Truncation selection and diffusion on random graphs

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Two-strategy evolutionary games on graphs have been extensively studied in the literature. A variety of graph structures, degrees of graph dynamics, and behaviours of replicators have been explored. These models have primarily been studied in the framework of facilitation of cooperation, and much excellent work has shed light on this field of study. However, there has been little attention to truncation selection as most models employ proportional selection (reminiscent of the replicator equation) or "imitate the best." Here we systematically explore truncation selection on random graphs, where replicators below a fitness threshold are culled and the reproduction probabilities are equal for all survivors. We employ two variations of this method: independent truncation, where the threshold is fixed; and dependent truncation, which is a generalization of "imitate the best." Further, we explore the effects of diffusion in our networks in the following orders of operation: diffusion-combat-offspring (DCO), and combat-diffusion-offspring (CDO). For independent truncation, we find three regimes determined by the fitness threshold: cooperation decreases as we raise the threshold; cooperation initially rises as we raise the threshold and there exists an optimal threshold for facilitating cooperation; and the entire population goes extinct. We find that dependent truncation affects games differently; lower levels reduce cooperation for the hawk-dove game and increase it for the stag hunt, and higher levels produce the opposite effects. DCO reduces cooperation in the static case. However, CDO has approximately as much or more cooperation than the static case.

INTRODUCTION

The evolution of cooperation is frequently modelled by the Prisoner's Dilemma. However, this model faces a tragedy of the commons in which defection is favoured over cooperation. The Prisoner's Dilemma is a symmetric game with two strategies: cooperate (c) and defect (d) with payoff matrix

$$\mathbf{\Pi} = \begin{array}{c} \\ c \\ d \end{array} \begin{array}{c} \begin{array}{cc} c & d \end{array} \\ \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array} \tag{1}$$

where $T > R > P > S$. Though the socially optimal strategy profile is (c, c), due to the temptation to cheat, T, the suboptimal strategy profile (d, d) is an evolutionarily stable state (ESS) [15]. This game and others are frequently studied in the parameter space determined by: $R = 1$, $-1 \leq S \leq 1$, $P = 0$, and $0 \leq T \leq 2$ [29]. Thus, for $-1 \leq S < 0$ and $1 < T \leq 2$, we have the Prisoner's Dilemma. $0 < S \leq 1$ and $1 < T \leq 2$, we have the Hawk-Dove game and a mixed ESS. For $-1 \leq S < 0$ and $0 \leq T < 1$, we have the Stag Hunt game and bistability. And, for $0 < S \leq 1$ and $0 \leq T < 1$, we have the harmony game where the ESS is socially optimal. Figure 1 depicts the frequency of cooperators at the interior equilibrium (if there is one) or at the exterior ESS. For the area of parameter space that represents the Hawk-Dove game, this is the ESS. For the area of the Stag Hunt, this represents the size of the basin of attraction of cooperation.

A variety of evolutionary dynamics have been used to explore these games [19, 25]. Here we will focus on an extensively studied framework, evolutionary games on graphs [23, 28, 31], where agents are represented by vertices and interact with other vertices with which they share edges [11, 22]. Each vertex has a specific strategy that it follows. In many studies, including this one, we assume that the players always play the same pure strategy regardless of the strategies of their neighbours. From these interactions, vertices earn payoffs — the average or sum of which is their fitness — that determine survival by some selection method. Lattice models of this kind can increase cooperation [16] or reduce cooperation in the Snowdrift game [12], depending on the selection method and games employed. A variety of different invasion scenarios have been studied in this framework [9], and it has been shown that cooperators can successfully invade [18].

Once payoffs have been assigned and fitnesses calculated, selection occurs. Each vertex compares its fitness to those of its neighbours to determine what strategy will occupy the vertex next turn. A common selection mechanism used in spatial games is proportional selection, where a vertex will randomly choose one of its neighbours, and adopt the neighbour's strategy with probability proportional to the difference in their fitnesses [3],

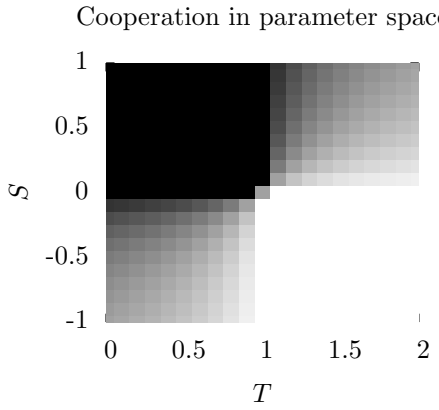

FIG. 1. Interpolated heatmap of cooperation in parameter space. White corresponds to defection and black to cooperation. In the harmony (top left quadrant), Hawk-Dove (top right quadrant), and Prisoner's Dilemma (bottom right quadrant) areas of parameter space, the colour represents the equilibrium frequency of cooperation (white is All Defect, black is All Cooperate, and grey an intermediate amount of cooperation). In the Stag Hunt area (bottom left quadrant), we have bistability. Thus, the heatmap represents the magnitude of the basin of attraction of cooperation.

which is equivalent to the replicator equation for an infinite population [14]. Another common selection mechanism is "imitate the best," in which the focal vertex will compare its fitness (the sum of all interactions with its neighbours) to the fitnesses of neighbouring vertices [11]. Its strategy will then become the strategy of the vertex with the greatest fitness. If there is a tie, it will be determined randomly from the maximal fitness neighbours.

Truncation selection occurs when a proportion of the population is culled and the survivors reproduce to fill the gap in the population. However, the reproduction rate is equal amongst all survivors (it's not scaled by fitness). Two types of truncation selection are dependent and independent [21]. In dependent truncation, the top τ proportion of the population survives and reproduces, while the bottom $1-\tau$ is culled. For $\tau = 1/n$, where n is the number of neighbours, we have the "imitate the best" rule. In independent truncation, replicators with fitnesses greater than some fitness threshold ϕ survive and reproduce, and those below it are culled. Note that reproduction is not dependent upon the degree to which a replicator is above the threshold for survival. This asymmetry in selection results in significant differences from the replicator equation, potentially displaying chaos and significant levels of cooperation where none are represented in the replicator equation employing identical games [5–8, 21]. A model that employs a degree of independent truncation is studied in [37]. Vertices are removed from the graph if their fitnesses are below a threshold. Vertices created as replacements have preferential connections to vertices with high fitnesses. After this process, there is proportional selection.

A variety of graphs have been explored, ranging from lattices with periodic or aperiodic boundaries, to small world graphs, and to random regular graphs [3]. Scale-free networks with different levels of degree-degree correlations and enhanced clustering have been shown to facilitate cooperation [26]. Cooperators perform better on random regular graphs than they do on regular small world graphs, which perform better than square lattices [13].

Dynamic graphs are graphs where the edges change over time. By altering the degree of dynamism of the graph, a variety of mechanisms (such as the Red Queen) can lead to high levels of cooperation [32]. This process can be random or determined by vertex behaviour [34]. In the behavioural model, vertices may choose to break edges by examining the payoffs earned from neighbours with whom they share them [4, 24], breaking edges with non-cooperating neighbours [27], or form edges with those vertices that have high payoffs [35, 36]. Other means to study this behaviour include models where the agents move on a plane [2, 10]. They interact with those within some Euclidean distance, which in some models is heterogeneous [37]. After a certain time they reproduce. Cooperation can be supported in such models, but only when the agents' velocities are low [20]. Scale-free graphs are the most resilient to this effect [17].

Another method of graph dynamism is diffusion, where vertices swap places in the graphs, or, equivalently, vertices swap strategies with neighbouring vertices. The order of the operations: contest, C; diffusion (graph dynamism), D; and offspring, O, heavily affects the results [30, 33]. CDO ordering of operations often inhibits the effects of graph structure [30].

Here we systematically explore independent and dependent truncation selection on random graphs, since it has not been sufficiently studied in the literature. Additionally, we study diffusion with both DCO and CDO operations. We compare our results to models that use proportional selection.

METHODS

Let $G(V, E)$ be an undirected graph with vertex set V and edge set E. $V_i = \{v_j : \{v_i, v_j\} \in E\}$ is the set of neighbours of vertex v_i. We construct a random graph using the Erdős-Rényi $G(n, p)$ model with expected vertex degree, $E[|V_i|] = 5$, and population size, $|V| = 500$. We assign to vertices the cooperator strategy with probability 0.5, and the remaining vertices are defectors. We run the simulation for 200 turns and employ synchronous combat and reproduction. The order of operations each turn is: contest, offspring, and diffusion for CDO; and

diffusion, contest, and offspring for DCO.

During the combat phase, players interact with all their neighbours, and earn payoffs from these interactions. From this we calculate the fitness of v_i, $f_i = \sum_{v_j \in V_i} \pi_{ij}/|V_i|$. The payoffs come from $\pi_{ij} \in \Pi$ (payoff matrix 1). We vary T and S with increments of 0.1.

Diffusion occurs by randomly selecting vertices to swap strategies with their neighbours n times per turn. We run simulations with mean diffusion rates, $d = n/|V| = 0$ to 25. However, we present the results for $d = 1$, since higher diffusion rates did not significantly affect our results.

During the offspring phase, we employ three different selection/updating rules: proportional, dependent truncation, and independent truncation. For each vertex, we examine it and its neighbours' fitnesses and employ our selection method to determine what strategy will occupy the vertex next turn. For proportional selection, v_i with strategy s_i will randomly choose a neighbour, v_j, and adopt its strategy, s_j, with probability $P(s_i \to s_j)$,

$$P(s_i \to s_j) = \begin{cases} \frac{f_j - f_i}{\max\{1,T\} - \min\{0,S\}} & \text{if } f_j - f_i > 0, \\ 0 & \text{otherwise.} \end{cases} \quad (2)$$

This method is identical to the replicator equation in the limit [14]. This selection mechanism is proportional to the differences between the payoffs of the vertices.

For dependent truncation, we determine the top $\lfloor \tau(|V_i| + 1) + 0.5 \rfloor$ vertices from each v_i and their neighbours and set the strategy of v_i to the strategy of a randomly selected vertex from this set. For independent truncation, for each v_i we determine the set

$$V_i' = \{v_j \in V_i \cup \{v_i\} : f_j \geq \phi \max\{1, T\} + (1-\phi) \min\{0, S\}\} \quad (3)$$

where $0 < \phi < 1$, and select randomly from this set to update the strategy of v_i. Note that independent truncation can result in $V_i' = \emptyset$, and thus we may have empty vertices. These empty vertices hold no strategy and do not compete with neighbours. However, they are still a part of the graph and thus offspring may be born at them. We ran simulations for τ from 0.05 to 0.95 in increments of 0.05, and ϕ from -1 to 2 (the range of possible fitnesses) in increments of 0.1. Finally, we averaged our results over 100 simulations for each parameter combination.

RESULTS

Proportional selection

To enable comparison with the truncation selection results, in Figure 2 we plot the interpolated heatmap for proportional selection with no diffusion, and $d = 1$ for

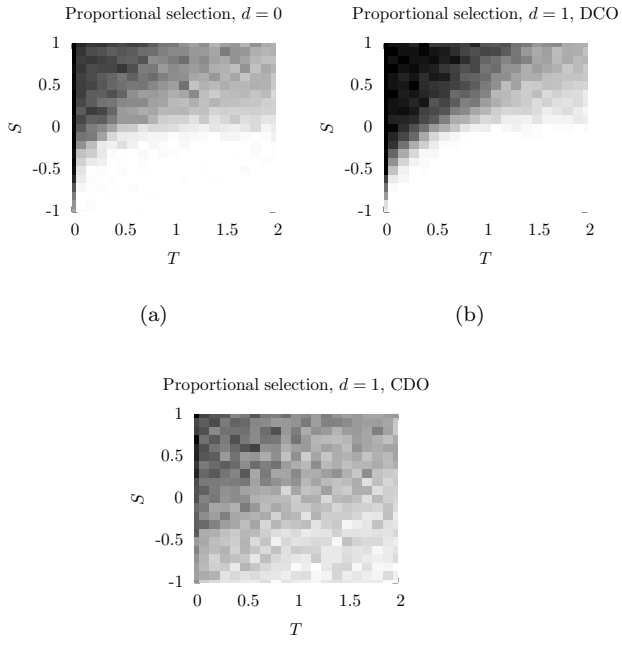

FIG. 2. Interpolated heatmap of average cooperation over 100 simulations for proportional selection with simulation length of 200 turns and $d = 0$ (**a**), DCO $d = 1$ (**b**), and CDO $d = 1$ (**c**). White corresponds to defection and black to cooperation.

DCO and CDO. Not shown here are results for $d > 1$, because we did not observe an appreciable impact from those rates. We observe less cooperation in these three cases than in Figure 1. This observation matches similar results in the literature, where clustering in structured models facilitates cooperation in the Stag Hunt game, and inhibits it in the Hawk-Dove game [28]. We observe less cooperation in Figure 2 than in Figure 1, since the clustering coefficient, $\bar{C} = p = 0.02$, is low for our graph [1]. Notice that the results for DCO do not differ significantly from the no diffusion case. However, CDO diffusion increases cooperation as observed in the hawk-dove, stag hunt, and harmony domains of parameter space. Cooperators within a cluster of cooperators will have a higher fitness than defectors in a defector cluster. Thus, cooperators that diffuse into a defector cluster will propagate, whilst defectors that diffuse into a cooperator cluster will likely die. This effect has been similarly observed in [30, 33].

Independent truncation

We observe a variety of behaviours for independent truncation that can be classified into three regimes that are dependent upon the fitness threshold, ϕ: $\phi \in [-1, 0)$, $\phi \in [0, 1)$, and $\phi \in (1, 2]$. In the first, cooperation de-

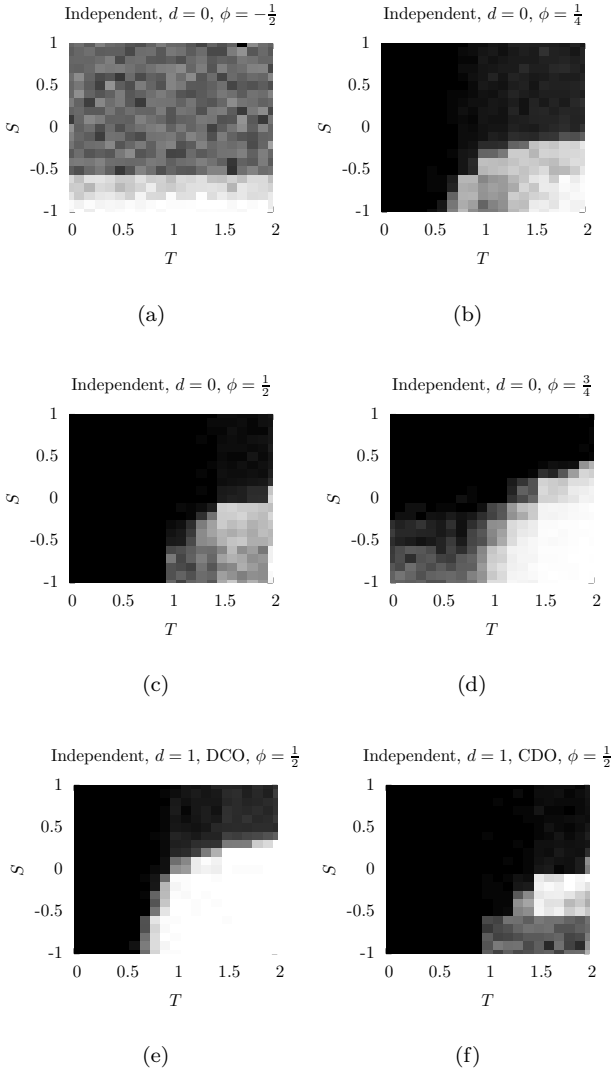

FIG. 3. Interpolated heatmap of average cooperation over 100 simulations for independent truncation with simulation length of 200 turns. Black corresponds to the density of cooperators. Note that unlike the proportional selection and dependent truncation heatmaps, white corresponds to the density of defectors and empty vertices (which do not occur in those other models).

creases as we increase ϕ. In the second, cooperation initially rises. And, in the third, no cooperation is present as extinction occurs.

Figure 3 portrays a variety of interesting heatmaps of the independent truncation model. In panels (a)-(d) we explore the effects of various values of ϕ for the no diffusion case. These results are summarized in Figure 4, which plots the density of cooperators, ρ_c, in each game region for various ϕ.

For independent truncation, we may be able to alter the nature of fixed points by altering ϕ [21]. The possible fitness values range from -1 to 2, and from this we have

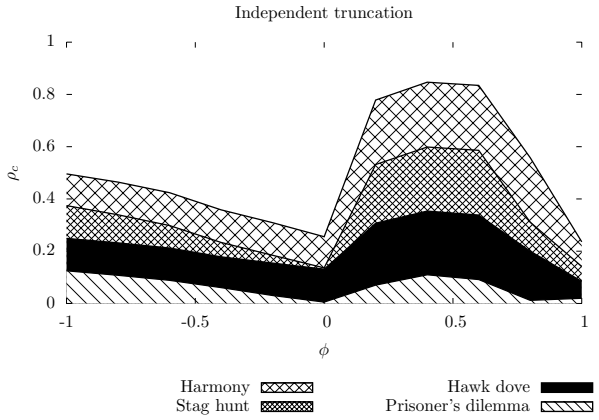

FIG. 4. Cooperator density, ρ_c, of each game for various ϕ.

three regimes: $\phi \in [-1, 0)$, $\phi \in [0, 1)$, and $\phi \in (1, 2]$. All players will make the threshold $\phi = -1$, and thus we would expect, and observe, $\rho_c = 1/2$. As we increase ϕ to 0, we will only select against cooperators, since we may have $S < 0$, but $T \geq 0$. Therefore, we observe less cooperation as ϕ rises to 0. Panel (a) of Figure 3 depicts this case for $\phi = -1/2$; we observe little cooperation below the line $S = -1/2$.

For $\phi \in [0, 1)$, selection will occur on both strategies. We observe more cooperation than in panels (b)-(d) of Figure 3 than the ESS predicts (Figure 1) and than we observe in the proportional selection model (Figure 2). Cooperation increases for all games as ϕ is raised. Cooperation reaches a peak and then decreases (Figure 3).

For $\phi > 1$, cooperators cannot survive, since their maximum fitness is 1. Therefore, populations could only exist of defectors, which earn a payoff of 0 playing one another. Therefore, they too will become extinct. Thus, we don't plot this parameter range.

When we incorporate diffusion into our models, we do not observe significant effects for $d > 1$ than we do for $d = 1$. The DCO results depicted in Figure 5 are qualitatively similar to the no diffusion case in Figure 3. However, we have less cooperation in the regime $\phi \in [0, 1)$ for the DCO model. Diffusion permits defectors to invade clusters of cooperators and thereby disrupt them, reducing cooperation. We can see this effect in the heatmaps of panels (c) and (e) of Figure 3. The impact is greatest in the prisoner's dilemma region, but also affects parameter space bordering it.

The CDO model bears many of the same phenomena as the non diffusion and DCO cases: cooperation initially decreases as we increase ϕ from -1, and increases for $\phi > 0$. However, we observe far greater densities of cooperators as we continue to increase ϕ, and the rise in cooperators does not decrease as it does in the other models. Rather, the population is nearly entirely cooperating at $\phi = 1$. This occurs because cooperators in

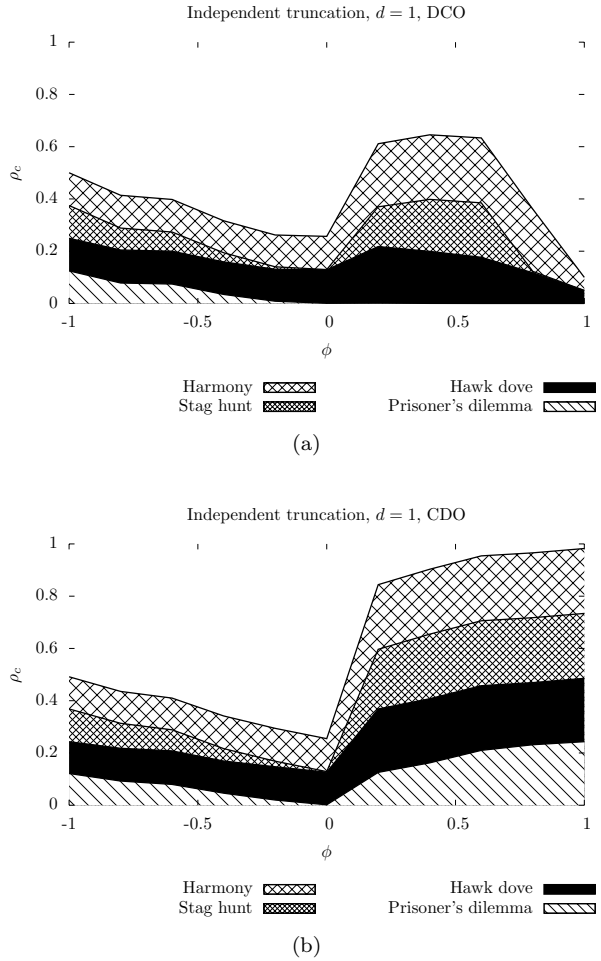

FIG. 5. Cooperator density, ρ_c, of each game for various ϕ.

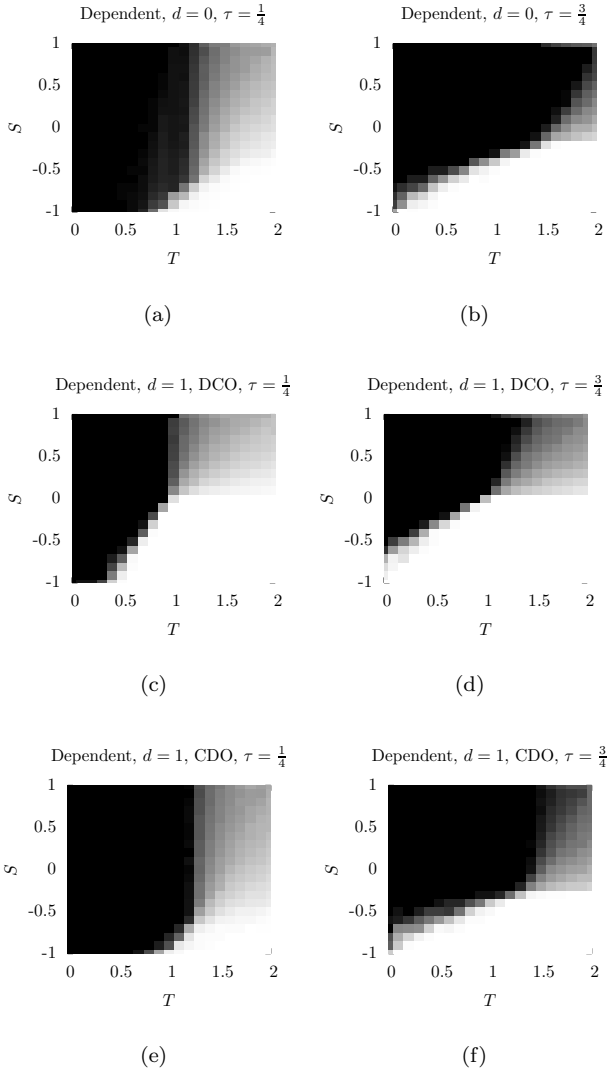

FIG. 6. Interpolated heatmap of average cooperation over 100 simulations for dependent truncation with simulation length of 200 turns. White corresponds to defection and black to cooperation.

a cooperator cluster earn good payoffs with their neighbours, and then may disperse into defector regions, where they will dominate the defectors due to their higher fitnesses. For $\phi > 1$, extinction occurs for the previously discussed reasons.

Dependent truncation

In general, we observe more cooperation in dependent truncation than we do in proportional selection. Further, the levels of truncation across the space of game parameters is roughly the same (as depicted in Figures 7 and 8). However, the proportion of replicators that survive, τ, affects each game differently.

Figure 6 depicts the heatmap results for dependent truncation for a variety of interesting cases. By comparing the figures in the left column with those on the right, we may observe the effects of low and high τ upon cooperation. There is no effect upon the harmony game; all players cooperate. There is little effect upon the low levels of cooperation for the prisoner's dilemma. However, increasing τ increases cooperation in the hawk dove game and reduces it for the stag hunt. We can see this summarized in Figures 7 and 8 for various values of τ.

Panels (c) - (f) of Figure 6 display the effects of the DCO vs CDO algorithms with $d = 1$, $\tau = 1/4$ and $\tau = 3/4$. We observe more cooperation for CDO than DCO, which is true regardless of τ as is summarized in Figure 8. Further, these figures contain the same phenomenon in the case with no diffusion; as τ increases, cooperation in the hawk dove game increase while it decreases in the stag hunt.

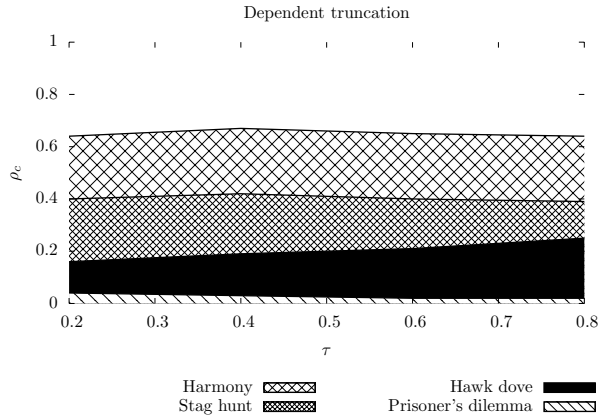

FIG. 7. Cooperator density, ρ_c, of each game for various τ.

DISCUSSION

Here we have systematically explored diffusion and different selection mechanisms on a random graph of cooperators and defectors. We have expanded the analysis of these selection mechanisms from proportional selection and "imitate the best" to incorporate two truncation schemes and various levels of truncation.

We have uncovered two interesting regimes for independent truncation: cooperation decreases as we increase the threshold parameter, ϕ; and cooperation increases for $\phi > 0$ where it will peak in the diffusionless and DCO cases and reach nearly 100% cooperation in the CDO case before the whole population becomes extinct for $\phi > 1$.

The impact of diffusion is most profound for one diffusion event per player on average, $d = 1$. We ran simulations up to $d = 25$ and observed only negligible effects upon our results. The DCO algorithm permits the disruption of clusters of cooperators by allowing defectors on the edge of the cluster to diffuse into it, where they exploit and outcompete their cooperating neighbours. In the CDO algorithm, however, players play their neighbours and then diffuse. Thus, cooperators in clusters earn good fitnesses and then may diffuse into defector clusters, where fitnesses are low. Defectors that diffuse into cooperative clusters will have low fitnesses earned from their defector neighbours, and thus cannot become established within the cooperative clusters and thereby disrupt them.

Dependent truncation is an extension of "imitate the best." However, we vary how many of the best players from which we choose for reproduction (by choosing τ). For low τ, we select from the very best of the population. For high τ, the majority of the players may be chosen to reproduce. τ has different effects on the density of cooperators for different games. While the harmony and prisoner's dilemma were not much affected, the hawk dove and stag hunt were. As we raise τ, we increase cooperation in the hawk dove game, but decrease it in the stag hunt. This phenomenon occurs with and without diffusion (and for both DCO and CDO).

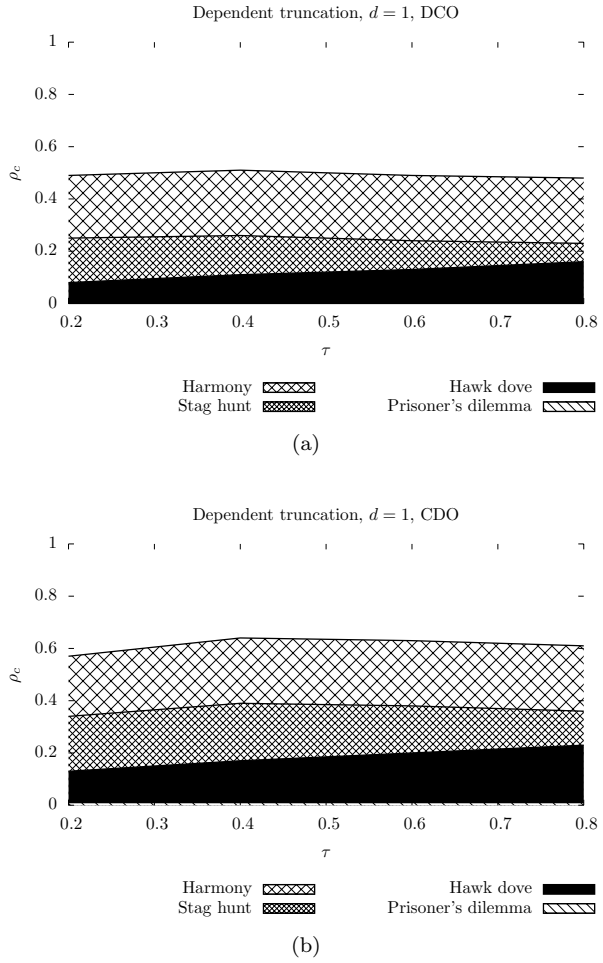

FIG. 8. Cooperator density, ρ_c, of each game for various τ.

We have a couple of suggestions for future work to expand on the ideas in this paper. For one, we should explore stochastic payoffs, which have been shown to have a significant impact upon non-spatial models [8, 21]. Further, we believe that a systematic exploration of other graphs would be a worthwhile endeavour.

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