mixed populations, an arbitrarily small-but-positive exit pay-off, $\epsilon > 0$, is sufficient to destabilize defection; see electronic supplementary material, remark 1. If there is also a viable cooperation-promoting mechanism in the form of iterations or reputation, cooperators can invade the population as long as their initial fraction is above ϵ (electronic supplementary material, figure S2B).

Combining the exit option with network reciprocity produces outcomes that differ greatly from those in well-mixed populations [5]. We find that in networked populations an arbitrarily small-but-positive exit pay-off typically leads to the coexistence of cooperators, defectors, and exiters through cyclic dominance. Coexistence by way of cyclic dominance is a subject of intense study in the contexts of biodiversity [40,46–49] and competition in microbial populations [50–52]. The results with more than three species in ecosystems, in fact, lend support to the conjecture that global oscillations are a general characteristic of realistic food webs

[53]. Curiously, taking finite-size effects into account shows that cyclic dominance may in some instances compromise biodiversity and even cause extinction [54]. In the context of the evolution of cooperation, cyclic dominance often supports cooperation despite a large temptation to defect [55], and in evolutionary games with more than three strategies an important finding is that cyclic dominance provides an escape route from the negative impacts of antisocial punishment [56]. For a detailed review of this extremely rich topic, see [41]. In the evolutionary game considered herein, it is particularly interesting that square-dense network structures, such as the regular lattice, keep cyclic dominance local. By contrast, networks without squares, such as random regular networks, turn cyclic dominance into a global phenomenon. Dramatic oscillations may ensue (electronic supplementary material, figure S3), giving rise to sudden extinction of exiters and subsequent unexpected domination of defectors.

Parallels between our exiters and well-known loners, which rose to prominence as a mechanism behind cyclic dominance [3,42,43], undoubtedly invite comparisons between the two. Loners are similar to exiters in that they opt out of the game to avoid getting exploited by defectors; in doing so, loners differ from exiters in that they generate a small-but-positive pay-off for the co-player in the game, regardless of whether this co-player is a cooperator, defector, or another loner. In this sense, the fact that exiters are just as responsible for cyclic dominance in networked populations as loners shows that non-zero pay-offs received by cooperators and

defectors when interacting with loners are practically irrelevant for the observed dynamic phenomena. The exit option can thus be deemed if not more basic, then at least more economical than the loner option. Exiters, furthermore, leave both cooperators and defectors completely hanging when they walk away from the game, which seems to correspond to various real-world situations. To exemplify, if completion of a scientific project rests on collaboration, two genuinely cooperative researchers should be able to complete the project as planned. If one of the researchers has free-riding tendencies, the project may still get completed, but the invested effort will be asymmetric. If, however, one researcher outright abandons the project for another project with a smaller but immediate pay-off, the remaining researcher is left with little hope for success.

The view that the exit option is beneficial for cooperation is being challenged by a new psychological study [57]. In their social-dilemma experiment, the authors find that, with the introduction of exit rights, exiting replaces defection, which is in line with our model's predictions. This further leads to an increase in the relative cooperation frequency, where 'relative' refers only to games without exiters. In absolute terms, however, the cooperation frequency decreases because many players choose to exit. In the model, whether more exiting leads to more or less cooperation depends on the exact set-up. A larger temptation b typically gives more power to defectors over cooperators; however, with more defectors in the system, exiters also gain more space to spread, ultimately generating the situation in which more exiting is accompanied by less cooperation (e.g. figure 3*b*). A larger exit pay-off ϵ mostly gives more power to exiters over defectors; however, with more exiters in the system, cooperators also gain more space to spread, ultimately generating the situation in which more exiting is accompanied by more cooperation (e.g. figure 5*a*). It should not be forgotten here that, as the exit pay-off becomes too large, exiters completely overpower the other two actor types. Haesevoets *et al.* [57] conclude that 'both research and practice can gain greatly in richness by giving more consideration to exit options in the study of cooperation', which is—given the richness of our results—a sentiment that we wholeheartedly agree with.

Exit rights have, to a degree, been studied at the interface between social and biological sciences. The most used methodology has been simulations with a focus on relative strategy

effectiveness in iterated games [58–60]. The results suggest that an exit option is beneficial for cooperation because exiting precludes exploitation by defectors. More recently, attention has turned towards social-dilemma experiments in which exiting has been realized through the ability to switch partners. The results also suggest that exiting benefits cooperation [61,62]. Our conclusion is somewhat more nuanced—while exit rights can help, they are certainly not a panacea.

Returning to the example of the Chinese famine, our results agree with Lin [13] in that having an exit option could save cooperation in the system. It is hard to interpret more of our results in that context; in conforming the model to networked evolutionary games, we lost the connection to that motivational example. Instead, we discovered that a seemingly minute adjustment to include exiters, leads to a plethora of dynamic phenomena. This shows that *nuances matter* even if we restrict ourselves to the goal of economic and evolutionary game theory, that is, to elucidate incentives for rational behaviours. If we wanted to raise the bar and proceed to modelling general human behaviour [20,63], details of the model would be even more important.

Data accessibility. The code used in the study is freely available at doi.org/10.17605/OSF.IO/GRHSB.

Authors' contributions. C.S., M.J., L.S. and M.P. conceived the research. C.S. and M.J. performed the simulations. All co-authors discussed the results and wrote the manuscript.

Competing interests. We declare we have no competing interests.

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