



Vacancies in growing habitats promote the evolution of cooperation

Hye Jin Park^a, Christian Hilbe^b, Martin A. Nowak^{c,d}, Beom Jun Kim^e, Hyeong-Chai Jeong^{f,*}

^a Department of Physics, Inha University, Incheon, 22212, Republic of Korea

^b Max Planck Research Group 'Dynamics of Social Behavior', Max Planck Institute for Evolutionary Biology, Plön, 24306, Germany

^c Department of Mathematics, Harvard University, Cambridge, MA, 02138, United States

^d Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, 02138, United States

^e Department of Physics, Sungkyunkwan University, Suwon, 16419, Republic of Korea

^f Department of Physics and Astronomy, Sejong University, Seoul, 05006, Republic of Korea

ARTICLE INFO

Keywords:

Evolution of cooperation
Population dynamics
Phase transition

ABSTRACT

We study evolutionary game dynamics in a growing habitat with vacancies. Fitness is determined by the global effect of the environment and a local prisoner's dilemma among neighbors. We study population growth on a one-dimensional lattice and analyze how the environment affects evolutionary competition. As the environment becomes harsh, an absorbing phase transition from growing populations to extinction occurs. The transition point depends on which strategies are present in the population. In particular, we find a 'cooperative window' in parameter space, where only cooperators can survive. A mutant defector in a cooperative community might briefly proliferate, but over time naturally occurring vacancies separate cooperators from defectors, thereby driving defectors to extinction. Our model reveals that vacancies provide a strong boost for cooperation by spatial selection.

1. Introduction

Cooperation pervades all scales of life, from large collective endeavors like hunting in humans to the microscopic production of a common resource in yeast (Wiessner, 2002; Rand and Nowak, 2013; Balshine-Earn et al., 1998; Greig and Travisano, 2004; Biernaskie, 2011; Pacheco et al., 2009). Yet explaining how these instances of cooperation have evolved is not straightforward. Cooperation usually imposes a cost on the focal player while generating a benefit for the opponent. As a consequence, cooperators are at an evolutionary disadvantage when competing with free-riding defectors. Understanding how cooperation can emerge despite this disadvantage is a major goal of evolutionary game theory (Smith, 1982; Nowak, 2006a,b; Szabó and Fáth, 2007; Sigmund, 2010; Broom and Rychtář, 2013).

One key mechanism for the evolution of cooperation is spatial selection (or spatial reciprocity) (Nowak and May, 1992; Szabó and Tóke, 1998; Nowak and Sigmund, 2004; Fletcher and Doebeli, 2009; Antal et al., 2009). In this case, cooperators are more likely to direct their help towards other cooperators. One way to achieve assortment is by phenotypic similarity (Antal et al., 2009). In that case, individuals only cooperate with those who match their own phenotypic attributes. Another way to achieve assortment is spatial structure (Killingback and Doebeli, 1996; Szabó et al., 2000; Hauert and Doebeli, 2004; Ohtsuki et al., 2006; Santos et al., 2006; Szabó and Fáth, 2007; Santos

et al., 2008; Hauert et al., 2008; Perc, 2009; Perc and Szolnoki, 2010; Hadjichrysanthou et al., 2011; Débarre et al., 2014; Allen et al., 2017; Su et al., 2019; Fotouhi et al., 2019). In that case, cooperators only interact with those in a close spatial proximity. Traditionally, studies of spatial reciprocity focus on fixed population structures, or on populations of constant size (Perc et al., 2013). Variable population sizes have been introduced relatively recently to spatial games, considering the interaction of population growth and strategy evolution (Nowak et al., 1994; Hauert et al., 2006; Wakano et al., 2009; Ross-Gillespie et al., 2009; Lion, 2009; Sekiguchi and Nakamaru, 2009; Melbinger et al., 2010; Wang et al., 2012; Sanchez and Gore, 2013; Smaldino, 2013; Liming and Wu, 2014; Szolnoki et al., 2014; Constable et al., 2016; Moreno-Fenoll et al., 2017; Rodriguez-Brenes et al., 2020; Wang and Perc, 2021). Here we introduce a simple model of spatial games in growing populations where absorbing phase transitions occur. We use this model to show that naturally arising vacancies between growing habitats can dramatically enhance the positive effects of spatial structure.

To this end, we study a model in which individuals populate a one dimensional (1D) lattice. Individuals engage in a pairwise interaction with each neighbor. In these interactions, they can either cooperate or defect. The outcome of the local interactions, together with the global quality of the environment, determine an individual's fitness.

* Corresponding author.

E-mail addresses: hyejin.park@inha.ac.kr (H.J. Park), hcj@sejong.ac.kr (H.-C. Jeong).

<https://doi.org/10.1016/j.jtbi.2023.111629>

Received 18 June 2023; Received in revised form 23 September 2023; Accepted 28 September 2023

Available online 5 October 2023

0022-5193/© 2023 Elsevier Ltd. All rights reserved.

Individuals with a low fitness are more likely to die (Huang et al., 2015; Park et al., 2019). Once a death event happens, it introduces a vacancy. Since cooperators adjacent to defectors are most liable to die, these vacancies naturally arise where cooperators and defectors meet. As a result, we show that vacancies tend to separate cooperative regions from clusters of defectors. In this way, they naturally introduce additional assortment. By taking advantage of the properties of one-dimensional lattice, we analytically draw the boundary between cooperator- and defector-dominant phases in the parameter space. Vacancies thus represent a mechanism for the evolution of cooperation in growing spatial communities.

2. Method

As a minimal model to describe the individuals' social interactions, we use a variant of the prisoner's dilemma called 'donation game' (Sigmund, 2010; Bahk et al., 2019). Each site of the 1D lattice can either be occupied by a cooperator (C), a defector (D), or it can remain empty (E). Players interact with each of their immediate neighbors. If the adjacent site is empty, the player's payoff for the respective interaction is zero. Otherwise, cooperators pay a cost c to provide a benefit b to their neighbor. Defectors pay no cost and provide no benefit. The result of these interactions can be summarized by the payoff matrix

$$\begin{array}{c}
 C \\
 D
 \end{array}
 \begin{array}{ccc}
 C & D & E \\
 \left(\begin{array}{ccc}
 b-c & -c & 0 \\
 b & 0 & 0
 \end{array} \right)
 \end{array}
 \quad (1)$$

In this payoff matrix, the focal player chooses a row, whereas the neighbor's type determines the column. The respective entry is then the payoff of the focal player. In the following, we normalize the benefit to $b = 1$, and we consider the case of a social dilemma, $0 < c < 1$.

As a result of these pairwise interactions, players obtain a total payoff of p . This payoff in turn affects the players' longevity. Specifically, we assume that a player's death rate is proportional to the death probability,

$$d = \frac{1}{1 + Ae^{wp}}, \quad (2)$$

In this equation, the parameter $w \geq 0$ corresponds to the strength of selection. It reflects how strongly an individual's survival is tied to its payoff. In the limiting case $w = 0$, payoffs are irrelevant. Here, all individuals have the same death probability $d = 1/(1 + A)$. For positive w , individuals with higher payoff are expected to survive for a longer time.

The other parameter $A > 0$ reflects the quality of the environment. In the limiting case that A approaches zero, survival is impossible, independent of how well players perform in the prisoner's dilemma. In the other limit when A is sufficiently large, the death rate approaches zero and populations tend to grow without vacancies. Because nothing prevents defectors from being the neighbors of cooperators, cooperative communities tend to get invaded and go extinct. In the following, we thus focus on the most interesting case when the quality of the environment A is intermediate.

To explore the evolutionary dynamics of the population, we study population growth from a single seed. The seed can either be a cooperator or a defector. We set the seed position as the origin of the lattice. Moreover, we define the habitat as the region from the leftmost occupied site L to the rightmost occupied site R . The size of the habitat $H(t)$ at time t is therefore

$$H(t) = R(t) - L(t) + 1. \quad (3)$$

In each time step, we randomly choose one of the $H + 2$ sites between $L - 1$ and $R + 1$. If the site is occupied, its inhabitant dies with death probability d , as defined by Eq. (2). Otherwise, if the site is empty, it can be colonized by an offspring of its neighbors. When both adjacent sites are empty, the chosen site remains empty. When only one neighboring site is occupied, its offspring takes the empty site. Finally,

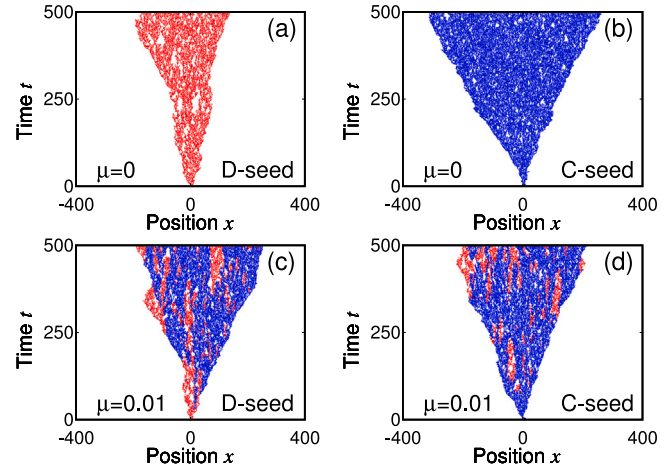


Fig. 1. Population growth from (a) D-seed with $\mu = 0$, (b) C-seed with $\mu = 0$, (c) D-seed with $\mu = 0.01$, and (d) C-seed with $\mu = 0.01$. We used $w = 1$, $A = 1$, and $c = 0.4$. White, red and blue sites represent empty sites, D- and C-inhabitants, respectively.

when both adjacent sites are occupied, they both are equally likely to reproduce. During reproduction, mutations may occur. The offspring adopts the parent strategy with probability $1 - \mu$ and the opposite strategy with probability μ . As usual, we define one Monte Carlo (MC) step as $H + 2$ such tries. Because the size of the habitat can change during a MC step, we define $H(t)$ to be the habitat size in the beginning of the MC step at time t .

3. Results

Fig. 1 shows four representative growth scenarios. We distinguish populations originating from either a single defector (left panels) or a single cooperator (right panels). In addition, we explore scenarios without and with mutation (top and bottom panels, respectively). In the absence of mutations, habitats grow with approximately constant rate. The exact growth rate depends on the seed. Habitats seeded with a cooperator grow faster. In contrast, in the presence of mutations, the steady states are independent of the initial seed. For the parameters in Fig. 1, cooperators eventually dominate the population even if the population originates from a single defector.

To get a more quantitative understanding of these results, we compute the population's survival probability $s(t)$, defined by

$$s(t) = \frac{a(t)}{M}. \quad (4)$$

Here, $a(t)$ is the number of simulations in which the population still exists at time t , out of M growth simulations in total. The infinite time limit of the survival probability $S_\infty = \lim_{t \rightarrow \infty} s(t)$ can then serve as an order parameter. It distinguishes environments that allow for the survival of the population from environments that guarantee extinction. We say the population is in the *active phase* when S_∞ is positive. In contrast, when S_∞ is zero, we speak of the *absorbing phase*. In the absorbing phase, all populations disappear eventually and no further dynamics occur (Hinrichsen, 2000; Chae et al., 2021).

Because the death probability (2) is one for $A = 0$, extinction is guaranteed in poor environments. Conversely, because the death probability approaches zero for large A , survival is almost certain in rich environments. It follows that as A gradually increases from zero, there is a unique threshold at which the system transitions from the absorbing to the active phase. Without mutations, this transition point A_c^θ depends on the cost of cooperation c and the seed type $\theta \in \{C, D\}$. To obtain the exact position of the transition point A_c^θ , Fig. 2(a),(b) plots $s(t)$ versus t on a log-log scale. At the transition point, the survival probability $s(t)$ shows power-law decay, $s(t) \sim t^{-\delta}$ (Hinrichsen, 2000),

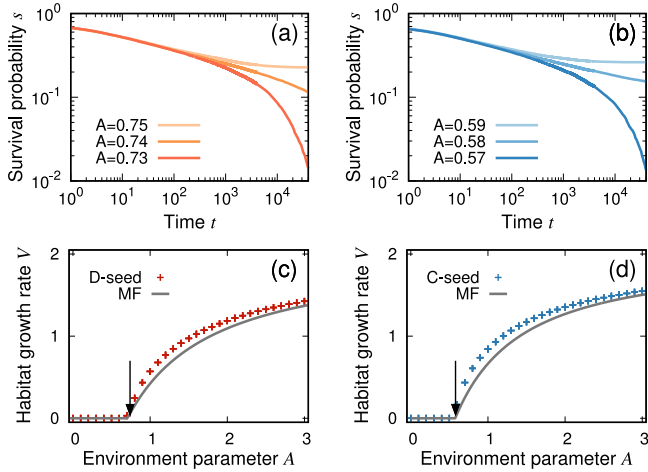


Fig. 2. Survival probabilities S and habitat growth rates V for $c = 0.7$ and $w = 1$. (a) S of the D-population at $A = 0.75, 0.74$ and 0.73 . (b) S of the C-population at $A = 0.59, 0.58$ and 0.57 . (c) V of the D-population. The plus symbols are the simulation results, averaged from 5000 independent survival samples at $t = 5000$, and the solid lines are MF calculations. The arrows indicate the transition points, $A_c^D = 0.74$ and $A_c^C = 0.58$ obtained in (a) and (b).

yielding a straight line in the plot. For $c = 0.7$ and $w = 1$, the power-law criterion yields $A_c^D \approx 0.74$ for defecting populations and $A_c^C \approx 0.58$ for populations of cooperators. The exponent δ is close to the directed-percolation exponent, $\delta_{DP} \approx 0.16^1$ (Hinrichsen, 2000).

We can also approximate the transition point A_c^θ by estimating the habitat's mean growth rate. This growth rate V should be positive in the active phase and approach zero close to the transition point. The value of V is determined by the motion of the habitat boundaries,

$$V = \langle \dot{H} \rangle = \langle \dot{R} \rangle - \langle \dot{L} \rangle = 2\langle \dot{R} \rangle, \quad (5)$$

where we have used the mirror symmetry $|\langle \dot{R} \rangle| = |\langle \dot{L} \rangle|$. To compute $\langle \dot{R} \rangle$, we distinguish two cases. The habitat expands if site $R + 1$ is selected. In that case, the site is populated by its neighbor and the right boundary moves from R to $R + 1$. On the other hand, the habitat shrinks if site R is chosen and its inhabitant dies. In that case, the amount by how much the habitat shrinks depends on the exact configuration of the players. In the following, we estimate the boundary velocity by assuming mean-field (MF) configurations. That is, we assume all sites within the habitat boundaries have the same occupation probability ρ . Under this approximation, the probability that the habitat shrinks by k sites when an inhabitant at the boundary dies becomes $(1 - \rho)^{k-1} \rho$.

For a D-population, an individual's death probability is $d_D = 1/(1 + A)$, independent of the population configuration. Hence its growth rate according to MF theory is given by

$$\begin{aligned} V_{MF}^D &= 2 \left(1 - d_D [\rho + 2\rho(1 - \rho) + 3\rho(1 - \rho)^2 + \dots] \right) \\ &= 2 \left(1 - \frac{d_D}{\rho} \right), \end{aligned} \quad (6)$$

which depends on the MF density ρ . This density in turn satisfies

$$\dot{\rho} = (1 - \rho)(2\rho - \rho^2) - d_D \rho. \quad (7)$$

in the interior of the habitat (see Supplemental material). Here, the first and the second summand describe the birth and the death process,

¹ We obtained absorbing transition points up to the third decimal point, $A_c^D = 0.742$ and $A_c^C = 0.579$. At those estimated absorbing transition points, the exponent δ is approximately 0.16 for both D-populations and C-populations ($\delta \approx 0.16$).

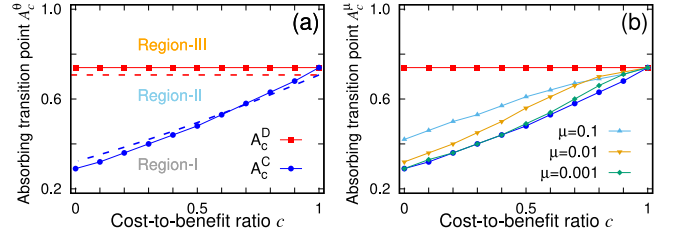


Fig. 3. (a) Absorbing transition points A_c^θ for the seed S for different values of cost-to-benefit ratio c with $S = D$ (red squares) and C (blue circles). The dashed lines are the boundaries obtained by MF approximation. In region-I, populations become extinct independent of the seed type, while in region-III both populations can survive. In region-II, a C-population can grow while a D-population always vanishes. (b) Absorbing transition points A_c^θ for finite mutation probabilities, $\mu = 0.001, 0.01$, and 0.1 . Here, $w = 1$, $M = 10000$, and $t = 4000$.

respectively. Using the MF density $\rho_{MF}^D = (3 - \sqrt{1 + 4d_D})/2$ in the steady state ($\dot{\rho} = 0$), we obtain

$$V_{MF}^D = 2 \left[1 - \frac{2}{3(A + 1) - \sqrt{(A + 1)(A + 5)}} \right]. \quad (8)$$

In spite of the well known weaknesses of MF theory in low dimensions, this growth rate reflects the corresponding simulation results remarkably well, see Fig. 2(c). In particular, by setting $V_{MF}^D = 0$ we obtain an estimated transition point of $A = 1/\sqrt{2} \approx 0.71$, which is close to the value $A_c^D = 0.74$ obtained from Fig. 2(a). For C-populations (see Supplemental material), we observe a similar match between MF calculations and simulation results, see Fig. 2(d).

In a next step, we use the two methods to compute the thresholds A_c^C and A_c^D for arbitrary cost levels, see Fig. 3(a). Because homogeneous populations of defectors have a higher death probability than populations of cooperators, we find that $A_c^C < A_c^D$ for all costs $c < 1$. That is, with respect to the quality of the environment, there is a window $A_c^C < A < A_c^D$ in which only cooperative populations can survive. Because A_c^C is an increasing function of c whereas A_c^D is flat, this window is largest for small cooperation costs. The window vanishes as the cooperation cost approaches the benefit $b = 1$ of cooperation.

While the previous analysis requires homogeneous populations (and hence a vanishing mutation rate), we can analyze the population dynamics with mutations analogously. In that case, the steady state composition of a population becomes independent of the initial seed. Instead, the absorbing transition point A_c^μ is now determined by the cooperation cost c and the mutation probability μ . In Fig. 3(b), we present A_c^μ for $\mu \in \{0.001, 0.01, 0.1\}$, together with A_c^C and A_c^D . We observe that as mutations become rare, the transition points decrease. As $\mu \rightarrow 0$, they approach the transition point A_c^C of a homogeneous population of cooperators.

For positive mutation rates, we can also measure how abundant cooperators are in the steady state. In Fig. 4, we show their frequency x_C as a heat map in the $A - c$ parameter space for $w = 1$ and $\mu = 0.001$. As expected, cooperators dominate the population for $A_c^C < A < A_c^D$. More surprisingly, however, they remain predominant in a large part of the region in which $A > A_c^D$, especially when the cooperation cost is small.

To analytically characterize the parameter region in which cooperators are predominant, we can again make use of MF methods. To this end, we consider the competition at the boundary between a cooperative cluster and a cluster of defectors. Because the cooperating individual directly at the boundary has a lower payoff than the adjacent defector, this cooperator is more likely to die. However, because cooperative clusters are more densely populated than clusters of defectors, the cooperative cluster shrinks comparably little. Furthermore, cooperative clusters tend to grow faster into vacant regions. By taking

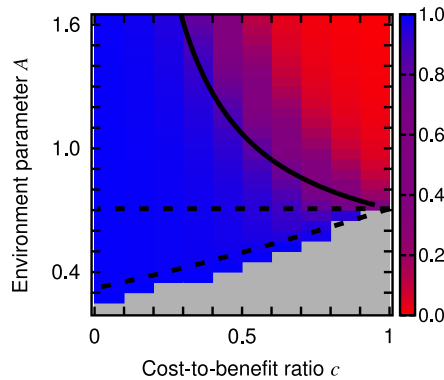


Fig. 4. Heat map of the steady state cooperator frequency x_c in the $A-c$ parameter space for $w = 1$ and $\mu = 0.001$. In the gray colored region, populations always vanish. The lower and the upper dashed lines represent the MF absorbing transition lines for C- and D-populations (without mutation). The solid line is the MF phase boundary that separates regions in which either cooperation or defection is predominant, respectively.

these opposing effects into account, the MF boundary velocity \dot{B}_{MF}^D of the D-domain next to the C-domain is given by

$$\dot{B}_{MF}^D = v \left(\frac{\alpha_1^D}{\rho_{MF}^D} + \frac{\alpha_0^C}{\rho_{MF}^C} \right) - \frac{\alpha_1^D}{\rho_{MF}^D} + v (\alpha_1^C - \alpha_0^C) \rho_{MF}^C. \quad (9)$$

Here, $v = V_{MF}^D / (V_{MF}^D + V_{MF}^C)$, and α_i^θ is the death probability of type $\theta \in \{C, D\}$ when there are i cooperators in the neighborhood (see Supplemental material). The resulting phase boundary, obtained by solving $\langle \dot{B}_{MF}^D \rangle = 0$, again recovers the simulation results remarkably well, as indicated by the black solid line in Fig. 4.

4. Concluding remarks

We have studied an individual-based evolutionary game model of a growing habitat. An individual's fitness is affected by the environment as well as interactions with its neighbors. As the quality of the environment deteriorates, there is an absorbing phase transition from growing to empty populations. While this transition exists for both cooperative and defecting populations, the transition point A_c^C for cooperators is smaller than the respective point A_c^D for defectors. It follows that in between, for $A_c^C < A < A_c^D$, there is a window in which only cooperators can survive. In our model, variable population sizes induced by spatial interactions are an essential factor to promote cooperation, as they induce the extinction of defectors in isolation while cooperators can survive.

The resulting cooperative communities are robust even in the presence of mutations. Once a defecting mutant arises, naturally arising vacancies quickly lead to the defectors' isolation. In this way, cooperative clusters can continue to spread whereas clusters of defectors are driven to extinction. Using MF approximation, we are able to accurately estimate A_c^C , A_c^D and the phase boundary between parameter regions in which either cooperators or defectors are predominant.

Vacancies arise from our longevity interpretation of fitness. Traditionally, fitness is taken as a measure of an individual's fecundity. Players with high fitness are more likely to reproduce (Nowak, 2006a; Sigmund, 2010; Szabó and Fáth, 2007). In contrast, we interpret fitness as longevity, which controls how likely players are to die (Huang et al., 2015; Park et al., 2019). When individuals die, they leave behind a vacancy. These vacancies act as a strong driver for cooperation, as they further enhance the cooperators' positive assortment.

In this paper, we have treated the quality of the environment as a constant. Instead, seasonal and stochastic fluctuations often introduce additional noise with profound effects on the evolutionary dynamics (Ashcroft et al., 2014; Baron and Galla, 2018). Moreover, populations themselves often shape the environment they inhabit (Hilbe et al.,

2018; Tilman et al., 2020). A particularly relevant case occurs when large populations induce the environment to deteriorate. In that case, the environment can be expected to remain close to the two absorbing transition points: In a good environment, the population will increase until the environment is depleted and population growth approaches zero. A constant positive population size requires the parameter A to move towards a value close to A_c^C . This observation suggests an important role of vacancies for the evolution of cooperation. As populations coevolve along with their environment, they settle at a state in which natural vacancies arise at a rate most favorable to cooperation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

H.J.P. was supported by the National Research Foundation of Korea (NRF) grant funded by the Korea government (MSIT) Grant No. RS-2023-00214071. C.H. acknowledges generous funding by the Max Planck Society and by the European Research Council (ERC), Horizon 2020 Grant E-DIRECT (850529). B.J.K was supported by the National Research Foundation of Korea (NRF) grant funded by the Korean government (MSIT), Grant No. 2019R1A2C2089463. H.C.J was supported by the National Research Foundation of Korea (NRF) grant funded by the Korea government (MSIT), Grant No. 2021R1F1A1063238. This work was supported by INHA UNIVERSITY Research Grant as well (H.J.P.).

Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.jtbi.2023.111629>.

References

- Allen, B., Lippner, G., Chen, Y.-T., Fotouhi, B., Momeni, N., Yau, S.-T., Nowak, M.A., 2017. Evolutionary dynamics on any population structure. *Nature* 544, 227–230.
- Antal, T., Ohtsuki, H., Wakeley, J., Taylor, P.D., Nowak, M.A., 2009. Evolution of cooperation by phenotypic similarity. *Proc. Natl. Acad. Sci.* 106 (21), 8597–8600.
- Ashcroft, P., Altrock, P.M., Galla, T., 2014. Fixation in finite populations evolving in fluctuating environments. *J. R. Soc. Interface* 11, 20140663.
- Bahk, J., Baek, S.K., Jeong, H.-C., 2019. Long-range prisoner's dilemma game on a cycle. *Phys. Rev. E* 99, 012410. <http://dx.doi.org/10.1103/PhysRevE.99.012410>.
- Balshine-Earn, S., Neat, F.C., Reid, H., Taborsky, M., 1998. Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. *Behav. Ecol.* 9 (5), 432–438.
- Baron, J.W., Galla, T., 2018. How successful are mutants in multiplayer games with fluctuating environments? Sojourn times, fixation and optimal switching. *R. Soc. Open Sci.* 5 (3), 172176. <http://dx.doi.org/10.1098/rsos.172176>.
- Biernaskie, J.M., 2011. Evidence for competition and cooperation among climbing plants. *Proc. R. Soc. B: Biol. Sci.* 278 (1714), 1989–1996. <http://dx.doi.org/10.1098/rspb.2010.1771>.
- Broom, M., Rychtář, J., 2013. *Game-Theoretical Models in Biology*. Imprint Chapman and Hall/CRC.
- Chae, S., Lee, N., Baek, S.K., Jeong, H.-C., 2021. Assortative clustering in a one-dimensional population with replication strategies. *Phys. Rev. E* 103, 032114. <http://dx.doi.org/10.1103/PhysRevE.103.032114>.
- Constable, G.W.A., Rogers, T., McKane, A.J., Tarnita, C.E., 2016. Demographic noise can reverse the direction of deterministic selection. *Proc. Natl. Acad. Sci. USA* 113 (32), E4745–E4754.
- Débarre, F., Hauert, C., Doebeli, M., 2014. Social evolution in structured populations. *Nature Commun.* 5, 3409.
- Fletcher, J.A., Doebeli, M., 2009. A simple and general explanation for the evolution of altruism. *Proc. R. Soc. B: Biol. Sci.* 276 (1654), 13–19. <http://dx.doi.org/10.1098/rspb.2008.0829>.
- Fotouhi, B., Momeni, N., Allen, B., Nowak, M.A., 2019. Evolution of cooperation on large networks with community structure. *J. R. Soc. Interface* 16 (152), 20180677. <http://dx.doi.org/10.1098/rsif.2018.0677>.

- Greig, D., Travisano, M., 2004. The Prisoner's Dilemma and polymorphism in yeast SUC genes. *Proc. R. Soc. B* 271, S25–S26. <http://dx.doi.org/10.1098/rsbl.2003.0083>.
- Hadjichrysanthou, C., Broom, M., Rychtář, J., 2011. Evolutionary games on star graphs under various updating rules. *Dynam. Games Appl.* 1 (3), 386. <http://dx.doi.org/10.1007/s13235-011-0022-7>.
- Hauert, C., Doebeli, M., 2004. Spatial structure often inhibits the evolution of cooperation in the snowdrift game. *Nature* 428 (6983), 643–646. <http://dx.doi.org/10.1038/nature02360>.
- Hauert, C., Holmes, M., Doebeli, M., 2006. Evolutionary games and population dynamics: maintenance of cooperation in public goods games. *Proc. R. Soc. B: Biol. Sci.* 273 (1600), 2565–2571. <http://dx.doi.org/10.1098/rspb.2006.3600>.
- Hauert, C., Wakano, J.Y., Doebeli, M., 2008. Ecological public goods games: Cooperation and bifurcation. *Theor. Popul. Biol.* 73 (2), 257–263. <http://dx.doi.org/10.1016/j.tpb.2007.11.007>.
- Hilbe, C., Šimsa, S., Chatterjee, K., Nowak, M.A., 2018. Evolution of cooperation in stochastic games. *Nature* 559, 246–249.
- Hinrichsen, H., 2000. Non-equilibrium critical phenomena and phase transitions into absorbing states. *Adv. Phys.* 49 (7), 815–958. <http://dx.doi.org/10.1080/00018730050198152>.
- Huang, W., Hauert, C., Traulsen, A., 2015. Stochastic game dynamics under demographic fluctuations. *Proc. Natl. Acad. Sci.* 112 (29), 9064–9069. <http://dx.doi.org/10.1073/pnas.1418745112>.
- Killingback, T., Doebeli, M., 1996. Spatial evolutionary game theory: Hawks and doves revisited. *Proc. R. Soc. B* 263 (1374), 1135–1144. <http://dx.doi.org/10.1098/rspb.1996.0166>.
- Liming, W., Wu, F., 2014. Effects of empty sites on cooperation in the prisoner's dilemma game based on social diversity. In: Solís-Perales, G. (Ed.), *Discrete Dyn. Nat. Soc.* 2014, 907052. <http://dx.doi.org/10.1155/2014/907052>, Publisher: Hindawi Publishing Corporation.
- Lion, S., 2009. Relatedness in spatially structured populations with empty sites: An approach based on spatial moment equations. *J. Theoret. Biol.* 260 (1), 121–131. <http://dx.doi.org/10.1016/j.jtbi.2009.05.035>, URL: <https://www.sciencedirect.com/science/article/pii/S0022519309002409>.
- Melbinger, A., Cremer, J., Frey, E., 2010. Evolutionary game theory in growing populations. *Phys. Rev. Lett.* 105, 178101. <http://dx.doi.org/10.1103/PhysRevLett.105.178101>.
- Moreno-Fenoll, C., Cavaliere, M., Martínez-García, E., Poyatos, J.F., 2017. Eco-evolutionary feedbacks can rescue cooperation in microbial populations. *Sci. Rep.* 7 (1), 42561. <http://dx.doi.org/10.1038/srep42561>.
- Nowak, M.A., 2006a. *Evolutionary Dynamics*. Harvard University Press.
- Nowak, M.A., 2006b. Five rules for the evolution of cooperation. *Science* 314 (5805), 1560–1563. <http://dx.doi.org/10.1126/science.1133755>.
- Nowak, M.A., Bonhoeffer, S., May, R.M., 1994. More spatial games. *Int. J. Bifurcation Chaos* 04 (01), 33–56. <http://dx.doi.org/10.1142/S0218127494000046>.
- Nowak, M.A., May, R.M., 1992. Evolutionary games and spatial chaos. *Nature* 359 (6398), 826–829. <http://dx.doi.org/10.1038/359826a0>.
- Nowak, M.A., Sigmund, K., 2004. Evolutionary dynamics of biological games. *Science* 303 (5659), 793–799. <http://dx.doi.org/10.1126/science.1093411>.
- Ohtsuki, H., Hauert, C., Lieberman, E., Nowak, M.A., 2006. A simple rule for the evolution of cooperation on graphs and social networks. *Nature* 441, 502–505.
- Pacheco, J.M., Santos, F.C., Souza, M.O., Skyrms, B., 2009. Evolutionary dynamics of collective action in N-person stag hunt dilemmas. *Proc. R. Soc. B* 276, 315–321.
- Park, H.J., Pichugin, Y., Huang, W., Traulsen, A., 2019. Population size changes and extinction risk of populations driven by mutant interactors. *Phys. Rev. E* 99, 022305. <http://dx.doi.org/10.1103/PhysRevE.99.022305>.
- Perc, M., 2009. Evolution of cooperation on scale-free networks subject to error and attack. *New J. Phys.* 11 (3), 033027. <http://dx.doi.org/10.1088/1367-2630/11/3/033027>.
- Perc, M., Gómez-Gardeñes, J., Szolnoki, A., Floría, L.M., Moreno, Y., 2013. Evolutionary dynamics of group interactions on structured populations: A review. *J. R. Soc. Interface* 10 (80), 20120997.
- Perc, M., Szolnoki, A., 2010. Coevolutionary games—A mini review. *Biosystems* 99 (2), 109–125. <http://dx.doi.org/10.1016/j.biosystems.2009.10.003>.
- Rand, D.G., Nowak, M.A., 2013. Human cooperation. *Trends Cogn. Sci.* 17, 413.
- Rodríguez-Brenes, I.A., Wodarz, D., Komarova, N.L., 2020. Beyond the pair approximation: Modeling colonization population dynamics. *Phys. Rev. E* 101, 032404. <http://dx.doi.org/10.1103/PhysRevE.101.032404>.
- Ross-Gillespie, A., Gardner, A., Buckling, A., West, S.A., Griffin, A.S., 2009. Density dependence and cooperation: Theory and a test with bacteria. *Evolution* 63 (9), 2315–2325. <http://dx.doi.org/10.1111/j.1558-5646.2009.00723.x>.
- Sanchez, A., Gore, J., 2013. Feedback between population and evolutionary dynamics determines the fate of social microbial populations. *PLoS Biol.* 11 (4), 1–9. <http://dx.doi.org/10.1371/journal.pbio.1001547>.
- Santos, F.C., Pacheco, J.M., Lenaerts, T., 2006. Evolutionary dynamics of social dilemmas in structured heterogeneous populations. *Proc. Natl. Acad. Sci.* 103 (9), 3490–3494. <http://dx.doi.org/10.1073/pnas.0508201103>.
- Santos, F.C., Santos, M.D., Pacheco, J.M., 2008. Social diversity promotes the emergence of cooperation in public goods games. *Nature* 454, 213–216.
- Sekiguchi, T., Nakamaru, M., 2009. Effect of the presence of empty sites on the evolution of cooperation by costly punishment in spatial games. *J. Theoret. Biol.* 256 (2), 297–304. <http://dx.doi.org/10.1016/j.jtbi.2008.09.025>, URL: <https://www.sciencedirect.com/science/article/pii/S0022519308005067>.
- Sigmund, K., 2010. *The Calculus of Selfishness*. Princeton University Press.
- Smaldino, P.E., 2013. Cooperation in harsh environments and the emergence of spatial patterns. *Chaos Solitons Fractals* 56, 6–12. <http://dx.doi.org/10.1016/j.chaos.2013.05.010>.
- Smith, J.M., 1982. *Evolution and the Theory of Games*. Cambridge University Press.
- Su, Q., Li, A., Wang, L., Eugene Stanley, H., 2019. Spatial reciprocity in the evolution of cooperation. *Proc. R. Soc. B: Biol. Sci.* 286 (1900), 20190041. <http://dx.doi.org/10.1098/rspb.2019.0041>.
- Szabó, G., Antal, T., Szabó, P., Droz, M., 2000. Spatial evolutionary prisoner's dilemma game with three strategies and external constraints. *Phys. Rev. E* 62, 1095–1103. <http://dx.doi.org/10.1103/PhysRevE.62.1095>.
- Szabó, G., Fáth, G., 2007. Evolutionary games on graphs. *Phys. Rep.* 446 (4), 97–216.
- Szabó, G., Töke, C., 1998. Evolutionary prisoner's dilemma game on a square lattice. *Phys. Rev. E* 58, 69–73. <http://dx.doi.org/10.1103/PhysRevE.58.69>.
- Szolnoki, A., Antonioni, A., Tomassini, M., Perc, M., 2014. Binary birth-death dynamics and the expansion of cooperation by means of self-organized growth. *Europhys. Lett.* 105 (4), 48001. <http://dx.doi.org/10.1209/0295-5075/105/48001>.
- Tilman, A.R., Plotkin, J.B., Akçay, E., 2020. Evolutionary games with environmental feedbacks. *Nature Commun.* 11, 915.
- Wakano, J.Y., Nowak, M.A., Hauert, C., 2009. Spatial dynamics of ecological public goods. *Proc. Natl. Acad. Sci.* 106 (19), 7910–7914.
- Wang, X., Perc, M., 2021. Emergence of cooperation in spatial social dilemmas with expulsion. *Appl. Math. Comput.* 402, 126149. <http://dx.doi.org/10.1016/j.amc.2021.126149>.
- Wang, Z., Szolnoki, A., Perc, M., 2012. Percolation threshold determines the optimal population density for public cooperation. *Phys. Rev. E* 85, 037101. <http://dx.doi.org/10.1103/PhysRevE.85.037101>.
- Wiessner, P., 2002. Hunting, healing, and hxaro exchange: A long-term perspective on !Kung (ju/'hoansi) large-game hunting. *Evol. Hum. Behav.* 23 (6), 407–436. [http://dx.doi.org/10.1016/S1090-5138\(02\)00096-X](http://dx.doi.org/10.1016/S1090-5138(02)00096-X).