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Linking Individual and Collective Behavior in Adaptive Social Networks

Flávio L. Pinheiro,[1,2,3] Francisco C. Santos,[1,3] and Jorge M. Pacheco[2,3,4]
[1]INESC-ID and Instituto Superior Técnico, Universidade de Lisboa, 2744-016 Porto Salvo, Portugal
[2]Centro de Biologia Molecular e Ambiental da Universidade do Minho, 4710-057 Braga, Portugal
[3]ATP-group, P-2744-016 Porto Salvo, Portugal
[4]Departamento de Matemática e Aplicações da Universidade do Minho, 4710-057 Braga, Portugal

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Adaptive social structures are known to promote the evolution of cooperation. However, up to now the characterization of the collective, population-wide dynamics resulting from the self-organization of individual strategies on a coevolving, adaptive network has remained unfeasible. Here we establish a (reversible) link between individual (micro)behavior and collective (macro)behavior for coevolutionary processes. We demonstrate that an adaptive network transforms a two-person social dilemma locally faced by individuals into a collective dynamics that resembles that associated with an N-person coordination game, whose characterization depends sensitively on the relative time scales between the entangled behavioral and network evolutions. In particular, we show that the faster the relative rate of adaptation of the network, the smaller the critical fraction of cooperators required for cooperation to prevail, thus establishing a direct link between network adaptation and the evolution of cooperation. The framework developed here is general and may be readily applied to other dynamical processes occurring on adaptive networks, notably, the spreading of contagious diseases or the diffusion of innovations.

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Complex networks provide a powerful representation of the underlying web of social ties that interconnect individuals in a given community or population [1–5]. As time unfolds, individuals may adjust their behaviors (or their social ties), which typically induces changes in the social network they are embedded in (or in their individual behavior). It is thus no surprise that the heterogeneous structures we often find in empirical analyses result from the interplay between at least these two coevolving mechanisms. Naturally, one expects the emerging features of a complex network to depend on the nature of the interactions between peers. For instance, if what is at stake is the spreading of a disease, healthy individuals ought to break (secure) the links with infected (healthy) individuals, provided they know they are (not) infected [6–8], whereas social dilemmas of cooperation [3,9–11] by considering individuals with different preferences (regarding the maintenance of interactions) often lead to more complex decision processes. The time dependence of both social structure and individuals' choices can be conveniently described by means of a coevolutionary process [3,4,11] where individual behavior is allowed to evolve *at par* with the structure of the underlying social network [11]. The latter implies that links are possibly rewired depending on whether individuals are satisfied or not with a given interaction. A simple implementation of such a model [11] —see below for details and Ref. [12] for related approaches —accounts for many of the stylized facts one expects to happen when social behavior and social structure coevolve [13]: adaptation of individual preferences and behaviors, together with resolution of conflicts of interest reflecting the process at stake. In particular, as detailed below, when conflicts of interest are described by the paradigmatic prisoner's dilemma (PD) of cooperation—which from a rational point of view would lead to widespread defection —network adaptation favors cooperation at a population-wide level. Consequently, and despite the fact that, locally, every individual engages in a PD game, globally, the game being played must be a different one.

But which one? Of which type? With which features? These questions remain open and are of fundamental importance given that, often, all we can gather empirically (e.g., from populations of microbes to human societies [14]) are time-series data of aggregate information, without direct information on individual behavior. An intuitive example of our empirical constraints regards epidemic outbreaks: What one often collects is aggregate statistical information of the community as a whole, instead of individual information that may allow practitioners to infer directly from the data the characteristics of the, say, virus infectiousness [7]. Thus, and similar to many other areas of physics, it becomes ubiquitous to establish a (reversible) link between individual and collective behavior in the analysis of coevolutionary processes.

In this Letter, we develop a novel framework able to capture the nontrivial link between the nature of individual (local) interactions and the population-wide (global) dynamics observable in adaptive structures.

Figure 1 provides an overview of what is known to date by means of computer simulations regarding the

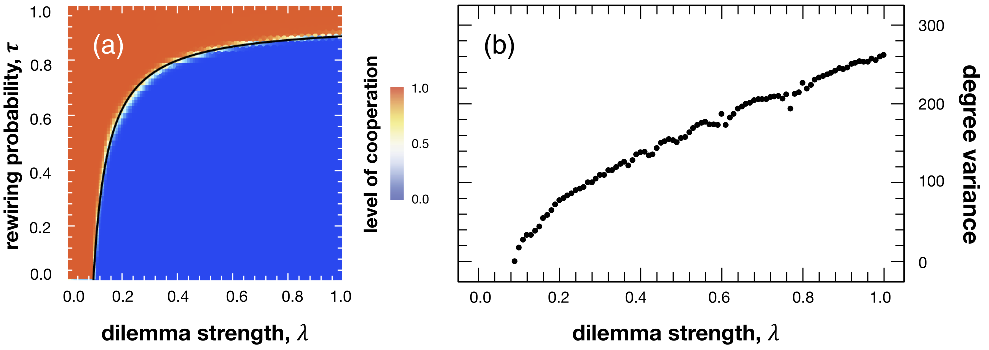

FIG. 1. Level of cooperation and network heterogeneity under coevolutionary dynamics. (a) We computed numerically the level of cooperation in the domain bounded by $0.0 \leq \lambda \leq 1.0$ and $0.0 \leq \tau \leq 1.0$. It is given by the average final fraction of cooperators after 5×10^3 generations (1 generation equals Z discrete strategy time steps, where Z is the population size) and averaged over 10^5 independent simulations starting from a configuration with equal abundance of strategies. Orange (blue) regions denote parameter values for which cooperators (defectors) dominate. These two regions are separated by a narrow transition line, approximately given by $\tau(\lambda) \approx a - 1/(b\lambda - 1)$ (solid black line, $a \approx 0.93$, $b \approx 20$). (b) Variance of the degree distribution of the equilibrium network as a function of λ, obtained along the curve $\tau(\lambda)$. Clearly, the stronger the social dilemma, the more heterogeneous the network becomes, in this way allowing for cooperators to increase their chances of overturning defectors in the population. Furthermore, network heterogeneity is most pronounced along the line $\tau(\lambda)$ marking the transition between full cooperation and full defection [11]. Other parameters are $\beta = 10.0$, $Z = 10^3$, and average network connectivity $\langle k \rangle = 8$.

coevolution of cooperation and network topology [11], when the social dilemma at stake is a PD. The relative time scales of network adaptation and behavioral evolution are controlled by the parameter τ: When $\tau = 0$, no network adaptation occurs; when $\tau = 1$, no behavioral adaptation occurs, which, as shown in Fig. 1, has a profound impact in the emergence of cooperation. One starts from a homogeneous random network [15], where all individuals have the same number of links, and let individual behavior and network structure coevolve at variable rates. Individuals engage in a PD in which mutual cooperation provides a reward $R = 1$, mutual defection a punishment $P = 0$, whereas when a C meets a D, the C gets a sucker's payoff, $S = -\lambda$, while the D gets a temptation, $T = 1 + \lambda$ ($\lambda \geq 0$ is the dilemma strength, such that increasing λ implies a stronger attraction into a full-D configuration). Time proceeds in discrete steps, with the coevolutionary process allowing, in each step, for link rewiring with probability τ and behavioral update with probability $(1 - \tau)$. Behavioral update is modeled via the so-called pairwise comparison rule [16], a birth-death process in which an individual i with strategy s_i (here C or D) imitates a neighbor m with (a different) strategy s_m with probability given by the Fermi distribution from statistical physics (where the inverse temperature β provides here a measure of the strength of natural selection): $p_{i,m} = \{1 + \exp[-\beta(f_m - f_i)]\}^{-1}$, with f_j accounting for the fitness of individual j, associated with the payoff accumulated over all interactions with their neighbors [16]. Network adaptation assumes that C's (D's) seek for C's to cooperate with (to exploit), while avoiding connections with D's: An individual is satisfied with all his C neighbors, being dissatisfied with the remaining. Hence, given a link between individuals A and B, if A is satisfied, she will try to keep the link; if dissatisfied, she will try to rewire the link to one of her second neighbors, accounting for the myopic nature of individuals regarding the entire social network. Following Ref. [11], when linked individuals A and B have a conflict regarding rewiring, resolution is fitness driven, the will of A prevailing with probability $\sigma = \{1 + \exp[-\beta(f_A - f_B)]\}^{-1}$. Different variants of this model have been considered [12], leading to qualitatively similar results. Naturally, the framework developed here is applicable to different choices of link rewiring, as well as to pairwise interactions of different nature, as discussed below.

As is well known [10,17], in the mean-field approximation C's are not evolutionary viable. But when interactions proceed along the links of a social network, C's do not necessarily get extinct [3], even when no network adaptation takes place ($\tau = 0$), as shown at the bottom part of Fig. 1(a). Most importantly, network adaptation paves the way for cooperation to prevail, even for game parameters that would render cooperation unfeasible in nonadaptive networks, as one can easily check by following trajectories of constant λ in Fig. 1(a). The faster the rate of network adaptation, the more C's get an evolutionary edge over D's. Moreover, for $\tau > 0$, our results suggest that the adaptive nature of the network nicely accounts for the heterogeneity observed in realistic social networks [1,2], in which a minority of nodes has a much larger degree than the majority. This is shown in Fig. 1(b), where we plot the degree variance of the networks emerging from coevolutionary simulations, as we move along the critical line $\tau(\lambda)$ depicted in Fig. 1(a), highlighting also the tight interplay between behavioral and network evolution.

To shed light on the link between individual and collective behavior, let us consider a network with Z nodes and L (undirected) links, and let every pair of linked individuals play a PD game of strength λ. Let us consider a large ensemble (Ω) of coevolutionary time series, each of which starts from an arbitrary fraction k/Z of C's placed at random on the initial network, that we shall take to be a homogeneous random network of degree $\langle k\rangle$ [15,18]. For a given time t, individual i, and coevolutionary simulation w, we compute the quantity $T_{i,w}(k,t) = (1/k_i)\sum_{m=1}^{k_i} p_{i,m}[1-\delta(s_i,s_m)]$ [$\delta(a,b)=1$ if $a=b$, and 0 otherwise], where $p_{i,m}$ stands for the probability that individual i imitates neighbor m (out of her k_i neighbors). We use $T_{i,w}(k,t)$ to compute the (ensemble) average probability that, in each behavioral update time step t, the number of C's in the population increases (+) or decreases (−) by one individual:

$$T^{\pm}(k,t) = \frac{1}{Z\Omega(k)}\sum_{w=1}^{\Omega(k)}\sum_{i=1}^{D_s,C_s} T_{i,w}(k,t). \qquad (1)$$

In Eq. (1), $\Omega(k)$ $[0 \le \Omega(k) < \Omega]$ is the number of times that a population configuration containing k C's was observed at time t in the ensemble Ω of all simulations performed. Equation (1) allows us to compute the (time-dependent) drift term,

$$\Gamma^A(k,t) = T^+(k,t) - T^-(k,t), \qquad (2)$$

that constitutes a network-dependent analog of the gradient of selection used in the analysis of the stochastic evolutionary dynamics in finite well-mixed populations [16,17]. Thus, $\Gamma^A(k,t)$ provides population-wide information of the coevolutionary dynamics, which now carries, nonetheless (time-dependent mean-field) information on the adaptive network structure. In the following, we shall rewrite $\Gamma^A(k,t)$ in generation units (by performing a partial time average over 1 generation, given by Z discrete behavioral update steps) as $\Gamma^A(k,t_g) = (1/Z)\sum_{t=Z(t_g-1)}^{Zt_g}\Gamma^A(k,t)$.

Figure 2 shows what happens at a population-wide scale as a function of time t_g in the coevolution of cooperation and adaption. At $t_g = 0$, the whole population engages in a PD game; this means that $\Gamma^A(k,0) < 0$ for any value of k. At this stage, what is best for an individual is also true for the population as a whole. As time unfolds, however, there is typically a critical number of generations (g_C) above which we observe the emergence of two (finite population analogues of) internal fixed points, that we denote by x_L and x_R (shown in Fig. 2 for $\tau = 0.4$); systematically, x_L has the structure of a probability repeller (leading to coordination dynamics, represented by open circles), whereas x_R has the structure of a probability attractor (coexistence dynamics, solid circles). As Fig. 2 shows, x_L and x_R separate from each other with time until they reach a stable location associated with a stationary phase of $\Gamma^A(k,t_g)$.

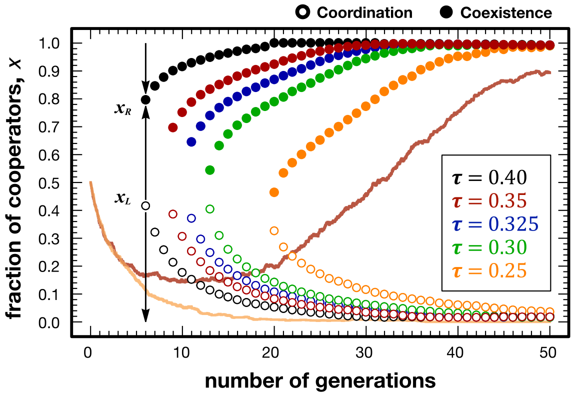

FIG. 2. Global PD dynamics in adaptive networks. Evolution of the internal fixed points of $\Gamma^A(k,t)$ for the different rewiring probabilities τ indicated, from top to bottom (bottom to top), for the coexistence (coordination) points. Solid lines display two prototype time series that start at $x = k/Z = 0.5$, one coevolving towards 100% D's ($\tau = 0.25$) and the other coevolving towards 100% C's ($\tau = 0.35$), this latter succeeding after crossing the coordination threshold provided by $\Gamma^A(k,t_g)$. Other parameters are $\lambda = 0.2$, $\beta = 10.0$, $N = 10^3$, $\langle k\rangle = 4$.

Importantly, the emergence of x_L and x_R depends sensitively on the value of τ: The larger the value of τ, the sooner x_L and x_R emerge as a result of the coevolutionary process. This is clearly shown in Fig. 2, where the order of appearance of the pair (x_L, x_R) follows the values of τ from top to bottom in the figure legend. Needless to say, the sooner the emergence of the pair (x_L,x_R), the more likely the self-organization among C's and D's will favor C's to fall into the basin of attraction of x_R, which will dictate the overall prevalence of cooperation. This, of course, reflects the predominant scenario, which is valid in a stochastic sense.

Solid lines in Fig. 2 display the evolution of C's for two representative coevolutionary time series, both starting from a random configuration containing $k = Z/2$ C's. Their color code uniquely identifies the rewiring probability τ ($\tau = 0.25$ for the orange line, lower curve, and $\tau = 0.35$ for the brown line, upper curve). At the start, the number of C's tends to decrease, as one would expect under a population-wide PD-like evolutionary dynamics. However, this is a transient regime: As strategy correlations build up *at par* with a coevolving network, we observe the emergence of a new population-wide dynamics at g_C, where the pair (x_L,x_R) emerges into the dynamics. In this new coevolutionary landscape, C's are now able to succeed provided $x > x_L$. Failing to achieve that will lead to the demise of cooperation. Both outcomes are illustrated in Fig. 2. Indeed, while for $\tau = 0.35$ the transient state is short enough (≈6 generations), thus allowing the fraction of cooperators x to remain above the time-dependent location of x_L, for $\tau = 0.25$ the transient is so large (≈20 generations) that by the time the pair (x_L, x_R) appears, x is already below x_L, compromising the viability of cooperators in the population, as shown by the corresponding solid line.

This analysis shows that, in adaptive networked populations, there will be a critical value of τ above which cooperation prevails (in a stochastic sense). This prevalence is associated with the capacity of the population to overcome the coordination barrier that emerges, at a population-wide scale, out of the coevolutionary processes of strategy and structure adaptation.

It is worth commenting on the significance and impact of the emergence of the pair of internal equilibria (x_L, x_R). As Fig. 2 suggests, this pair converges to the approximate limits $x_L \approx 0$ and $x_R \approx 1$ as $t_g \to \infty$. This is, however, highly unlikely: Strictly speaking, a single D in a population of $Z-1$ C's will always be advantageous, independent of the underlying network structure, whereas a single C in a population of $Z-1$ D's will always be disadvantageous, and thus the pair (x_L, x_R) cannot converge exactly to (0,1). Nevertheless, to the extent that x_R emerges at values higher than the actual fraction x of C's present in the population at that time, it will foster the increase of C's in the population, which in turn will promote an increase in the value of x_R. In this sense, the role of x_L becomes more important than that of x_R in what concerns the viability of cooperation.

It is further important to point out that work carried out in the framework of N-person coordination games shows that one of the most prominent features of the associated evolutionary dynamics resides, precisely, in the emergence of a pair (x_L, x_R) with exactly the same structure and nature [17], in a wide region of the game parameter spectrum, a feature that does not occur in two-person games, such as the PD we started from. Thus, one may state that, globally, two-person games on adaptive networks are transformed into effective N-person coordination games. To make this statement more explicit we change, in the following, the social dilemma from a PD to a two-person coordination game, of ubiquitous importance from philosophy to economics and evolution [17], and which renders cooperation feasible. Indeed, at a mean-field level, cooperation will thrive provided there is a critical mass of cooperators to begin with. In other words, we change the nature of the pairwise interaction and, similarly to Fig. 2, we investigate the global dynamics of the population. The results, shown in Fig. 3, provide a scenario that is remarkably similar to that obtained by means of a PD (although one needs smaller adaptation rates in order for cooperation to prevail), providing additional evidence of the unifying role one obtains, at a global level, by studying the coevolution of behavior and network structure.

Overall, both processes under consideration—strategy evolution and structural evolution—contribute to a positive assortment of C's. Indeed, the strategy update process leads to what can be qualitatively described as a C's (D's) breed C's (D's) type dynamics. Yet, the complexity of the underlying social dilemma leads to a symmetry break in the outcome of the update process: Unlike C's, whose success reinforces their growth, D's become victims of their own success [3,19]. When coevolving at par with network adaptation, this asymmetry is reinforced by a new symmetry break associated with links that connect two C's and links that have at least one D: the former are resilient to adaptation, contrary to the latter, which will be resilient only if D's are much more fit than C's. As our results demonstrate, such asymmetry also contributes to an assortment of C's at the same time that it fosters the segregation of D's. The joint contribution of both processes facilitates the emergence of cooperation, which becomes feasible in the entire parameter range of the game as long as network adaptation proceeds fast enough.

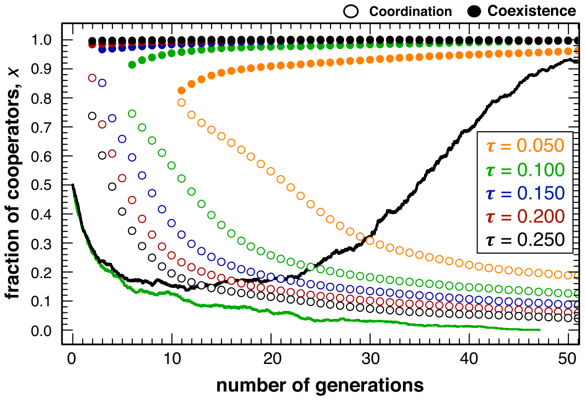

FIG. 3. Global coordination dynamics in adaptive networks. Evolution of the internal fixed points of $\Gamma^A(k,t)$ for the different rewiring probabilities τ indicated, where we use the same notation as in Fig. 2. Despite the different nature of the pairwise interaction, one obtains here the emergence (at different times, depending on τ) of a pair of (analogues of) fixed points, in full analogy with Fig. 2. Other parameters are $R = 1$, $P = 0$, $T = 0.9$, $S = -0.25$, $\beta = 10.0$, $N = 10^3$, $\langle k \rangle = 4$.

To conclude, a crucial issue of complex systems research and, more recently, of computational social science, is to understand how societies behave as a collective, knowing beforehand how individuals interact with each other. Conversely, if all we know is how societies behave collectively (as happens all too often in microbiology), is there anything we can say about how individuals interact with each other? This Letter shows how to develop a reversible link between individual and collective behavior. We show how network adaptation changes the cooperation dilemma, as it is locally perceived, into a coordination problem at a global level, exhibiting an N-person coordination structure impossible to anticipate from the two-person interaction we started from. Interestingly, such a coordination problem ultimately dictates the collective dynamics and therefore each individual's choices, even if, locally, individual perception remains unchanged and individuals cannot observe or even anticipate such global dynamics. The simplicity (and computational efficiency) of the present implementation renders this framework readily applicable to other time-dependent processes that occur on adaptive networks [8,20].

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[1] L. A. N. Amaral, A. Scala, M. Barthelemy, and H. E. Stanley, Proc. Natl. Acad. Sci. U.S.A. **97**, 11149 (2000).
[2] A.-L. Barabási, *Linked: How Everything is Connected to Everything Else and What It Means* (Plume, New York, 2002); S. N. Dorogovtsev and J. F. Mendes, *Evolution of Networks: From Biological Nets to the Internet and WWW* (Oxford University Press, Oxford, 2003).
[3] G. Szabó and G. Fáth, Phys. Rep. **446**, 97 (2007).
[4] M. Perc and A. Szolnoki, BioSystems **99**, 109 (2010).
[5] J. H. Fowler and N. A. Christakis, Br. Med. J. **337**, a2338 (2008).
[6] T. Gross, C. J. Dommar D'Lima, and B. Blasius, Phys. Rev. Lett. **96**, 208701 (2006).
[7] S. Van Segbroeck, F. C. Santos, and J. M. Pacheco, PLoS Comput. Biol. **6**, e1000895 (2010).
[8] S. Funk, M. Salathé, and V. A. A. Jansen, J. R. Soc. Interface **7**, 1247 (2010).
[9] P. Kollock, Annu. Rev. Sociol. **24**, 183 (1998).
[10] K. Sigmund, *The Calculus of Selfishness* (Princeton University Press, Princeton, NJ, 2010).
[11] F. C. Santos, J. M. Pacheco, and T. Lenaerts, PLoS Comput. Biol. **2**, e140 (2006).
[12] J. M. Pacheco, A. Traulsen, and M. A. Nowak, Phys. Rev. Lett. **97**, 258103 (2006); J. M. Pacheco, A. Traulsen, H. Ohtsuki, and M. A. Nowak, J. Theor. Biol. **250**, 723 (2008); S. Van Segbroeck, F. C. Santos, A. Nowé, J. M. Pacheco, and T. Lenaerts, BMC Evol. Biol. **8**, 287 (2008); S. Van Segbroeck, F. C. Santos, T. Lenaerts, and J. M. Pacheco, Phys. Rev. Lett. **102**, 058105 (2009); F. Fu, C. Hauert, M. A. Nowak, and L. Wang, Phys. Rev. E **78**, 026117 (2008); J. Poncela, J. Gómez-Gardeñes, A. Traulsen, and Y. Moreno, New J. Phys. **11**, 083031 (2009); F. Fu, T. Wu, and L. Wang, Phys. Rev. E **79**, 036101 (2009).
[13] K. Fehl, D. J. van der Post, and D. Semmann, Ecol. Lett. **14**, 546 (2011); P. Bednarik, K. Fehl, and D. Semmann, Proc. R. Soc. B **281**, 20141661 (2014).
[14] K. S. Korolev, J. B. Xavier, and J. Gore, Nat. Rev. Cancer **14**, 371 (2014); D. Lazer *et al.*, Science **323**, 721 (2009); J.-P. Onnela, J. Saramäki, J. Hyvönen, G. Szabó, D. Lazer, K. Kaski, J. Kertész, and A.-L. Barabási, Proc. Natl. Acad. Sci. U.S.A. **104**, 7332 (2007).
[15] F. C. Santos, J. F. Rodrigues, and J. M. Pacheco, Phys. Rev. E **72**, 056128 (2005).
[16] G. Szabó and C. Tőke, Phys. Rev. E **58**, 69 (1998); A. Traulsen, M. A. Nowak, and J. M. Pacheco, Phys. Rev. E **74**, 011909 (2006).
[17] J. Hofbauer and K. Sigmund, *Evolutionary Games and Population Dynamics* (Cambridge University Press, Cambridge, England, 1998); B. Skyrms, *The Stag Hunt and the Evolution of Social Structure* (Cambridge University Press, Cambridge, England, 2004); J. M. Pacheco, F. C. Santos, M. O. Souza, and B. Skyrms, Proc. R. Soc. B **276**, 315 (2009).
[18] H. Ohtsuki, M. A. Nowak, and J. M. Pacheco, Phys. Rev. Lett. **98**, 108106 (2007).
[19] F. C. Santos and J. M. Pacheco, J. Evol. Biol. **19**, 726 (2006).
[20] F. L. Pinheiro, M. D. Santos, F. C. Santos, and J. M. Pacheco, Phys. Rev. Lett. **112**, 098702 (2014).