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The role of emotions in the maintenance of cooperative behaviors

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Abstract – Our attention is focused on how individual emotions influence collective behaviors, which captures an aspect of reality missing from past studies: free riders may suffer some stress, which could adapt jointly with the individual stress intensity and size of the gaming group. With an evolutionary game theoretical approach, we gain the fixation probability for one mutant cooperator to invade and dominate the whole defecting population. When the stress intensity exceeds a threshold, natural selection favors cooperators replacing defectors in a finite population. We further infer that lower stress intensity is sufficient for one mutant cooperator to become fixed with an advantageous probability in a larger population. Moreover, when the gaming group is smaller than the population size, the more the return from the public goods, the lower the threshold of stress intensity required to facilitate the full dominance of cooperators. We hope our studies may show that individual sentiments or psychological activities will open up novel explanations for the puzzle of collective actions.

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Introduction. – Social dilemmas are situations in which the optimal decision for an individual is not optimal, or is even harmful, for the society as a whole. Rational agents, who try to maximize their own well-being, may thus attempt to free ride and reap undeserved rewards, i.e. benefit from the "social" contributions of others without providing their own in exchange. Resolving a social dilemma entails providing a rationale on how a behavior that is costly for an individual but beneficial for the society can be maintained by means of natural selection. A common mathematical framework of choice for addressing the many subtleties of cooperation within groups of selfish individuals is the evolutionary game theory [1–11]. Many real-life situations are often associated with collective actions based on joint decisions made by multiple individuals. This type of problems is best dealt with in the frame of N-person games, such as the public goods game, which has been a classical mathematical metaphor illustrating the problem of cooperation and cheating through group interactions [12–15]. Irrespective of their decision, each group member receives an equal share of public goods after the accumulative contributions are multiplied by a

factor that takes into account the added value of collaborative efforts. The dilemma posed by this model is thus a conflict between the choice (defection) that maximizes each individual player's reward and the choice (cooperation) that maximizes the reward for the group as a whole.

A variety of solutions for this dilemma have been discussed in the past studies and suggested to be capable of boosting cooperation. The theory of kin selection focuses on cooperation among individuals that are genetically closely related, whereas theory of direct reciprocity focus on the selfish incentives for cooperation in bilateral longterm interactions [16–19]. Greenbeard genes are a special form of kin selection. The theories of indirect reciprocity and costly signalling indicate how cooperation in larger groups can emerge when the cooperators can build a reputation [20–23]. Recently studied ways of promoting cooperation in public goods games include the introduction of volunteering [24], social diversity [25], reward [26], social learning [27], group size [28], to name but a few. Besides, punishment has also turned out to be an effective mechanism to prevent cheating even under full anonymity [29].

There is now a rich literature on whether and how various forms of punishment are effective in bringing about cooperation [30–37].

In addition, evolutionary psychologists have also expressed a keen interest in trying to answer the puzzle of human collective action. For instance, the role of moral emotions in the resolution of the collective dilemma game has recently become the matter of considerable debate [38,39]. These emotions originate in social relationships and are built on reciprocal evaluations and judgements of the self and others. It is inspired by the fact that: a substantial number of people may exhibit social preferences, implying that they are not solely motivated by self-interest but also care positively or negatively for the payoffs of relevant reference agents. Choosing for immediate individual rewards in a social dilemma situation gives rise to moral emotions (jealousy, guilt, stress, etc.), a normal feeling beset by the ordinary human being. Intriguingly, research from psychology and behavioural economics have provided experimental evidence of that such moral emotions lead to prosocial or cooperative behaviors of humans.

We note that earlier studies on the ability of emotions for driving cooperative behaviors put much emphasis on getting insights by performing human experiments [40–44]. This leaves us with a situation in which the psychological activities can also be investigated by means of mathematical models to obtain a comprehensive understanding. To shed light on this issue, we develop a simple argument to delineate how the collective actions are affected by the emotions of free riders. Although rich conditions may be required by the emergence of emotions, here we employ a simplification of the concept of "stress" faced by defectors as a first step. Further, free riders may incur some cost due to this unpleasant experience when they are thrown into the stress or even shame condition. In particular, we assume that this cost is in the form of payoff reduction, denoting that stress can be seen as a kind of loss aroused by the potential sense of social fairness and justice believed by humans.

Besides, for a more realistic setting, this inflicted cost is closely related to the stress intensity of the focal defector (seen as internal causes) and size of the gaming group (seen as external causes) it participates in. It seems plausible that defectors may endure relatively slight stress when they submerge in a larger gaming group. Also, empirical evidences tell us that individuals differ in autonomous morality, leading to the heterogeneity of stress intensity within populations. From this perspective, we can thereby assume that defectors may bear larger cost when suffering stronger stress intensity and participating in smaller gaming group. Thus, this work aims to construct a platform reflecting the interplay of individual emotions and dilemma games, and measure its ability in achieving and sustaining cooperation.

The rest of the paper proceeds as follows. First we describe the studied model. Next, we derive analytical

expressions for the fixation probability of one mutant cooperator to take over a finite defecting population. Finally, we sum up our observations and provide concluding comments based on them.

The extended public goods game. — Before continuing, it is important to review the typical public goods game (PGG). It is proposed to illustrate the problem of cooperation and cheating through group interaction, which is still a matter of lively debate. Cooperation (to maximize reward for the group) and defection (to maximize reward for the individual) are the two strategies that are usually at the heart of such social dilemma.

In a typical PGG played in a group of n interacting agents, each player must independently and simultaneously decide whether or not they wish to bear the cost of cooperation and thus to contribute to the common pool. The collected sum is multiplied by a factor r(1 < r < n) and then redistributed to the n players equally, irrespective of their individual contributions. Thus, why should a self-interested individual contribute anything to a public good that —once it exists— an individual can consume regardless of whether it contributed or not?

Herein, our extended public goods game (EPGG) with binary (all or none) contributions, follows identical rules to those of the typical PGG described above, except that defectors are likely to suffer some stress in terms of payoff reduction. However, altruistic individuals, *i.e.* cooperators here, will suffer no stress. Our simplified game theoretical description of such problems assumes that each cooperator (C) makes a contribution of 1 to the respective public goods under consideration, while nothing is contributed by a defector (D).

In this EPGG, we employ c_k and d_k as the payoff for an individual cooperating and defecting, respectively, when there are n-k cooperators in the other n-1 group members $(1 \le k \le n)$. Regardless of whether it contributes or not, each member will evenly gain the benefit (n-k)r/n. The difference is that cooperation will incur an additional cost 1-r/n, while defection may suffer stress closely related with stress intensity α and size of gaming group n. Therefore, c_k and d_k can be respectively described as

$$c_k = \frac{r(n-k+1)}{n} - 1,$$
 (1)

$$d_k = \frac{r(n-k)}{n} - \frac{\alpha}{n}. (2)$$

Solving $c_k > d_k$ immediately gives us $\alpha > n - r$ (1 < r < n). If defectors suffer stress with an intensity larger than n - r, then cooperation in this EPGG is a dominant strategy, and thus a traditional evolutionary stable strategy in the deterministic model [45].

Fixation probability and evolutionarily stable strategy. – Our main concern is to derive the fixation probability for one mutant cooperator to take over the finite defecting population. We posit a large, well-mixed

population of size N. From time to time, a random sample of n players is chosen to participate in an EPGG. Fitness of an individual is determined by its expected payoff in the game assuming weak selection. At each time step, an individual is chosen for reproduction with the probability proportional to its fitness. The individual produces its copy that replaces another randomly chosen individual.

Below, we intend to derive the fixation probability for one mutant cooperator to invade and take over the population playing defection. Let i denote the number of cooperators in a finite N population, and thus N-i represents the number of defectors. The probability follows the hypergeometric distribution that an individual in a group of n members plays the EPGG with other n-k cooperators and k-1 defectors. That is, this probability is $\binom{i-1}{n-k}\binom{N-i}{k-1}/\binom{N-1}{n-1}$ for a cooperator and $\binom{i}{n-k}\binom{N-i-1}{k-1}/\binom{N-1}{n-1}$ for a defector. Hence, the expected payoff for a cooperator and a defector in this population is respectively given by

$$F_i = \sum_{k=1}^{n} \frac{\binom{i-1}{n-k} \binom{N-i}{k-1} c_k}{\binom{N-1}{n-1}},$$
 (3)

$$G_i = \sum_{k=1}^n \frac{\binom{i}{n-k} \binom{N-i-1}{k-1} d_k}{\binom{N-1}{n-1}}.$$
 (4)

Note that here $\binom{a}{b}$ is defined as a binomial coefficient when $a \ge b$ and otherwise as zero when a < b.

Next, following [46], the fitness of a cooperator and a defector is respectively defined as

$$f_i = 1 - \omega + \omega F_i, \tag{5}$$

$$g_i = 1 - \omega + \omega G_i, \tag{6}$$

where ω measures the selection intensity. Particularly, $0<\omega\ll 1$ means weak selection where the payoffs gained from game playing make a small contribution to the fitness.

Selection dynamics can be formulated as a Moran process, which is a simple birth-death process [47]. At each time step, one agent is chosen for reproduction proportional to its fitness. One identical offspring is being produced and replaces a randomly chosen individual, thus N is constant. The same individual could be chosen for reproduction and death. At each time step, the number of cooperators can either increase by one, stay the same, or decrease by one. Therefore, the probabilities to change from i to i+1 cooperators, and from i to i-1 cooperators are respectively given by

$$p_{i,i+1} = \frac{if_i}{if_i + (N-i)g_i} \cdot \frac{N-i}{N}, \tag{7}$$

$$p_{i,i-1} = \frac{(N-i)g_i}{if_i + (N-i)g_i} \cdot \frac{i}{N}.$$
 (8)

Herein the number of cooperators i in the population of size N could be $0, 1, \ldots, N-1$, or N.

Then the probability to keep on having i cooperators

$$p_{i,i} = 1 - p_{i,i+1} - p_{i,i-1}. (9)$$

This mentioned process has two absorbing states, $p_{0,0} = 1$ and $p_{N,N} = 1$, that is, full cooperating population and full defecting population. If the population has reached either one of those states, then it will stay forever.

Let ρ_c denote the fixation probability of a single mutant C to take over a population of D [46]. Thus, the fixation probability of C, ρ_c , with which a population at state i = 1 eventually reaches state i = N is given by

$$\rho_c = \frac{1}{1 + \sum_{j=1}^{N-1} \prod_{i=1}^j \frac{g_i}{f_i}}.$$
 (10)

For neutral mutants with $f_i = g_i$ in a finite population of N individuals, their fixation probabilities are 1/N. We refer to D as stochastically robust against the invasion of C if natural selection opposes C replacing D, or formally, $\rho_c < 1/N$ [46]. Herein, we consider the case of weak selection where ω approaches zero.

According to Kurokawa and Ihara [48], for the general n-player game, the fixation probability ρ_c of C in a defecting population, is approximately given by

$$\rho_c \approx \frac{1}{N} \cdot \frac{1}{1 - \frac{(AN - B)w}{n(n+1)}},\tag{11}$$

where

$$A = \sum_{k=1}^{n} k(c_k - d_k), \tag{12}$$

$$B = -n^2 d_n + \sum_{k=1}^{n-1} k d_k + \sum_{k=1}^{n} (n+1-k)c_k.$$
 (13)

Hence, $\rho_c > 1/N$ holds and thus the selection favors C replacing D if AN > B. According to Kurokawa and Ihara [48], the condition AN > B can be reformulated as

$$(N-n)\sum_{k=1}^{n}k(c_k-d_k)+(n+1)\sum_{k=1}^{n-1}k(c_{k+1}-d_k)>0. (14)$$

Inserting c_k and d_k calculated above into eq. (14) leads to K > 0, where

$$K = (N - n)\left(\frac{r}{n} + \frac{\alpha}{n} - 1\right) + (n - 1)\left(\frac{\alpha}{n} - 1\right). \tag{15}$$

In a scenario like this, small N(N=n) helps $\alpha/n-1$ to play a key role in the evolutionary outcomes. Alternatively, large N benefits $r/n+\alpha/n-1$ to be the vital factor. Then eq. (11) can be correspondingly reformulated as

$$\rho_c \approx \frac{1}{N} \cdot \frac{1}{(1 - wK/2)}.\tag{16}$$

Solving K > 0 brings $\alpha > \alpha^*$, where this threshold α^* of stress intensity will thus be

$$\alpha^* = \frac{Nn - Nr + nr - n}{N - 1}.\tag{17}$$

These findings are indications that if the stress intensity surpasses the threshold value, natural selection favors one mutant cooperator to invade and take over the defecting population playing the EPGG.

Let us continue to ask whether C is more likely to replace D than vice versa. The ratio of the fixation probabilities can be calculated as follows

$$\frac{\rho_c}{\rho_d} = \prod_{i=1}^{N-1} \frac{f_i}{g_i} \approx 1 + \frac{\omega}{n} \left[N \sum_{k=1}^n (c_k - d_k) - n(c_1 - d_n) \right], \quad (18)$$

where ρ_d is the fixation probability for one mutant defector to take over the population of N cooperators, or the probability that the number of cooperators evolves from i = N - 1 to i = 0.

If $\rho_c/\rho_d > 1$, it is more likely that one mutant cooperator becomes stabilized in a population of defectors than one mutant defector becomes fixed in a population of cooperators. With a view to $c_k - d_k = r/n + \alpha/n - 1$ and $c_{k+1} - d_k = \alpha/n - 1$ in our studied system, eq. (18) can be reformulated as

$$\frac{\rho_c}{\rho_d} \approx 1 + \frac{\omega}{n} \left[(N - n) \sum_{k=1}^n (c_k - d_k) + n \sum_{k=1}^{n-1} (c_{k+1} - d_k) \right]
= 1 + \omega K.$$
(19)

Consequently, $\rho_c/\rho_d > 1$ is equivalent to K > 0 and therefore derives $\alpha > \alpha^*$ again.

Looking further ahead, eqs. (16) and (19) lead to

$$\rho_d \approx \frac{1}{N} \cdot \frac{1}{(1 + wK/2)},\tag{20}$$

where K > 0 results in $\alpha > \alpha^*$ and $\rho_d < 1/N$, implying that natural selection opposes one mutant defector taking over the cooperating population. Summarizing the above results, $\alpha > \alpha^*$ helps us finally get

$$\rho_c > \frac{1}{N} > \rho_d. \tag{21}$$

Notably, cooperation is an evolutionary stable strategy in a finite population of size N when satisfying the following conditions: 1) a single mutant defector in a cooperating population has a lower fitness, and 2) fixation probability ρ_d of defecting mutant is lower than 1/N [46]. Herein, the condition 1) requires $F_{N-1} > G_{N-1}$ where

$$(N-n)(c_1-d_1) + (n-1)(c_2-d_1) > 0, (22)$$

where $c_1 - d_1 = r/n + \alpha/n - 1$ and $c_2 - d_1 = \alpha/n - 1$ in our studied system lead to K > 0 and $\alpha > \alpha^*$ again. At this point, condition 2) can also be met. Hence, cooperation is an evolutionary stable strategy for finite N in the case of $\alpha > \alpha^*$. Similarly, defection is not an evolutionary stable strategy for finite N since neither condition could be satisfied when $\alpha > \alpha^*$.

Lastly, we analyse the relatedness of threshold α^* with other model parameters, and firstly focus on

$$\frac{\partial \alpha^*}{\partial N} = \frac{r(1-n)}{(N-1)^2} < 0 \tag{23}$$

which indicates the larger the size of the population, the lower the threshold of stress intensity, which gives us many interesting hints about cooperation in social society. Moreover, the small values of eq. (23), when facing a sufficiently large population, imply an indistinctive effect of the population size on the game dynamics in that case.

Then, in the general case in which $n < N, \alpha^*$ monotonically decreases with increasing multiplication factor r, since

$$\frac{\partial \alpha^*}{\partial r} = \frac{n-N}{N-1} < 0 \tag{24}$$

when the group composition changes from generation to generation, the more the return from the public goods, the lower the threshold of stress intensity. However, this influence disappears under the assumption of n = N. Put differently, when the group consists only of permanent members, the stress intensity larger than the threshold can fully drive the full dominance of cooperators, irrespective of the multiplication factors.

Finally, we shift our attention to

$$\frac{\partial \alpha^*}{\partial n} = \frac{N+r-1}{N-1} > 0, \tag{25}$$

where α^* monotonically increases with greater n and reaches its maximum till n=N. As explained earlier in the model definition, larger n will reduce the stress cost α/n of the focal defector, and therefore enforce the payoff advantages of defectors when facing cooperators. Under this situation, the observation here that cooperators in a larger game group need larger stress intensity of the defectors to survive, is not surprising.

Conclusions. — Self-interest frequently causes individuals engaged in joint enterprises to choose actions that are counterproductive. Our work is initiated by questions related to the psychological activities of individuals engaging in collective actions. Everyday experiences tell us that free riders may suffer some stress stirred up by the potential social justice and moral principles, when reaping the benefits of cooperation by others. Within this model, this negative emotion is represented as an additional payoff loss that is born by players when defecting. As a closer approximation of the real world, this loss decreases with larger gaming group size and it can also be tuned by an intensity parameter. This raises the question of how the agent emotions affect the spread of strategies through a population of finite size.

Our work thus intends to investigate the potential role of emotions in triggering cooperative behaviors. Herein we gain the fixation probability for one mutant cooperator to invade and dominate the whole defecting population. When the stress intensity of defectors surpasses the threshold, cooperation is, while defection is not, an evolutionary stable strategy in finite population. Moreover, lower stress intensity can already drive the larger population to a state which assures substantial cooperation. Further, when the gaming group is smaller than the population size, the more the return from the public goods, the lower the threshold of stress intensity required to facilitate the dominance of cooperation. We can safely reach the conclusion that the proposed stress emotions experienced by free riders presents a viable escape hatch out of evolutionary stalemate, and may provide an alternative way to explore the sustainment of massive cooperation in real-life societies.

The fine-grained analysis gained above provides an intuitive understanding of the role played by stress in public goods games. However, the research reported here lends itself to multiple extensions. An immediate one, for example, would be to allow for the possibility of an emotional profile (e.g., including sympathy, envy, shame, etc.) endowed to gaming players. It should be stressed that up to now we have limited our study to where only positive acts, *i.e.* the stress suffered by free riders, are considered. However, one could think of scenarios in which emotions from a player will often be more complicated in natural settings. For instance, the intriguing work of [49,50] has revealed that even the negative part of an emotional profile can elevate the social welfare in collective actions of networked populations. Thus, investigating what happens by theoretical considerations when introducing the negative emotions seems a promising continuation of the results presented here. Another interesting future direction would be to address whether the presence of these different emotions altogether, and even the evolution of emotions, affect the dynamics of behaviors in the field of human cooperation. Further theoretical work is needed to clarify these issues and to accurately mimic reality.

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REFERENCES

- [1] AUMANN R. J., Irrationality in Game Theory, in Economic Analysis of Markets and Games: Essays in Honor of Frank Hahn, edited by Dasgupta P., Gale D., Hart O. and Maskin E. (MIT Press, Cambridge, Mass.) 1992, pp. 214–227.
- [2] AXELROD R., J. Confl. Resolut., 24 (1980) 3.
- [3] AXELROD R. and HAMILTON W. D., Science, 211 (1981) 1390.
- [4] SZÖLLŐSI G. J. and DERÉNYI I., Phys. Rev. E, 78 (2008) 031919.

- [5] AXELROD R. and DION D., Science, 242 (1988) 1385.
- [6] BERNHARD H., FISHERBACHER U. and FEHR E., Nature, 442 (2006) 912.
- [7] BOYD R., GINTIS H. and BOWLES S., Science, 328 (2010) 617.
- [8] Burtsev M. and Turchin P., Nature, 440 (2006) 1041.
- [9] DREBER A., RAND D. G., FUDENBERG D. and NOWAK M. A., Nature, 452 (2008) 348.
- [10] ZHANG J., ZHANG C. and CHU T., Chaos, Solitons Fractals, 44 (2011) 131.
- [11] SZOLNOKI A. and PERC M., Phys. Rev. E, 89 (2014) 022804.
- [12] BRANDT H., HAUERT C. and SIGMUND K., Proc. Natl. Acad. Sci. U.S.A., 103 (2006) 495.
- [13] HAUERT C., DE MONTE S., HOFBAUER J. and SIGMUND K., Science, **296** (2002) 1129.
- [14] SZOLNOKI A. and PERC M., Phys. Rev. E, **81** (2010) 057101.
- [15] ZHANG C., ZHANG J., XIE G. and WANG L., EPL, 90 (2010) 68005.
- [16] IMHOF L. A. and NOWAK M. A., Proc. R. Soc. Lond. B, 277 (2010) 463.
- [17] NOWAK M. A., Science, **314** (2006) 1560.
- [18] Ohtsuki H. and Nowak M. A., J. Theor. Biol., 247 (2007) 462.
- [19] PACHECO J. M., TRAULSEN A., OHTSUKI H. and NOWAK M. A., J. Theor. Biol., 250 (2008) 723.
- [20] NOWAK M. A. and SIGMUND K., Nature, 437 (2005) 1291.
- [21] NOWAK M. A. and SIGMUND K., Nature, 393 (1998) 573.
- [22] BRANDT H. and SIGMUND K., Proc. Natl. Acad. Sci. U.S.A., 102 (2005) 2666.
- [23] ELY J., FUDENBERG D. and LEVINE D. K., Games Econ. Behav., 63 (2008) 498.
- [24] HAUERT C., DE MONTE S., HOFBAUER J. and SIGMUND K., *Science*, **296** (2002) 1129.
- [25] SANTOS F. C., SANTOS M. D. and PACHECO J. M., Nature, 454 (2008) 213.
- [26] SZOLNOKI A. and PERC M., EPL, 92 (2010) 38003.
- [27] SIGMUND K., DE SILVA H., TRAULSEN A. and HAUERT C., *Nature*, **466** (2010) 861.
- [28] SZOLNOKI A. and PERC M., Phys. Rev. E, 84 (2011) 047102.
- [29] PIAZZA J. and BERING J. M., Evol. Psychol., 6 (2008) 487.
- [30] BRANDT H., HAUERT C. and SIGMUND K., Proc. R. Soc. Lond. B, 270 (2003) 1099.
- [31] ZHANG C., ZHANG J., XIE G. and WANG L., J. Stat. Mech. (2010) P12004.
- [32] HAUERT C., TRAULSEN A., BRANDT H., NOWAK M. A. and SIGMUND K., Biol. Theor., 3 (2008) 114.
- [33] DARCET D. and SORNETTE D., J. Econ. Interact. Coord., 3 (2008) 137.
- [34] Fehr E. and Gächter S., Nature, 415 (2002) 137.
- [35] SZOLNOKI A. and PERC M., J. Theor. Biol., 325 (2013) 34.
- [36] Perc M., Sci. Rep., 2 (2012) 344.
- [37] HELBING D., SZOLNOKI A., PERC M. and SZABÓ G., PLoS Comput. Biol., 6 (2010) e1000758.
- [38] Tangney J. P., J. Pers. Soc. Psychol., 61 (1991) 598.
- [39] VAN LANGE P. A. and VISSER K., J. Pers. Soc. Psychol., 77 (1999) 762.

- [40] Frank R. H., Emot. Rev., 3 (2011) 252.
- [41] KETELAAR T., Ancestral emotions, current decisions:
 Using evolutionary game theory to explore the role of
 emotions in decision-making, in Evolutionary Psychology,
 Public Policy and Personal Decisions (Lawrence Erlbaum
 Associates, Inc Mahwah, NJ) 2004, pp. 145–168.
- [42] Ketelaar T. and Tung Au W., Cogn. Emot., 17 (2003) 429
- [43] Nelissen R. M., Dijker A. J. and deVries N. K., J. Exp. Soc. Psychol., 43 (2007) 280.
- [44] DE HOOGE I. E., ZEELENBERG M. and BREUGELMANS S. M., Cogn. Emot., 21 (2007) 1025.

- [45] MAYNARD SMITH J., Evolution and the Theory of Games (Cambridge University Press, Cambridge, UK) 1982.
- [46] NOWAK M. A., SASAKI A., TAYLOR C. and FUDENBERG D., *Nature*, **428** (2004) 646.
- [47] LIEBERMAN E., HAUERT C. and NOWAK M. A., *Nature*, **433** (2005) 312.
- [48] KUROKAWA S. and IHARA Y., Proc. R. Soc. Lond. B, 276 (2009) 1379.
- [49] SZOLNOKI A., XIE N.-G., WANG C. and PERC M., EPL, 96 (2011) 38002.
- [50] SZOLNOKI A., XIE N.-G., YE Y. and PERC M., Phys. Rev. E, 87 (2013) 042805.