The role of diversity in the evolution of cooperation

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ABSTRACT

Understanding the evolutionary mechanisms that promote and maintain cooperative behavior is recognized as a major theoretical problem where the intricacy increases with the complexity of the participating individuals. This is epitomized by the diverse nature of Human interactions, contexts, preferences and social structures. Here we discuss how social diversity, in several of its flavors, catalyzes cooperative behavior. From the diversity in the number of interactions an individual is involved to differences in the choice of role models and contributions, diversity is shown to significantly increase the chances of cooperation. Individual diversity leads to an overall population dynamics in which the underlying dilemma of cooperation is changed, benefiting the society as whole. In addition, we show how diversity in social contexts can arise from the individual capacity for organizing their social ties. As such, Human diversity, on a grand scale, may be instrumental in shaping us as the most sophisticated cooperative entities on this planet.

1. Introduction

Merriam Webster defines diversity as "*the condition of having or being composed of differing elements*". Considering the broad scope of the term, it may legitimately be pointed out that the title of this manuscript is perhaps far more presumptuous than its actual contents. Indeed, we scratch at most of the surface of diversity in its relation to the evolution of cooperation. Even so, we find something that may be seen at first as counter-intuitive: Diversity promotes the evolution of cooperation. Or, at least, when one considers the different aspects of diversity that have been investigated so far.

Historically, the evolution of cooperation has been studied in the absence of diversity (Hardin, 1968; Axelrod and Hamilton, 1981; Hofbauer and Sigmund, 1998; Nowak and Sigmund, 2004; Nowak, 2006b, 2006a; Sigmund, 2010). It was found more reasonable to deal with the evolution of cooperation in a population of (primitively) identical individuals, as defined by conventional evolutionary game theory (EGT) (Maynard-Smith, 1982; Hofbauer and Sigmund, 1998; Sigmund, 2010). Every individual can potentially interact with anybody else in an infinite population, having access to the same portfolio of actions (a.k.a.

strategies): for instance, to *cooperate* or to *defect*. Such cooperators (Cs) and defectors (Ds) typically engage in binary encounters where success is determined by games like the (in)famous Prisoner's dilemma (PD), in which case the evolutionary dynamics relentlessly condemns Cs to extinction. Even when spatial reciprocity (Axelrod, 1984; Nowak and May, 1992; Szabó and Fáth, 2007) was unveiled as a viable mechanism for the emergence of cooperation, Cs and Ds were lined up in an ordered, military-like parade with toroidal endings (for the muse of mathematicians) where each myopic agent interacted only with her four (or eight) immediate neighbors (see for instance Fig. 1B). As such every agent was topologically identical to any other agent in the population. The success of this framework was immense since it showed that cooperation is evolutionary viable within a narrow window of game parameters. Still this approach ignored something as natural as diversity in the neighborhood structure (Amaral et al., 2000; Albert and Barabási, 2002; Dorogotsev and Mendes, 2003; Onnela et al., 2007). Indeed, empirical studies have shown that modern societies are grounded in strongly diverse and heterogeneous networks of exchange and cooperation, in which some individuals play radically different roles depending on their social position, which may or may not be related to the number of actual interactions (see example in Fig. 1a). Incorporating this diversity into the EGT context introduced differences in the way the dilemma is perceived by each individual (Santos and Pacheco, 2005, 2006; Santos et al., 2008; Pacheco et al., 2009a), as it becomes contingent on her social context. Within EGT, this

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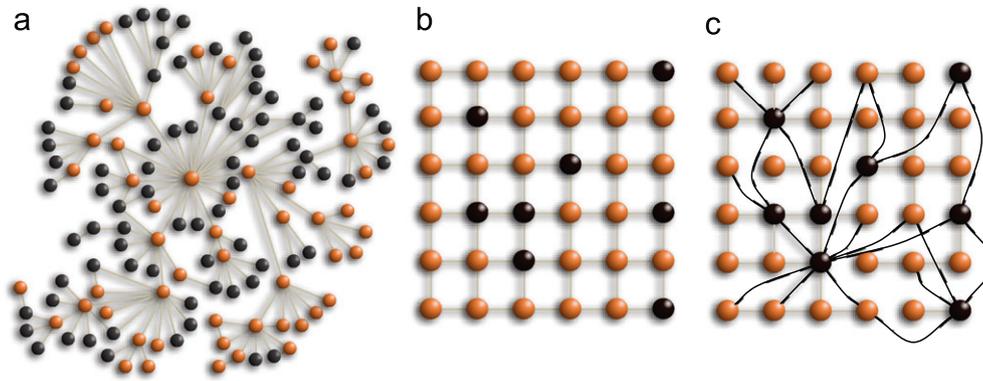E-mail address: pacheco@cii.fc.ul.pt (J.M. Pacheco).

Fig. 1. Topological diversity. (a) Both interaction patterns between individuals, and social influence of so-called role models exhibit distributions that are markedly heterogeneous, where diversity is ubiquitous, as shown. This contrasts with panel (b), a typical example of a homogeneous network (organized in a so-called "von Neumann" neighborhood) where all nodes are topologically equivalent. In panel (c) we show what happens when individuals are given the opportunity to break up unwanted links (here favorable partners and pictured in black) while maintaining the good ones. This simple yet natural mechanism disrupts the topological equivalence of panel (b), which is reflected in the finite variance of the distribution of the number of acquaintances in the population (see also Fig. 2a).

diversity in interaction patterns is only a first form. In addition, diversity can also exist in the collection of strategic and learning behaviors. In case of the first, we will address in the following the effect of differences in cooperative investment (Santos et al., 2008; Pacheco et al., 2009a). In case of the latter, some individuals, may simply be chosen more frequently as role models than others, producing a significant effect in the flow of behavioral changes caused by the evolutionary dynamics. In addition, diversity in individuals' game strategy (McNamara et al., 2004), imitation capacity (Szolnoki and Szabó, 2007; Perc and Szolnoki, 2008; Szolnoki and Perc, 2008; Szolnoki et al., 2008c) or learning approach (Van Segbroeck et al., 2010b) may produce significantly different outcomes in equivalent games.

As we show in the following, the combined effects resulting from heterogeneous social interactions may lead not only to a boost in the overall levels of cooperation (Abramson and Kuperman, 2001; Santos and Pacheco, 2005, 2006; Santos et al., 2006b, 2008; Gómez-Gardeñes et al., 2007; Masuda, 2007; Poncela et al., 2007; Szabó and Fáth, 2007; Szolnoki et al., 2008b; Perc and Szolnoki, 2010), but also to a symmetry breaking of the game itself, as well as the introduction of large variance in the distribution of wealth, associated here with the ensuing accumulated game payoffs (Santos et al., 2008; Pacheco et al., 2009a).

After showing how the combined influence of both the number and frequency of interactions contributes to enlarge the chances of Cs, one may naturally wonder what are the origins of such diversity. To address this point, let us imagine for a second that individuals engage in a game of cooperation. Both Cs and Ds prefer to interact with Cs, given the benefit of such an interaction for their own payoff. Let us imagine each individual has the choice to break up the links with those who "hurt" her, maintaining the links with those that do not. Figs. 1b and c show what happens.

As soon as individuals have a choice, the corseted symmetry of the underlying network of contacts is broken, no matter how they break the contacts or to whom they re-direct their attention. In other words, diversity in frequency and number of interactions emerges naturally when humans make decisions, even when one starts from a non-diverse setup (Skyrms and Pemantle, 2000; Ebel and Bornholdt, 2002; Eguiluz et al., 2005; Pacheco et al., 2006a; Santos et al., 2006a; Hanaki et al., 2007; Tanimoto, 2007; Gross and Blasius, 2008; Szolnoki et al., 2008a; Poncela et al., 2009; Szolnoki and Perc, 2009; Van Segbroeck et al., 2009). Clearly, the so-called heterogeneous networks, which arise naturally whenever people make decisions, constitute an ubiquitous feature of the pattern of contacts between individuals in general, and humans in particular, whenever individuals may impose their

preferences in what concerns their social ties. In the following sections, we will show that diversity, in its different guises, promotes cooperation.

2. Staging cooperation in an evolutionary and diverse setting

In a black and white world of unconditional behaviors, individuals may decide to behave as Cs or Ds. When pairs of individuals interact, the outcome can often be conveniently described in terms of a symmetric two-player game of cooperation. When both decide to cooperate, each receives a reward R for mutual cooperation, whereas mutual defection results in a punishment value P for both. Also, if one player cooperates while the other defects, then the D player receives a payoff T – often described as the temptation to defect – while the C player receives a payoff S, the sucker's payoff. Several dilemmas of cooperation result from different ranking of these four entries. Among those, the Stag-hunt or coordination dilemma arises when $R > T > P > S$, representing a dilemma in which the *fear* of being cheated by a D player ($P > S$) may provide a reason for defecting instead of cooperating. Also, whenever $T > R$ individuals may be tempted (or *greedy*) to play D towards a C, since deceiving a cooperator becomes the best possible outcome. In the absence of fear ($P < S$), *greed* leads to the chicken or snowdrift games (**SG**, $T > R > S > P$), whereas whenever both tensions are present ($T > R$ and $P > S$) we obtain the popular **PD** ($T > R > P > S$), where defection always provides the best possible profit in a pairwise interaction with unknown opponents. Inevitably this leads rational players to opt for (mutual) defection, even if players would be better off under a mutual cooperation.

This game-theoretical reasoning implies a rational attitude of players. Humans, however, often address complex problems differently, observing and retaining the experiences and successes of others. In particular, it is likely that the individual propensity to cooperate will be influenced by the actions and achievements of others, as previously shown in the context of donations to collective endeavors (Carman, 2003; Rees et al., 2009; Fowler and Christakis, 2010). This so-called social learning dynamics (Tomasello and Call, 1997; Rendell et al., 2010; Sigmund, 2010) can be conveniently described in the framework of **EGT**. The outcome resulting from all interactions in which an individual participates dictates the social success or fitness of an individual which, in turn, drives the social learning dynamics of Cs and Ds, as individuals tend to copy their acquaintances whenever these appear to be more successful. We consider that each individual i

adopts the strategy of a randomly selected (social) neighbor j with probability p given by the Fermi function (from statistical physics) $p = [1 + e^{-\beta(f_j - f_i)}]^{-1}$, where β (an inverse temperature in physics) controls the intensity of selection and $f_i(f_j)$ stands for the fitness of individual $i(j)$ (Szabó and Tőke, 1998; Traulsen et al., 2006). For $\beta \ll 1$, selection is weak and individual fitness is but a small perturbation to random drift in behavioral space. On the contrary, large values β enhance the influence of the payoff values in the individual fitness, and both the role played by the network of interactions and the social context of each individual. We shall, therefore, study the social learning dynamics of cooperation in this context ($\beta = 10.0$, unless stated otherwise).

In the following we simplify the game parameter space by fixing the payoff received from mutual cooperation and mutual defection ($R = 1$ and $P = 0$), in order to address all dilemmas in a single two-dimensional parameter space of *fear* (S) and *greed* (T) (Macy and Flache, 2002; Santos et al., 2006c). In the contour plots of Fig. 2, we show the outcome of evolution obtained from computer simulations on different classes of networks of $N = 10^3$ and average connectivity of $z = 4$, starting from an equal fraction of *C*s and *D*s.

All homogeneous graphs exhibit the same single-peak shape for the degree distribution (and ensuing cumulative degree distribution $D(k)$, also shown in Fig. 2). Here we employed homogeneous random networks (Horand) (Santos et al., 2005) which are obtained by repeatedly swapping the edges of randomly chosen pairs of links of a lattice, thereby removing all spatial correlations while preserving the homogeneous degree distribution of connectivities. In the opposite limit of diversity, we employed scale-free networks, generated using the Barabási–Albert (**BA**) model, which employs growth and preferential attachment (Barabási and Albert, 1999), whereas exponential networks, of intermediate diversity, were generated replacing the preferential attachment by uniform attachment in the **BA** model (Barabási and Albert, 1999; Albert and Barabási, 2002; Dorogotsev and Mendes, 2003). Different mechanisms can be used (Molloy and Reed, 1995; Dorogotsev et al., 2001; Albert and Barabási, 2002; Santos et al., 2006a; Poncela et al., 2008, 2009) to generate **SF** degree distributions portraying features not present in the **BA** model. In general, however, **SF** networks have in common a large diversity and lead to evolutionary dynamical behaviors which are qualitatively similar to those observed in **BA** networks (Santos et al., 2006b; Poncela et al., 2007, 2008, 2009; Devlin and Treloar, 2009; Perc, 2009), which may also depend on the way individual fitness is defined (Santos and Pacheco, 2006;

Masuda, 2007; Pusch et al., 2008; Szolnoki et al., 2008b). *Random Graphs* were generated by means of the Small-World model of Watts and Strogatz (1998) (Watts, 1999), in the limit of maximum heterogeneity (that is, rewiring probability equal to 1.0), which is compatible with the Erdos-Renyi random graphs, except that there are no vertices with connectivity smaller than $z/2$. In the limit of complete interaction networks, we recover a well-mixed population, which corresponds to a homogeneous graph of average connectivity $z = N - 1$. The equilibrium frequencies of cooperators were obtained for each value of T and S by averaging over 10^3 generations after a transient time of 5×10^3 generations. Each value in the contours was obtained from averaging over 10^4 simulations for each of 10 different realizations of each network class.

As we move from left to right in Fig. 2, we increase the diversity in the interaction patterns of the population, reflected in the variance of the degree distributions shown in the left panel. Empirical distributions collected from actual social networks fall somewhere between the limits considered in Fig. 2, where the dreary homogeneity and topological equivalence among nodes, typical of homogeneous networks (regular rings and lattices, among others), contrasts with the acute diversity of **SF** networks (Barabási and Albert, 1999; Amaral et al., 2000; Albert and Barabási, 2002; Dorogovtsev, 2010). In heterogeneous structures such as random, exponential and **SF** networks, different individuals will typically undergo a different number of interactions, as dictated by each individual's social context and pattern of connectivity. Given that the payoff accumulated by each individual dictates her success, diversity in social contexts will certainly have an impact on the evolution. Moreover, given that each individual context also defines the portfolio of role models an individual can chose from to revise her behavior, a heterogeneous social structure implies that some individuals may take profit from their social position to influence a larger number of members of the population than others.

These two types of diversity – in fitness and social influence – may offer some advantage to a minority of highly connected individuals (or particular strategies), irrespective of their strategic behavior. Indeed, both **C**s and **D**s may benefit from interacting a large number of times, and also by influencing more individuals than others. This said, the results in Fig. 2 may come as a surprise, as it shows that diverse environments significantly enlarge the chances of cooperation in every 2-person dilemma considered.

The analysis of the role played by a minority of highly connected individuals, as often found in **SF** networks and, to a
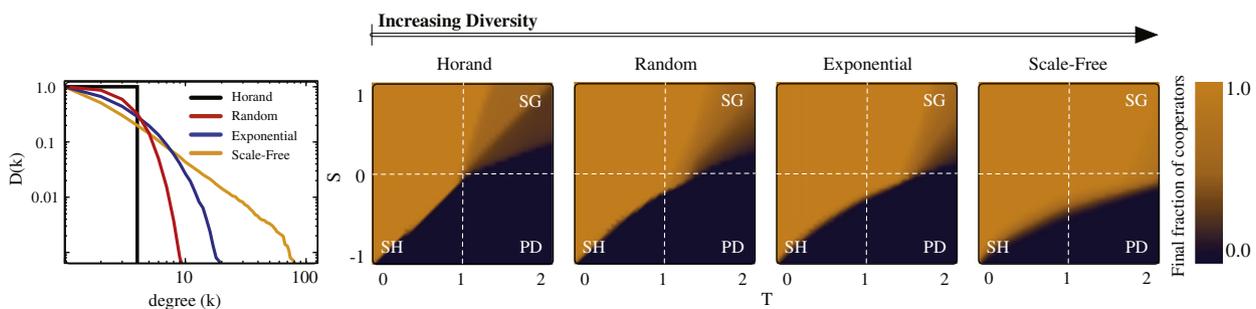

Fig. 2. Evolutionary dynamics in heterogeneous social structures. **Left Panel** Cumulative degree distributions $D(k)$ representing the distribution and diversity of the neighborhood sizes in the populations for four network classes ($N = 10^3$ and average degree $z = 4$). While in any type of homogeneous network the probability being surrounded by k other nodes is described by a single peak (we used homogeneous small-world networks (Santos et al., 2005) (randomly rewired in this example, HoRand), in *Random* networks this is defined by a Poisson distribution, whereas in *Scale-free* networks (**SF**) $D(k)$ follows a power-law (Dorogovtsev, 2010) . We also investigate a third class of networks, often referred as exponential, exhibiting a level of heterogeneity intermediate between the previous two (see main text for details). **Contour plots** Outcome of evolution for all 2-person symmetric games and diversity levels resulting from the network classes pictured on the left. Contours are drawn for a fixed difference between mutual cooperation and mutual defection ($R = 1$, $P = 0$), whereas the payoff T (temptation to defect or *greed*) is limited to the interval defined by $R \pm 1$ and the payoff S (*fear* from being cheated) ranges in the interval given by $P \pm 1$, spanning the three social dilemmas in main text: Stag–Hunt Game (**SH**), Snowdrift Game (**SG**) and Prisoner's dilemma (**PD**). Diversity generally promotes cooperation irrespective of the dilemma at stake (see main text for details on the simulations and population structures).

lesser extent, in random and exponential networks, may shed a light on this result. At a first glance, Ds would profit from being in pivotal positions of the network, in particular when surrounded by a significant number of Cs. By exploiting a large number of Cs, their choices will be most likely imitated by their cooperative neighbors. However, in doing so, the central defector will see her fitness reduced, as defectors' success is contingent on the number of Cs in the neighborhood. Few generations will be sufficient to make defectors vulnerable to the increasing influence of nearby Cs who maintained their Cooperative trait. **SF** networks provide ideal conditions for the existence of such cooperators. The existence of interconnected "hubs" with a broad range of connectivities creates star-like structures of different sizes, in which Cs may play a central role while managing to resist the invasion of highly successful Ds, by profiting from a large number of mutual cooperative exchanges. Whenever this happens, these cooperative leading fellows (at their own scale) do profit from their locally cooperative environment to become role models, even to those Ds who eventually end up as victims of their own success (Santos and Pacheco, 2006; Santos et al., 2006b, 2008).

3. Context dependent investments and symmetry breaking of the Prisoner's dilemma

At the heart of any study grounded on the Prisoner's dilemma game is the assumption that an act of cooperation entails a certain cost. As a result, the recipient of a cooperative act receives a benefit, whereas the conflict between individual and collective interests relies on the fact that the benefit is larger than the cost. In all these studies, every C pays a fixed cost c per game, providing the same benefit to the partner. However, in a heterogeneous setting there is no reason to assume that every C contributes the same to each game in which she participates. In fact, it is reasonable to assume that the amount that each individual contributes is correlated to the surrounding social context (Boehm, 1999; Santos et al., 2008; Pacheco et al., 2009a). As an example, the investments of Cs in each pairwise interaction may be limited to the available resources she has to dedicate to all her commitments. Hence, the contribution to each game will depend on the social context (number of partners) of each C, introducing an additional layer of diversity, i.e. variation in the investments made by cooperators. Real world situations should fall between these two investments paradigms: the conventional unlimited resources paradigm, where each individual may invest a fixed cost c per game; and a second where cooperators distribute an endowment c by all game interactions.

Before addressing the emergence of cooperation in these two extreme scenarios, it is relevant to note that diversity in contributions comes together with a variation in the benefits received. The relation between the investments and the ensuing collective returns can be described in a linear fashion, as it is commonly adopted in public goods game (Hardin, 1968; Kollock, 1998). Here, the benefits collected by the participants are proportional to the costs expended, providing not only the ideal ground to introduce variations in individuals' contributions, but also a natural pairing between game dynamics and social embedding. In its simplest form, a conventional public goods dilemma involves a pair of individuals who, independently decide to contribute (Cs) or not (Ds) an amount c to a common pool. The total amount is multiplied by an enhancement factor F and equally shared between the two participants. This reduces to a simple payoff matrix, in which $R=(F-1)c$, $S=Fc/2-c$, $T=Fc/2$ and $P=0$. For $c=1$, whenever $1 < F < 2$ we recover the "conventional" Prisoner's dilemma introduced above, as $T > R > P > S$.

Differently, if one considers that each individual shares a cost c over all pairwise interactions in which she/he participates, we obtain a distinct dilemma, which we shall call *Distributed Prisoner's dilemma* (**DPD**) (Pacheco et al., 2009a), as opposed to the above mentioned *Conventional Prisoner's dilemma* (**CPD**). Here, whenever a player A meets a player B, A gets a payoff $P_A = F(c_A s_A + c_B s_B)/2 - c_A s_A$, where $c_A(c_B)$ and $s_A(s_B)$ correspond to the investment and strategies of $A(B)$. When $s_A=1$ ($s_A=0$) the strategy is C (D). Hence, when playing C, her investment in each game will be contingent of her number of connections (k_A), such that each investment amounts to $c_A = c/k_A$. As a result, diversity in connectedness leads to a break of symmetry of the game itself, producing a hardly predictable effect in the overall dynamics.

From the expression above, it is clear that the nature of the dilemma is not changed in homogeneous settings (no topological diversity), as it amounts to a rescaling of the payoff values. Yet, as shown in Fig. 3, in heterogeneous settings, that is, in the presence of topological diversity, the outcome of cooperation suffers a remarkable boost for the entire range of F, as a result of the diversity in the profile of individual contributions, which can be shown to increase with increasing heterogeneity of the underlying network and, therefore, with the diversity in the investments made in each encounter. The equilibrium frequencies of cooperators shown in Fig. 3 were obtained following the same simulation details of Fig. 2.

The computation of the fitness values associated with the number of connections of the node shows that a diverse investment scenario (**DPD**) increases significantly the chances of invasion of highly connected nodes by Cs, raising the odds for cooperative parties occupying the most influential positions of the social network (Santos et al., 2008; Pacheco et al., 2009a). This result was obtained in the limit where any contributing act is positively assessed, irrespective of its value. In other words, all contributions are seen as cooperative, indicating that a social norm in which the *act of giving is more important than the amount given* may be more efficient in promoting cooperation.

The remarkable boost of cooperation obtained in the case of the **CPD** and **DPD** when compared with homogeneous and/or well-mixed settings can be understood at a population-wide level, by examining the population-averaged gradients of selection G at work for the different dilemmas. G is here defined as the difference $G(x) = T^+(x) - T^-(x)$ between the average probability of
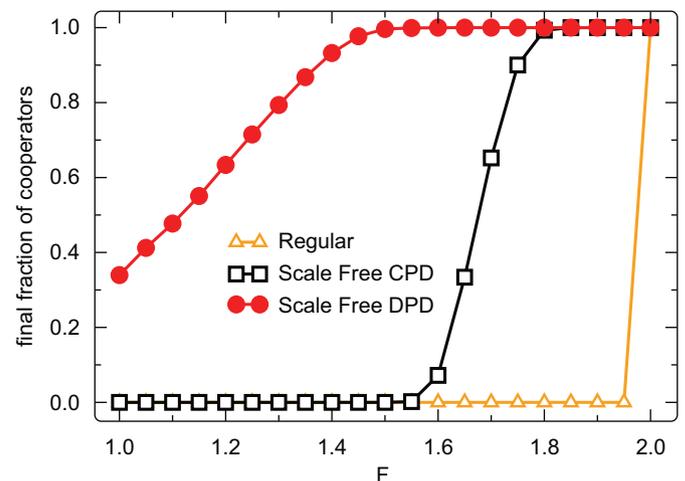

Fig. 3. Evolution of cooperation with context dependent investments. Final frequency of cooperators in scale-free for the two paradigms – **CPD** and **DPD** – compared with homogeneous regular networks, as function of the enhancement factor F. The advantage of Cs is dramatically in Context dependent investment paradigm in which the same cost is evenly shared among each one's neighbors (see text for simulation details).
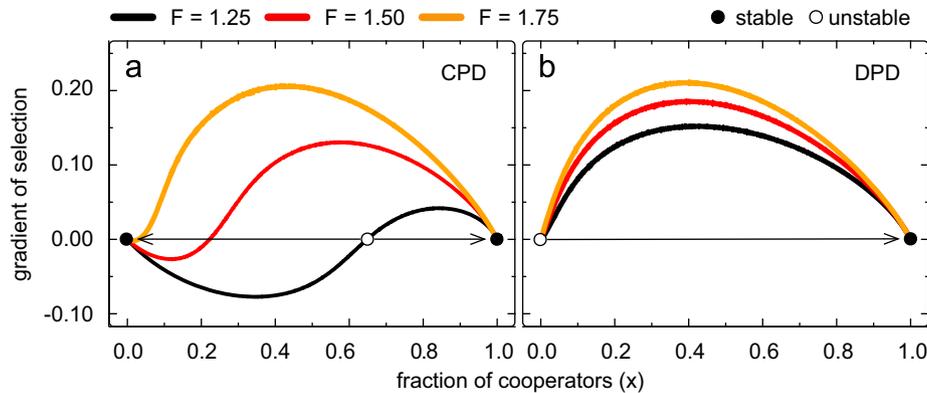
Fig. 4. Gradients of selection $G(x)$. (a) Under the CPD paradigm, Scale-free networks lead to the appearance of an unstable equilibrium x^* (open circle) and a scenario characteristic of a coordination game, paving the way for cooperator dominance for frequencies above x^*. (b) Under DPD, $G(x)$ becomes positive for (almost) all values of x ($x^* \sim 0$ for all values of F considered), leading to a scenario characteristic of a Harmony game, where cooperators dominate unconditionally. In both panels the networks employed had 1000 nodes and an average degree $z=4$. Each value of $G(x) = T^+(x) - T^-(x)$, where $T^+(x)$ ($T^-(x)$) is the average frequency of transitions increasing (decreasing) the number of **C**s for each random configuration with xN **C**s, was computed numerically by averaging over 10^5 different randomly generated configurations and networks, where each random configuration was generated assuming that each **C**(**D**) has, at least, one **C**(**D**) in her neighborhood, replicating the conditions observed in the numerical simulations.

increasing ($T^+(x)$) and decreasing ($T^-(x)$) the number of coopera-tors (Traulsen et al., 2006; Pacheco et al., 2009b; Santos and Pacheco, 2011) for a given fraction x of cooperators in the population. Whenever cooperation is favored by evolution, G will be positive (and negative otherwise). $G < 0$ constitutes the hall-mark of the **PD** in well-mixed populations (irrespective of the contribution scheme and fraction of cooperators), reflecting its defection dominance dynamics. Differently, in the presence of diversity, and despite the fact that individuals engage in pairwise instances of a **PD**, one can observe that, at a population wide level, the average gradient of selection reflects a coordination game in the case of the **CPD**, and a Harmony game, where cooperation dominates unconditionally, in the case of the **DPD**. Diversity in resource allocation stemming from the diversity of the underlying social structure leads cooperators to become dominant at the population wide level (Fig. 4).

4. Evolving diversity

So far, we have discussed the diversity effects emerging from heterogeneous social networks, neglecting the possibility that the social dynamics itself may play an important role in the origins of such diversity. As already argued in the introduction (see also Fig. 1), the feedback loop between behavior and network struc-ture, may give rise to a significant topological diversity. Moreover, even if both **C**s and **D**s are unsatisfied by interacting with **D**s, and seek **C**s to cooperate and exploit (respectively), network dynamics allows for an efficient assortment of cooperators, who together may prevail and take over the population. In addition, since **C**s are always regarded as the most interesting partners (irrespective of the game played), they attract a large number of links increasing their influence as role models in the rest of the population. The co-evolution of behavior and network dynamics can be studied in several ways, as is apparent from the increasing number of models addressing this issue (Skyrms and Pemantle, 2000; Ebel and Bornholdt, 2002; Zimmermann et al., 2004; Eguiluz et al., 2005; Pacheco et al., 2006a, 2008; Santos et al., 2006a; Hanaki et al., 2007; Tanimoto, 2007; Gross and Blasius, 2008; Poncela et al., 2008, 2009; Szolnoki et al., 2008a; Fu et al., 2009; Szolnoki and Perc, 2009). Here, we shall consider a minimal setting in which individuals engage in 2-person dilemmas of cooperation with their neighbors and, depending on how they are satisfied with their partners, they have the possibility to rewire their

connections to other individuals in the population. Hence, the game payoff induces an entangled co-evolution of strategy and structure, with the need for an extra time scale (τ_{net}) associated with topological evolution, which can be larger or smaller than the one defined for strategy evolution ($\tau_{strategies}$). The ratio $W = \tau_{strategies}/\tau_{net}$ provides a measure of the individuals' inertia to react against unfavorable neighbors: large values of W reflect populations in which individuals react promptly to adverse ties, whereas smaller values correspond to some overall inertia for topological change. Hence, a strategy update event is chosen with probability $(1+W)^{-1}$, and a structural update event being selected otherwise. In Fig. 5 we show the results from this co-evolution as a function of W. Starting from homogeneous and uncorrelated networks (Santos et al., 2005) (*HoRand*, see above), for $W = 0$, the network remains static, recovering the results of the contour on the left of Fig. 2. Yet, with increasing W, individuals become apt to adapt their ties with increasing efficiency, and as a result, the chances of cooperation are strongly enhanced.

In particular, in Fig. 5 we start from a homogeneous random network of 10^3 nodes, in which all nodes have the same number of edges ($z=30$), randomly linked to arbitrary nodes. The value of the average connectivity remains constant through evolution and was chosen such that cooperation would have limited chances to prevail on static networks, even under the presence of a diverse social structure. In addition, $z=30$ also reflects the average number of times reported in the literature for socials networks (Dorogotsev and Mendes, 2003; Dorogovtsev, 2010). As in Fig. 2, we start with 50% of cooperators randomly distributed in the population. A strategy update event is defined as before using the pairwise comparison rule (Traulsen et al., 2006). In a network update event, two randomly chosen connected individuals (A and B) decide unilaterally what they wish to do. Whenever both A and B are cooperators, both are satisfied with the edge and no rewiring takes place. The two other possibilities occur when either A and/or B are defectors, as at least one individual will necessarily be dissatisfied with the edge. The decision to rewire is contingent to the fitness values of A and B, such that more successful individuals will have higher probability of freely managing their social ties. When A wants to change the link whereas B does not, A will be able to rewire with a probability $p_w = [1 + e^{-\beta_W(f_A - f_B)}]^{-1}$ ($\beta_W = 0.005$, in Fig. 5), whereas with prob-ability $1 - p_w$, A stays linked to B. When both individuals want to redirect their links, a similar contest is used to decide who keeps the link. When decision is to rewire, the new destination is chosen
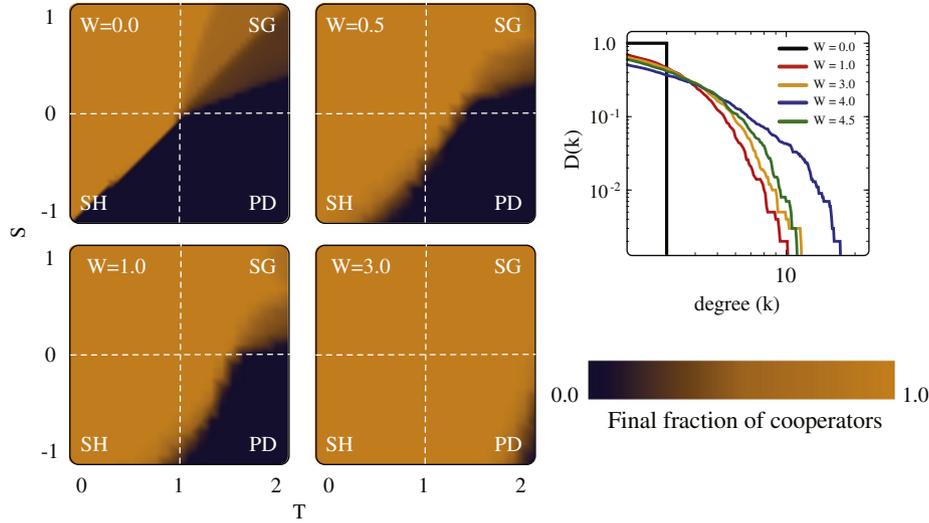
Fig. 5. Co-evolutionary dynamics of behavior and social structure. Contour plots) Final frequency of cooperators for different values of the time-scale ratio W for the same social dilemmas of Fig. 2. By increasing the speed at which individuals readjust their social ties, cooperation becomes viable irrespective of the game played. **Right panel** Cumulative degree distribution for the **PD** with $T=2.0$ and $S=-1.0$ ($R=1$ and $P=0$ in all panels) for different values of W. The diversity in the distribution of the number of connections (degree) results from fierceness of the competition between **C**s and **D**s. For low values of W ($W<1.0$), cooperators have no time to reshape their neighborhoods and increase the overall level of diversity in the network. A similar effect occurs whenever W is very large ($W>4.0$), since **C**s are so fast modifying their neighborhood that **D**s are promptly wiped out from the network without the need for the development of a large diversity. For intermediate values, networks develop strong degree heterogeneity, similar to the connectivity patterns found in real social networks (Amaral et al., 2000) reflecting the need and capacity of **C**s to fight back defectors by means of the development of a strong asymmetry of degrees.

randomly from the immediate neighbors of the former opponents, to cope with the limited individual information about all individuals in the population. We impose that individuals connected by a single link cannot lose this link, allowing all nodes to undergo evolution of strategies. We run 100 independent simulations for each set of parameters (T, S, W) and compute the final fraction of cooperators after 10^8 generations (Santos et al., 2006a). At the end of each evolution we also computed the cumulative degree distribution of the final networks, which are on the basis of the distributions of Fig. 3.

Due to the coupled dynamics of strategy and topology, the emerging social networks exhibit an overall diversity that accounts very well for the diversity of patterns recently found in acquired data on social networks (Amaral et al., 2000). In particular, diversity depends on the underlying social dilemma and the value W. Different challenges to cooperation lead to the evolution of different societal organization (see Fig. 5). Fierce competition between strategies leads to an increasing diversity, as an outcome of the self-organized interactions and decisions within the population.

5. Mind your neighbors, but react differently

In the previous sections, we focused on the effects of diversity in the local environment of **C**s and **D**s and showed how this diversity might emerge from individual myopic preferences regarding their partners. Invariably, however, in all these models **C**s (and **D**s) exhibit no differences of behavior among themselves. This situation contrasts with most social systems, where we recognize a large behavioral diversity: two **C**s (**D**s) may behave differently when confronted with the same situation. In particular, some individuals may have the propensity to swiftly change their social ties, whereas other may remain loyal even though they may be dissatisfied with such interactions (Van Segbroeck et al., 2008, 2009, 2010a). Moreover, social networks form and evolve through individuals' decisions based on the social context wherein they find themselves, such that some individuals may be socially

constrained not to change even when they want to. Eventually, the decision to change may be related with the information available concerning other potential partners, as more risk-averse individuals may find it riskier to seek for new neighbors (Eckel and Wilson, 2004). Hence, while in the previous section W reflected an average characteristic of the population, one may wonder how the diversity in the individual timescales of network adaptation can influence the prevalence cooperative actions.

We may answer this question analytically (Pacheco et al., 2006b, 2006a, 2008; Van Segbroeck et al., 2009, 2010a; Wu et al., 2010), hence providing some additional insights, if we ignore the details of the evolution of the network structure. To do so, let us consider that individuals are characterized by a strategy S_i ($i \in \{1,\ldots,2M\}$), which defines both the individual behavior in the games in which he/she is involved (**C** or **D**), and the rates at which he/she establishes new connections and destroys existing ones. We use α_i to denote the propensity with which S_i individuals form new connections, and γ_{ij} to denote the rate at which they remove existing connections with S_j individuals. ij-links are therefore established at a rate $\alpha_i \alpha_j$ and removed at a rate $\kappa_{ij} = (1/2)(\gamma_{ij} + \gamma_{ji})$. The corresponding linking dynamics of the network can be described by a set of ordinary differential equations (Pacheco et al., 2006b; Traulsen et al., 2006) $\dot{L}_{ij} = \alpha_i \alpha_j (N_{ij} - L_{ij}) - \kappa_{ij} L_{ij}$, where $L_{ij}(N_{ij})$ is the number (maximum number) of edges connecting individuals with strategies S_i and S_j (assuming a constant population size N). These differential equations lead to a equilibrium distribution of links given by $L^*_{ij} = N_{ij} \phi_{ij}$, where $\phi_{ij} = \alpha_i \alpha_j (\alpha_i \alpha_j + \kappa_{ij})^{-1}$ denotes the fraction of active ij-links. When the structure of the network evolves much faster than the individual strategies, the stationary regime is always reached before the next strategy update takes place. In this limit, the fitness of each individual S_i in the steady state becomes $f_i = \sum_j a_{ij} \phi_{ij} (N_{ij} - \delta_{ij})$ (Pacheco et al., 2006a; Traulsen et al., 2006) where a_{ij} is the original game payoff matrix. This is mathematically equivalent to the fitness of an S_i individual playing a game specified by the rescaled payoff matrix $A' = [a_{ij} \phi_{ij}]_{i,j=1,\ldots,2M}$ in a finite, well-mixed population. In practice, the requirement of a much faster network dynamics compared to strategy dynamics may be considerably relaxed, as the approximation above is valid
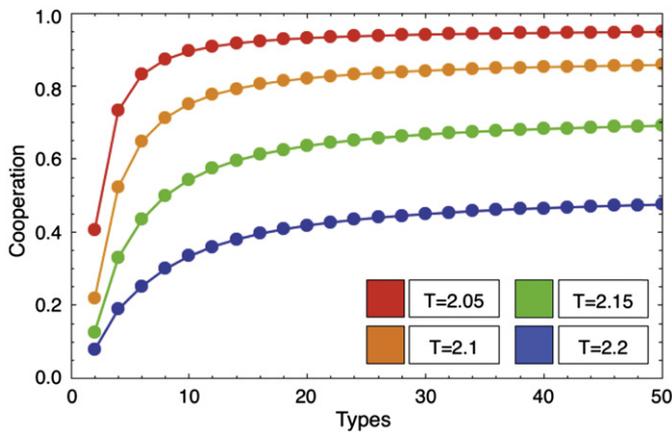
Fig. 6. Impact of behavioral differences concerning the way individuals manage their social ties. The population spends more time in a cooperative states when the number of possible types (M) increases, irrespective of the temptation to defect T in the Prisoner's dilemma ($R=2$, $P=1$, $S=3-T$, $N=100$, $\beta=0.1$, $\alpha=0.1$, $\delta=0.2$). See main text for details.

in a much wider range of scales than one could possibly anticipate (Pacheco et al., 2006a, 2006b; Van Segbroeck et al., 2010a).

Using the rescaled payoff matrix A', the evolutionary dynamics of $2M$ strategies can be conveniently described in the limit of rare mutations (Imhof et al., 2005; Fudenberg and Imhof, 2006) for the same update rule used before, in which the population will spend most of the time in monomorphic states of one of the strategies. The ensuing dynamics can be computed by means of the transition matrix of a Markov chain with $2M$ states, given by the probabilities that a mutant with strategy S_i will fixate in a population of $N-1$ individuals with strategy S_j (Traulsen et al., 2006), for all i and j. This matrix $\Lambda=[\Lambda_{ij}]_{i,j=1,\ldots,2M}$, in turn, can be used to determine the stationary distribution of strategies, that is, the fraction of time the population spends in each of the $2M$ available strategies, which is given by normalized left eigenvector of the eigenvalue 1 of Λ.

In Fig. 6, we consider $2M$ different strategies for players, where M is the number of distinct rates of removal of adverse ties that **C**s and **D**s may adopt. By adopting rates of unwanted ties falling into M subdivisions of the interval $[0.5-\delta, 0.5+\delta]$, with $[0.5-\delta, 0.5+\delta]$ and $\delta=0.2$ (Van Segbroeck et al., 2009), we show that increasing the number of ways of responding to adverse ties promotes cooperation, for several payoff matrices associated with the Prisoner's dilemma, but similar results are obtained for all dilemmas discussed in previous sections (Van Segbroeck et al., 2010a). The denser the spectrum of possible behavioral types, the more likely for cooperation to prevail. As such, adaptive social dynamics and behavioral differences benefit the entire community even though, as before, individuals still act in their own interest.

6. Conclusions

In this manuscript, we present an overview of diversity in its different guises, as such providing a ground for understanding the impact of diversity as a whole, and its role as a fundamental mechanism in promoting the emergence and maintenance of cooperation. Diversity at the level of interactions and behaviors provides new clues concerning the mechanisms that supply Humans with one of the key social features responsible for our evolutionary success: *Cooperation*.

In Section 2 we have addressed two types of diversity: (i) diversity in the number of interactions an individual is involved in and (ii) the possibility that some individuals are regarded as social

models more often than others. As consequence of (i), one is naturally led to include an additional layer of diversity (and complexity): (iii) diversity in contributions resulting from a fixed investment endowment that, as a cooperator, each individual is able to offer (see Section 3). In all these cases, behavior becomes dependent on one's social context and ranking (similar to our everyday life), and cooperation is strongly enhanced as a result of it. Cooperators in highly ranked positions are more capable to resist the invasion of defectors, while the latter are not able to profit from these pivotal social positions in the long run, as they become victims of their own success. This effect is further enhanced whenever different cooperators distribute their investments, contributing differently to the same game, whenever in a heterogeneous environment, such that diversity breaks the symmetry of the original 2-person game of cooperation. Enhancements also occur whenever individual cognition leads individuals to distribute their investments unevenly to their partners (Vukov et al., 2011). From a moral perspective, this increase of cooperation obtained from heterogeneous contributions, provides clues about the efficiency of rules of social assessments in which the act of giving is seen as more significant than the amount given, as it exploits the diverse nature of Human interactions to ensure high levels of cooperation. These results are here discussed for 2-person interactions, but are easily extendable to more complex N-person interactions (Santos et al., 2008; Santos and Pacheco, 2011).

Most of the results discussed here were based on the emergence of cooperation from an equal distribution of cooperators and defectors. Yet, once full cooperation is achieved, diversity may still play an important role. It can be shown that topological heterogeneity (as well as incipient cognition (Vukov et al., 2011)) holds back the invasion of free riders: Diversity promotes robustness. This fact is correlated with other interesting aspect not explicitly addressed here: The interplay between cooperation and social diversity has important implications in what concerns the distribution of wealth (fitness) in a population, whenever one considers the dynamics of cooperation from an economical viewpoint. The robustness of cooperation in diverse social settings seems to be related with a strong diversity in incomes, providing clues for the emergence of hierarchical structures in real systems (Santos et al., 2008; Vukov et al., 2011).

In Section 4, we discussed how this highly important topological diversity might emerge from the individuals' capacity to revise their social ties. The feedback between topological evolution and behaviors not only resolves the conundrum of cooperation irrespective of the dilemma played, but also creates the heterogeneous interaction structures, which provide the necessary diversity for cooperation to prevail. Diversity emerges naturally in situations where the fight between **C**s and **D**s is fiercer, leading to network structures with features commonly observed empirically.

Furthermore, in Section 5 we take into consideration that some social interactions may last longer than others, depending on the particular choices of individuals concerning the way they manage adverse ties. Some will try to break contact as soon as possible, whereas others remain in touch even though they are dissatisfied with the situation, creating a different form of behavioral diversity (McNamara et al., 2004; Van Segbroeck et al., 2009). In this framework, we show how cooperation blooms – and society as a whole benefits – the larger the behavioral diversity present in the population.

As such we provide ample support for the idea that diversity, on a grand scale, is instrumental not only to promote cooperation, but also to sustain it, even in the absence of complex community enforcement mechanisms, reputations or punishment (Hamilton, 1964; Wilson, 1975; Ostrom, 1990; Fehr and Gachter, 2000; Milinski et al., 2002; Skyrms, 2004; Nowak, 2006a; West et al., 2007; Sigmund et al., 2010).

Besides the models of diversity discussed here, other forms of diversity have been recently considered, which corroborate our message. For instance, in (Perc and Szolnoki, 2008; Szolnoki and Perc, 2008; Szolnoki et al., 2008c) it is shown how diversity in learning rates (some individuals tend to learn the best strategies faster than others) can support cooperative behavior. Similarly, in (Santos et al., 2011) it has been shown that, whenever individuals have the capacity to provide meaningless signals before each interaction and react accordingly, the fate of cooperation is strongly dependent on the diversity of signals available, illustrating the advantages of a complex signaling system (or proto-language). Moreover, all these insights correlate nicely with recent experiments investigating the role of diversity and globalization (Buchan et al., 2009) in human cooperation, offering a positive message concerning the advantages of a tolerant and socially diverse world.

Acknowledgments

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