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Evolution of conditional cooperation in a spatial public goods game

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Abstract

Spatial structure is one of the mechanisms that allows the evolution of cooperation, especially in dyadic interactions. However, when interactions occur within groups, the effectiveness of spatial structure is reduced, and additional mechanisms to sustain cooperation are needed. Conditional cooperation strategies are commonly adopted in strategic interaction, but not extensively investigated in the context of spatial reciprocity, despite potentially changing the dynamic of the evolution of cooperation. We propose and model a public good game where agents spatially interact in groups and adopt conditional cooperation strategies. We show that cooperation is evolving with no need for additional mechanisms apart from spatial structure when agents follow conditional strategies. We confirm the positive influence of productivity and cluster formation on the evolution of cooperation in spatial models. Our results are robust for two types of conditional cooperation strategies.

Author Summary

We study the evolution of cooperation using a computational model that allows us to simulate evolutionary dynamics and shows the conditions under which cooperation observed in collectives could emerge. Cooperation is a widespread behavior in biological and human systems that allows groups to function and thrive, but it constitutes a puzzle for evolutionary theories: how is it that individuals sacrifice resources to benefit the interest of the group? Can evolution favor this behavior? Previous studies have shown that constraining individuals to local interactions favors the emergence of cooperation, making altruistic behavior possible. However, when interactions are scaled to bigger groups, this spatial constraint alone is not sufficient for cooperation to evolve. We show that by just allowing the use of conditional strategies ("I cooperate if enough others cooperate"), which are commonly adopted by humans in real life, cooperation is sustained with no need for additional mechanisms other than spatial interaction. Our results show the effectiveness of conditional cooperation behavior and how simple behavioral rules help overcome some of the challenges posed by group interactions. These findings contribute to explaining the extended cooperation we find in nature and human societies.

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Introduction

Cooperation is essential for collectives and societies to thrive. Major transitions in human life history [1,2], the formation of higher-level organisms and organizations [3], and the ability to organize collective action [4] are all possible because of cooperation among individuals. Cooperation can be broadly defined as the act of paying a cost to benefit the group, but due to the underlying tension between individual and group interests, it creates a social dilemma: the maximization of the short-term material benefits to the self leads to lower group outcomes [5]. Put another way, what is good for the individual is not always good for the population [6]. For this reason, cooperation has been seen as an evolutionary puzzle: rationality and natural selection are assumed to favor selfish behavior, but cooperation is nevertheless achieved across biological and animal systems, reaching its largest scale in human societies, where cooperation occurs even among unrelated individuals [7]. Finding the mechanisms that explain the evolution of cooperation has been key for understanding how this behavior emerges in the first place, and under which conditions cooperation is sustained.

Computational models have been used to identify mechanisms and conditions that can solve the puzzle of cooperation. Spatial structure is among the five mechanisms that allow the evolution of cooperation [3,8,9]. By constraining interaction among individuals at the neighborhood level, forms of reciprocal beneficial behavior, also referred to as spatial reciprocity, can emerge. Nowak and May's spatial model [8] showed that cooperation, both in simple organisms and across species, can evolve even without accounting for more sophisticated and uniquely human abilities, such as norms, language, and culture if agents are located on a regular lattice.

Spatial models, by restricting interaction to a local scale, relax the assumption of agents randomly interacting with each other (i.e., having a well-mixed population) [8]. The local constraint of interactions allows for positive assortment [6], increasing the likelihood of cooperating agents interacting with other cooperators and reaping benefits from contributing. It is thanks to pattern formation that assortment emerges: cooperating agents can cluster and isolate from defectors [10,11,12,13].

Regular lattices provide an initial structure for more general and realistic population structures and social networks. More complex structures, in which agents are heterogeneously connected with one another [14,15,16,17], partner selection is possible [18,19], and connections are dynamically [20,21,22] and temporally [23,24] updated, can also be conductive of cooperative behavior. However, the underlying mechanism behind network reciprocity is nonetheless a generalization of spatial reciprocity, where agents can form clusters of cooperators and reduce opportunities to interact with defectors [3,9].

Many of the findings concerning spatial reciprocity arise from models that have adopted 2x2 games, like Prisoner's Dilemma, where interactions occur (i) among pairs of agents (ii) playing two behavioral strategies (cooperate or defect) [25]. When these two conditions change, the effectiveness of the spatial mechanism might vary. For example, when interactions are extended to groups, as in the case of Public Goods Games, spatial structure alone might not be sufficient to sustain cooperation because of the challenges sizable groups pose to cooperation [26,27]. Usually, group cooperation in spatial games is then achieved when other mechanisms like reputation and punishment [28,29], variable population density [30], and partner selection [31,32] are in place.

Models of the evolution of cooperation in spatial structure have mainly explored unconditional strategies (i.e. cooperate or defect) [25]. However, when it comes to human interactions, conditional behavior is commonly adopted, and most subjects consider others' actions when deciding whether to cooperate [33,34]. Conditional cooperation strategies, even in their simplest form, such as tit-for-tat, can lead to sustained cooperation in the context of repeated interaction among pairs, as in the case of direct reciprocity [35,36,37,38]. However, when moving to group interaction, conditional strategies, despite having the potential to punish and isolate defectors, can be less effective in sustaining cooperation by precluding the possibility of directly punishing defectors by withholding contribution in future encounters [7,26].

The effectiveness of conditional strategies when interaction occurs in groups in the context of spatial reciprocity has not been extensively investigated, with the exception of [19,29,39–42]. Similarly to [39], our study focuses only on conditional cooperation strategies, ignoring a wider and more complex strategy space [19,29,40–42]. We further investigate this aspect, testing the validity of previous results for variations in relevant model specifications to see if cooperation can be sustained in group interaction by allowing conditional cooperation strategies in a spatial game. We introduce conditional cooperation criteria based on thresholds [43] and test the robustness of the results when allowing for thresholds to emerge.

We study the evolution of cooperation in a spatial public goods game in which an agent interacts with its immediate neighbors and follows conditional cooperation strategies. Given that results obtained in spatial games are highly sensitive to model details [25], such as neighborhood structure and update rules (i.e. the way in which individual's strategies evolve) [8,10,44], we test whether similar results to those obtained by [39] can hold when interaction occurs in bigger groups (i.e. Moore neighborhood structure instead of von Neumann), and when agents social learning is guided by the use of unconditional update rule (i.e. "follow the best", as in [8], where agents copy neighbors' best payoff).

Agents contribute to the public good based on the observed number of other agents' cooperating, not just on other agents' intentions, as in [39]. Thus, the decision rule adopted in our model doesn't require agents to have information about others' strategies, making fewer assumptions about agents' cognitive abilities and their communication patterns, thereby creating a simpler condition in which cooperation can evolve. Agents follow a conditional cooperation rule based on thresholds as in [43], which we further implement by letting agents' conditional cooperation criteria evolve independently for each number of possible cooperating neighbors.

We demonstrate that high levels of public good contributions can evolve for different formulations of conditional cooperation in a simple spatial public goods game, even without including social norms, reputation, or punishment [29,43,45,46], by just allowing agents to react to others' behavior and act in a conditional way. We confirm the positive role of the productivity factor, especially when conditional cooperation criteria rely on thresholds. Conditional cooperation strategies that are based on threshold values reinforce the spatial reciprocity mechanism, allowing cooperation to evolve thanks to cluster formation. However, when allowing for conditional cooperation values to evolve independently, cooperation evolves, but to a smaller extent, and we don't see a clear emergence of thresholds in the conditional cooperation values condition. The evolution of cooperation is nevertheless robust for different formulations of conditional cooperation.

Model description

We consider a NxN torus where each cell is occupied by an agent who makes a decision, each round, about whether to contribute to a public good. Each agent shares a public good with 8 neighbors around the agent's cell. The contributions to the public good are multiplied by $r > 1$ and divided equally among the 9 agents in the neighborhood. If an agent does not contribute, the endowment c is kept by the agent. An agent decides to contribute according to a threshold value, i.e. if the number of contributing neighbors is expected to be a certain number of cooperators *nc*. We refer to the conditional cooperation rule adopted in this scenario as the *threshold condition*. For simplicity's sake, we assume myopic agents who use the observed number of cooperators in the previous round as the expectation for the next round. This means that contribution is conditional on the observed contributions of others.

The payoff y_i of an agent *i* is equal to

$$y_i = \sum_j^n \frac{[c \cdot r \cdot f(x_j)]}{9} + c \cdot (1 - f(x_i)) \tag{1}$$

Where

$$f(x_i) = 1 \quad IF\ i\ cooperates\ ELSE\ f(x_i) = 0 \tag{2}$$

And *x* is the action of the agent, f(x_i) = 1 is cooperate and f(x_i) = 0 is not cooperate, *c* is the endowment of the agent, *r* is the productivity of the public good for the agent, and *n* is the number of neighbors.

Agents make a decision to cooperate if *nc* of the 8 neighbors cooperated in the previous time step. Agents are initialized with an integer value of *nc* equal to 8, meaning they only cooperate if all 8 neighbors cooperated in the previous round. Each round, agents will check whether one of the neighboring agents has a higher payoff, and if so, it will copy the *nc* value of that neighbor. By doing so, we apply the unconditional update rule [8] to the conditional cooperation criteria. Similar to [43], the threshold is miscopied with a small probability ε . If a miscopy happens, the *nc* threshold gets initialized to a random value.

We also implemented an alternative version of the model, which we refer to as the *9 conditions*, where instead of a threshold *nc*, the agent has an independent decision whether to cooperate or not for each of the number of agents *j* that are cooperating in the neighborhood. The decision to cooperate or defect is represented by a strategy s_i where:

$$i = \sum_j^n f(x_j) \tag{3}$$

so

$$If \sum_j^n f(x_j) = i \ \ THEN\ s_i = 0\, ELSE\ 1 \tag{4}$$

Where s_i is the decision to cooperate (= 1) or not (= 0) for each of the nine options (0,..,8). Therefore, an agent who always defect will have s = {0,0,0,0,0,0,0,0,0} while an agent who only cooperate if 5 or more neighbors cooperate is represented as s = {0,0,0,0,0,1,1,1,1}. Note that we allow for more degrees of freedom than in the *threshold condition*, such that cooperating if 5 neighbors cooperate doesn't imply cooperating if 6 neighbors cooperate (i.e., agent strategy could be s = {0,0,0,0,0,1,0,0,0}). A possible strategy that could evolve is {0,0,0,0,1,1,1,0,0}, which indicates that an agent cooperates if a number of neighbors are cooperating but will freeride if most neighbors cooperate. The introduction of this variation allows us to test the robustness of the results for a conditional cooperation rule that can adapt more finely to the local conditions and test whether threshold values for conditional cooperation strategies could eventually evolve.

Results

We first explore how productivity level relates to the average level of cooperation after 2000 rounds. For each value of productivity level *r*, the model was run 200 times since it will lead to a stable reliable distribution of outcomes. The starting condition was that all agents have a *nc* equal to 8 and have not cooperated in round 0. This means that all agents are non-cooperative, contrarily to [39], in which all strategies are equally present at initialization. Despite the initial condition of non-cooperation, we see cooperation evolving, which is in line with what is found in other spatial models of cooperation in flat lattice surfaces, where clusters of cooperators spread to the whole population independent of the initial density of cooperators. Fig 1 shows that a higher *r* leads to more cooperation, which is consistent with previous results showing the positive effect of productivity level [27,39]. It is noticeable that the trajectory experiences a few jumps when the productivity level surpasses a certain threshold. The thresholds depend on the relationship between *r* and n_i, the number of cooperating neighbors of agent *i*. If $r = 9/(n_i - n_j + 1)$, the payoff y_i of a cooperating agent *i* is the same for a defecting agent *j* if the cooperator had n_i cooperating neighbors and the defector had n_j defecting neighbors. Thus, if an agent is imitating the strategy of the best-performing neighbor, it will not be able to distinguish between cooperative and defecting agents. For example, if $r = 3$, the payoff of an agent is the same for a cooperator and a defector if the defector had 2 more neighbors contributing to the public good than the cooperator during the last time step. If $r > 3$, the payoff of the cooperator is higher than a defector in that situation. This allows for an increase in cooperation. There are thresholds for $r = 2.25$ ($n_i - n_j = 3$), $r = 3$ ($n_i - n_j = 2$), and $r = 4.5$ ($n_i - n_j = 1$), which explains the observed jumps. Having payoff indifference in a strategy space in which the adoption of behavior follows the imitation of best payoffs of neighboring agents [8,10] allows for considerable improvement of cooperation, provided agents follow conditional cooperative behavior based on thresholds. The ambiguity that is created by payoff indifference increases the chances of lower conditional cooperation thresholds being adopted, helping spatial reciprocity to spread more effectively.

We then turn to the evolution of thresholds to assess their sensitivity to productivity levels and their role in promoting cooperation. Fig 2 shows the distribution of the evolved *nc*,

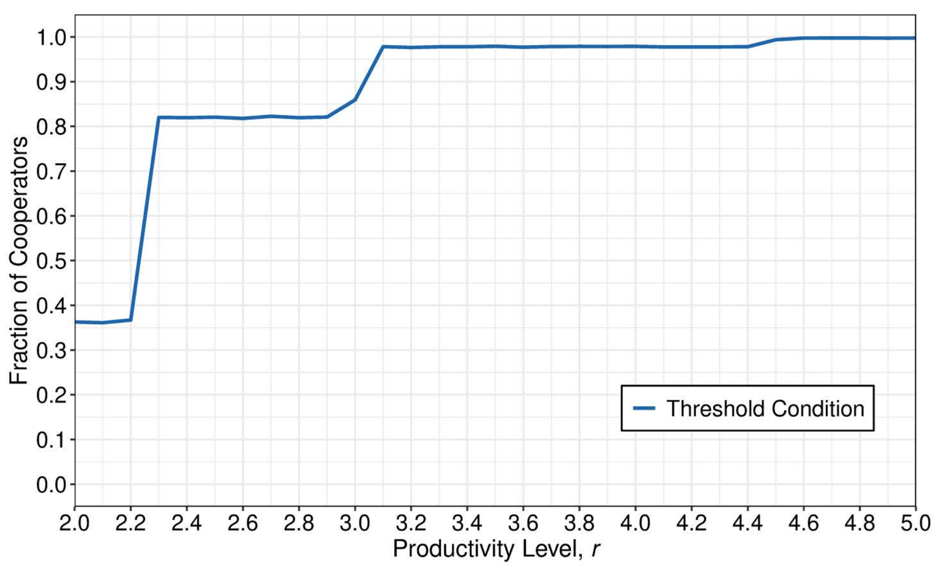

Fig 1. The fraction of agents who cooperated at the end of 2000 time steps as a function of the productivity of the public good *r*, with $N = 100$ and $\mu = 0.001$, in the *threshold condition*. Thresholds values of *r* emerge due to the relationship between *r* and number of cooperating neighbors, n_i When $r = 9/(n_i - n_j + 1)$, the payoff of a cooperating agent *i* is the same for a defecting agent *j*, increasing the likelihood of the cooperator's *nc* value to be selected.

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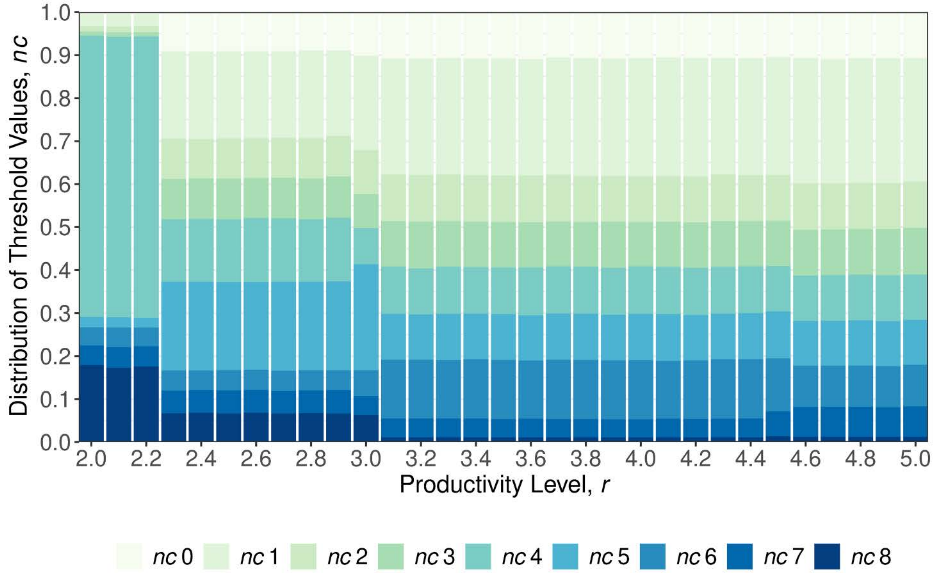

Fig 2. The distribution of threshold value *nc* at the end of 2000 rounds as a function of the productivity of the public good *r* in the *threshold condition.* High values of *nc* ($nc \geq 4$) are selected for low values of *r* ($r < 3$), meaning that the expected number of cooperating neighbors required to cooperate is higher when productivity levels are low.

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the threshold used by agents to decide when to cooperate. We see that for low values of the productivity level *r* of the public good the threshold is higher, typically 4 cooperative neighbors, than for high values of *r*. Thus, for a low level of productivity more neighbors need to be expected cooperators in order to cooperate.

If we look at individual simulations (Fig 3), we see that there is an initial low level of cooperation, with random initialization of *nc*, but due to mutations, pockets of agents with lower thresholds *nc* occur, which allow cooperation to spread. This is especially more widespread when $r > 3$. Although lower *nc* thresholds are widespread when $r > 3$, the number of cooperating neighbors is typically 8 (Fig 4). Hence, there is no strong selection pressure for *nc*, since any threshold will reinforce cooperation. When $r < 3$, and especially when $r < 2.25$, we see an increased share of neighbors not cooperating, increasing the importance of a minimum value of neighboring cooperators, *nc*, to reinforce cooperative outcomes.

Next, we examine the *9 conditions* scenario, in which agents make independent decisions to cooperate or defect for each number of cooperating neighbors. Again, we find high levels of cooperation, but not as high as when agents adopt thresholds in their conditional cooperation strategies (Fig 5).

The reason for this is that there are more ways for agents to take advantage of the local conditions and exploit cooperators. If we look at the spatial patterns of individual simulations (Fig 6), we see that there is less clustering in the *9 conditions* compared to the *threshold condition*. The patterns obtained in the *threshold condition* show that the benefit spatial reciprocity usually provides for cooperation in 2x2 games in terms of clustering, allowing cooperators to isolate defectors and reap the benefit from donations by positively assorting with other cooperators [8,25,47], can also be obtained when agents adopt conditional strategies in group interactions, consistently with what is found in [39]. However, compared to [39], cooperation is less diffused even for higher levels of *r,* because having conditional cooperation based on the number of cooperating neighbors - instead of agents' intentions to cooperate - doesn't allow the creation of a stable and diffused interface of

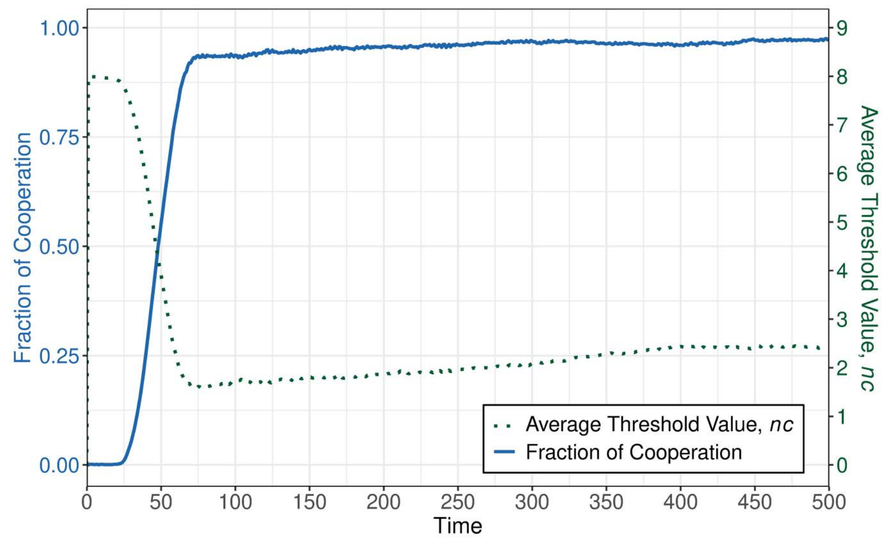

Fig 3. Time evolution of cooperation as measured by fraction of cooperation over time (solid line) and threshold values *nc* (dotted line) in individual simulation for *r* = 3.2 in the *threshold condition*. Cooperation spreads concurrently to the emergence of low values of *nc* due to mutation.

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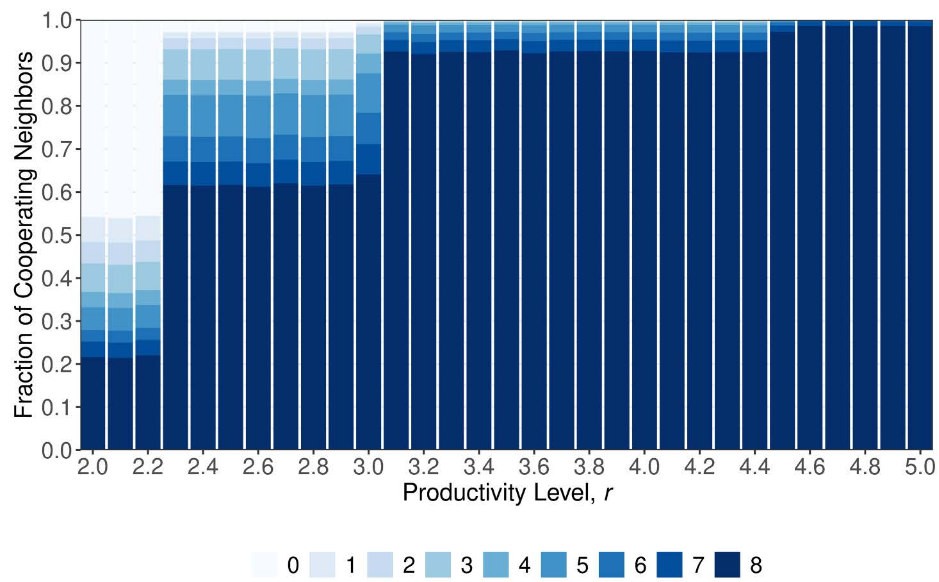

Fig 4. The distribution of the number of cooperating neighbors at the end of 2000 rounds as a function of the productivity of the public good *r* in the *threshold condition*. The high fraction of cooperating neighbors shows how selection against *nc* increasingly disappears for *r* >2.4 (Fig 2) since any threshold will reinforce cooperation.

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inactive cooperators that selectively stop cooperating with defectors but that are nevertheless promoting cooperation. Moreover, letting higher degrees of freedom in conditional cooperation strategies further undermines the effectiveness of spatial reciprocity in terms of clustering, which leads to lower levels of cooperation (Fig 6B). It is noticeable that cooperation emerges nevertheless, despite having defectors taking more benefits from cooperation than in [39].

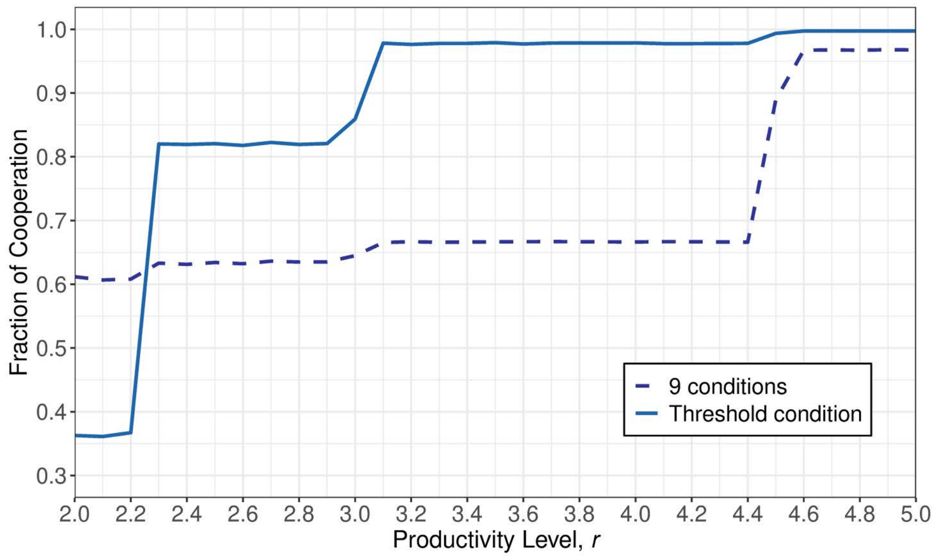

Fig 5. The fraction of agents who cooperated at the end of 2000 time steps as a function of the productivity of the public good *r*, with *N* = 100 and μ = 0.001, in the *threshold condition* (solid line) and *9 conditions* (dashed line). Cooperation levels in the *9 conditions* are reduced compared to the *threshold condition* because the higher degrees of freedom in the *9 conditions* increases the chances of taking advantages of local conditions.

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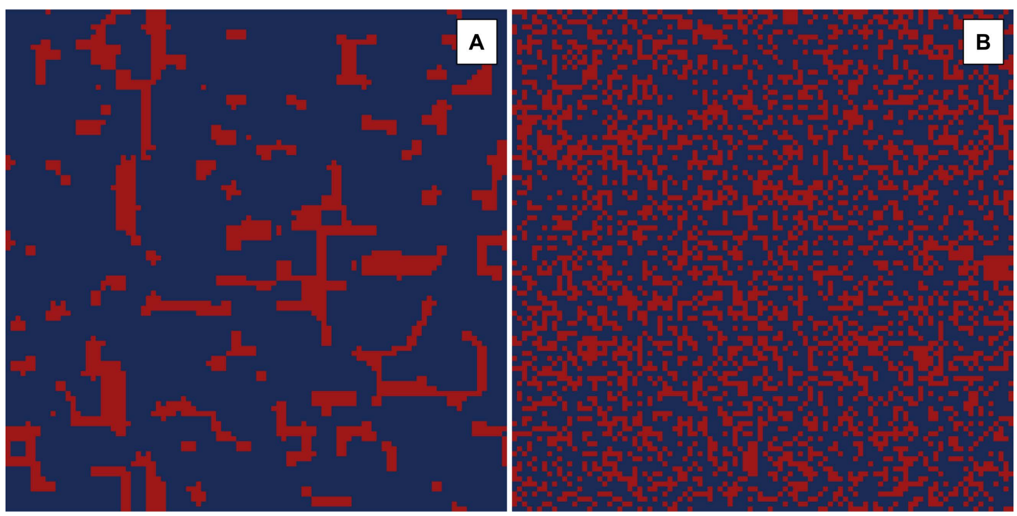

Fig 6. Evolutionary snapshots for cooperators (blue) and defectors (red) under (A) the *threshold condition* and (B) *9 conditions*. Results are obtained for *r* = 2.5 at *t* = 2000. The reduced clustering in (B) compared to (A) shows how the degrees of freedom in conditional cooperation strategies introduced by the *9 conditions* hinder the effectiveness of spatial reciprocity.

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The role of productivity in boosting cooperation is less pronounced in the *9 conditions* when compared to the *threshold conditions*. Despite thresholds occurring for the same values of *r* across the two scenarios (Fig 5), the jumps are less defined in the *9 conditions*, and only cooperation sizably increases when *r* reaches 4.5. The results obtained in the *9 conditions* resemble those obtained in the *threshold condition* only for high levels of *r* when cooperation in the public good becomes so profitable that the social dilemma almost disappears (when *r* =

5, the social dilemma disappears). Agents are typically surrounded by a majority of cooperating neighbors even in the *9 conditions*, and 7 or 8 cooperating neighbors when the productivity level is higher than 4.5 (Fig 7).

Concerning the evolution of strategies *s* that defines when an agent cooperates in the *9 conditions*, we see that there is a selection for $s_2 = 0$, $s_5 = 0$, and $s_8 = 0$ for 3 < r < 4.5 (Fig 8), whereas $s_3 = 1$, $s_4 = 1$, $s_6 = 1$, and $s_7 = 1$ are widespread. Selection is especially strong for $s_5 = 0$. The reason behind the evolution of s and the strong selection for $s_5 = 0$, is unclear, having 512 possible combinations of *s* for each agent. The evolution of *s* could be related to the distribution of cooperating neighbors. There are low values of 2 and 8 neighbors (Fig 7), for which we see corresponding low values of $s_2 = 1$, and $s_8 = 1$, and almost no case of 0 and 1 neighbors, for which we see values of s_0 and s_1 equally drawn to be 0 or 1. Finally, s_3, s_4, s_6, and s_7 are typically equal to 1, and agents often have between 3 to 7 cooperating neighbors. However, following this logic, the selection for $s_5 = 0$ is puzzling, given the considerable number of 5 cooperating neighbors. The relationship between *s* and the number of cooperating neighbors isn't able to fully provide an explanation for the dynamic of evolving *s* values for conditional cooperation, so further research is needed to explain this selection process.

When looking at individual simulations, we see that the surge in $s_5 = 1$ in the initial time steps allows the emergence of cooperation, but when the number of cooperators reaches the maximum and stabilizes, $s_5 = 1$ gets selected against - or at least decreases - and this is true irrespective of the value of r, especially when $r < 4.5$. Thus, $s_5 = 0$ might be the element that allows agents to take advantage of the local condition, especially when having a more pronounced social dilemma (r<4.5), breaking down the ability of cooperating agents to cluster and create bubbles of cooperation.

While we don't see a clear pattern formation in cooperation for $r < 4.5$, we do see clusters in the way $s_i = 1$ values evolve. In fact, when looking at individual simulations, we observe a spatially defined evolution of $s_i = 1$ (conditional cooperation) values, which form clustered patterns, while the evolution of the number of cooperating neighbors changes fast and without

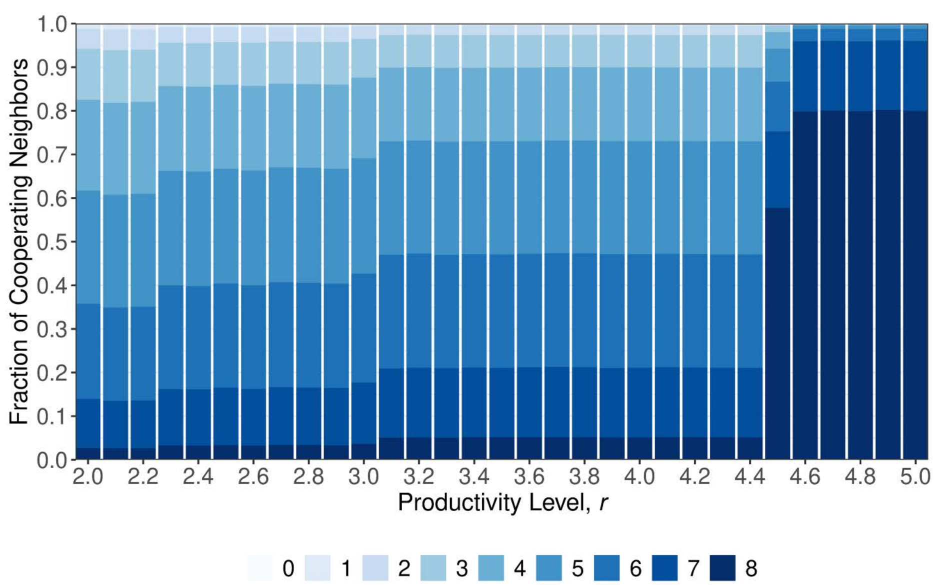

Fig 7. The distribution of the number of cooperating neighbors at the end of 2000 rounds as a function of the productivity of the public good *r* in *9 conditions*. A sizable number of cooperating neighbors is reached also in the *9 conditions*, although a spread of 7 and 8 cooperating neighbors only occurs for high levels of *r* ($r > 4.5$).

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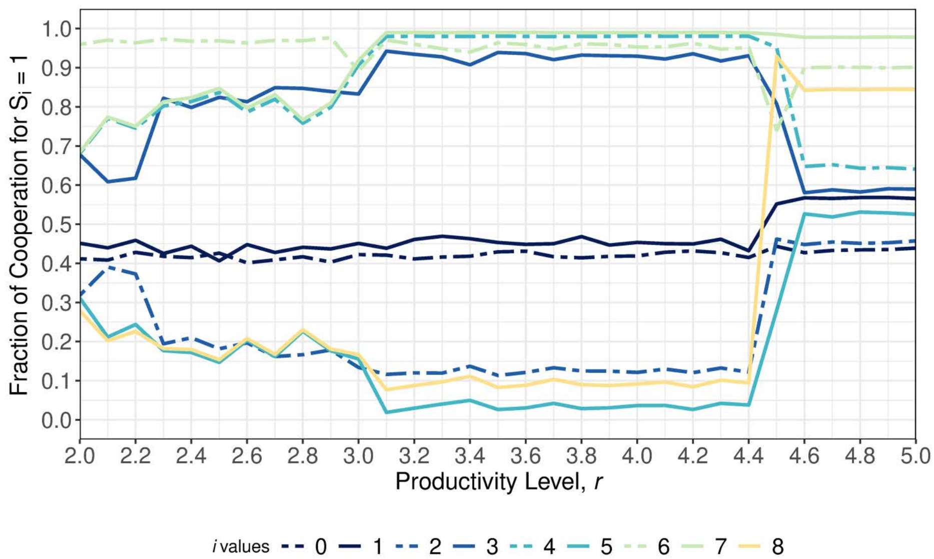

Fig 8. The average fraction of agents for which $s_i = 1$ as a function of the productivity of the public good *r*, with $N = 100$ and $\mu = 0.001$. The evolution of $s_i = 1$ values in the *9 conditions* doesn't lead to the emergence of $s_i = 1$ threshold values when allowing for higher degrees of freedom in conditional cooperation strategies for values of $r < 4.5$.

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following clearly defined patterns. Future research could investigate the relation between these two dimensions to verify whether the evolution of cluster formation in the conditional behavioral criteria ($s_i = 1$) affects the spatial evolution of cooperative behavior and cooperators' assortment in neighborhoods.

Finally, it is interesting to note that we don't see the emergence of threshold values of $s_i = 1$ (which could be the equivalent to the *nc* used in *threshold condition*) when allowing for high degrees of freedom in conditional cooperation decisions (at least for values of $r < 4.5$). When $r > 4.5$, there is a spread of 8 cooperating neighbors (Fig 7) and, contrary to the *threshold condition,* $s_i = 1$ is needed for agents with *i* equal to 6, 7, 8 where more than 98% of the time 6 or more neighbors are cooperating (Fig 7). For other *i*, s_i is not selective, and we see around 50% of the time $s_i = 1$ and $s_i = 0$ otherwise.

Discussion

Cooperation is evolving in a spatial public goods game with heterogeneous agents using conditional cooperation strategies. Spatial structures are known to sustain cooperation in dyadic interactions [10,11,12,13], but when interactions are scaled into groups, additional mechanisms are usually needed for cooperation to evolve [28,29,30,31,32]. We show that simply allowing for conditional behavior is effective in sustaining cooperation in spatial models. Building on previous results [39], we demonstrate that even when extending group size and constraining agents' decisions to others' previous behavior, cooperation evolves, despite more unfavorable initial conditions, and is maintained. Conditional cooperation strategies based on threshold values (*threshold condition*) are able to sustain spatial reciprocity when interaction is extended to groups, promoting pattern formation just like in 2x2 games [6,10,25]. The use of thresholds leads to a higher level of cooperation compared to conditional cooperation strategies with more degrees of freedom (*9 conditions*). The higher degree of freedom undermines cluster formation and, thus, cooperation.

Productivity levels positively impact the creation of the public good, which is consistent with previous findings [39]. This effect is particularly pronounced when conditional cooperation strategies follow threshold values (*threshold condition*). In this scenario, the payoff indifference that occurs among cooperators and defectors for certain values of r allows cooperation to surge. The ambiguity created by the payoff indifference can be beneficial for the evolution of cooperation in a context in which agents follow unconditional update rules [8,10] and conditional behavior based on threshold values, fostering the diffusion of spatial reciprocity. When, instead, conditional cooperation strategies are not restricted to threshold values (*9 conditions*), the effectiveness of the productivity factor in obtaining high levels of cooperation occurs only at higher levels of r.

Future research could explore different topographies of static networks, to understand whether the selection over particular values of $s_i = 1$ would occur similarly to what we found in the *9 conditions*, as well as exploring dynamic networks to understand whether the simple addition of conditional cooperation behavior can help the evolution of cooperation when interaction occurs in groups [9,48] and how it would affect network evolution.

Overall, the model points out that cooperation can evolve in a spatial public goods game without the need for additional mechanisms. Spatial reciprocity and conditional strategies combined with spatial structure can be sufficient to positively sustain the evolution of cooperation.

Material and methods

The model code and detailed documentation of the model are archived here: https://doi.org/10.25937/9mcr-2h92

Model implementation

The model is implemented in Netlogo 6.

Author contributions

Conceptualization: Francesca Federico, Raksha Balakrishna, Marco A. Janssen.

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Funding acquisition: Marco A. Janssen.

Methodology: Francesca Federico, Raksha Balakrishna, Marco A. Janssen.

Software: Francesca Federico, Raksha Balakrishna, Marco A. Janssen.

Supervision: Marco A. Janssen.

Visualization: Francesca Federico, Raksha Balakrishna, Marco A. Janssen.

Writing – original draft: Francesca Federico, Raksha Balakrishna, Marco A. Janssen.

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