Volatile social environments can favour investments in quality over quantity of social relationships

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Cooperation does not occur in a vacuum: interactions develop over time in social groups that undergo demographic changes. Intuition suggests that stable social environments favour developing few but strong reciprocal relationships (a ‘focused’ strategy), while volatile social environments favour the opposite: more but weaker social relationships (a ‘diversifying’ strategy). We model reciprocal investments under a quality–quantity trade-off for social relationships. We find that volatility, counterintuitively, can favour a focused strategy. This result becomes explicable through applying the theory of antagonistic pleiotropy, originally developed for senescence, to social life. Diversifying strategies show superior performance later in life, but with costs paid at young ages, while the social network is slowly being built. Under volatile environments, many individuals die before reaching sufficiently old ages to reap the benefits. Social strategies that do well early in life are then favoured: a focused strategy leads individuals to form their first few social bonds quickly and to make strong use of existing bonds. Our model highlights the importance of pleiotropy and population age structure for the evolution of cooperative strategies and other social traits, and shows that it is not sufficient to reflect on the fate of survivors only, when evaluating the benefits of social strategies.

1. Introduction

The evolution of cooperation is a central theme in biology [1,2]. Past theoretical work has elucidated how cooperative traits can be advantageous over non-cooperative traits that better exploit the public good of cooperation. While inclusive fitness theory explains why cooperation among kin can evolve [3–5], reciprocity theory explains how cooperation between individuals that are not necessarily related can be enforced by reward and punishment [6–8]. In animal societies, such reciprocal cooperations can lead to the build-up of social partnerships, as shown in humans [7,9], vampire bats [10,11], some nonhuman primates [12–14], some fishes [15,16] and some birds [17,18].

A gap exists between simple evolutionary models of cooperation and the complex psychology of helping decisions in animal societies [19,20]. In particular, Connor [19] argues that thinking ‘beyond the dyad’ (i.e. not considering solely fixed pairs of individuals) is necessary if we are to understand the evolution of cooperative strategies in animal societies (as assumed when taking the ‘biological market’ perspective [21]). For animals that live in complex societies, much cooperation takes place in the context of stable social bonds that seem analogous to human friendships. Yet, very few theoretical studies have investigated the evolution of cooperative strategies within an explicit social network and have considered how the network itself evolves as a result of individual interactions [18,22–24].

A particularly intriguing question is what cooperative strategy evolves when individuals face an unavoidable trade-off between quantity and quality.
2. The model

(a) Overview

We model individuals that live in groups of $N$ individuals. Group size is kept constant by recruitment of new group members as soon as an existing member has died.

All individuals share resources and thereby participate in the dynamics of social bond forming over their entire lifetime. Reproduction is asexual for simplicity, and generations are overlapping. While all individuals use the same structural rules of Bayesian updating of social bonds (details below), they differ in their a priori propensity to establish contact with individuals with whom they do not have an interaction history yet. For brevity, we call such individuals ‘strangers’, though note that they live permanently in the same group.

These propensities to establish contact with strangers are genetically encoded, with two independent traits that impact an individual’s propensity to (i) ask resources from strangers ($A_i$) or (ii) to give resources to strangers ($G_i$). High values indicate a tendency to diversify one’s social relationship portfolio, and low values indicate a focused approach to relationships. There is both resource-independent and resource-dependent mortality, and each vacancy created by death is replaced by a new recruit, with the parent chosen randomly from the population of living individuals. Selection on traits operates based on survival: individuals whose traits give them a reliable resource supply contribute disproportionately to future generations by virtue of them living longer. Recruits inherit their (single) parent’s trait with some mutation, allowing $A_i$ and $G_i$ to evolve, with the social network also changing as an emergent property of the population.

Inspired by vampire bat biology [10,11], we assume that each individual attempts to perform independent foraging at each time step, but this may fail, creating a constant supply of successful (satiated) and unsuccessful (needy) individuals who thereafter can interact socially, allowing resources to be donated to unsuccessful individuals. Note that we assume pre-existing willingness to help others (we do not give individuals the option to cheat), as our model is designed to investigate the evolution of focused versus diversified relationship tendencies, and the resultant narrow or broad social networks, rather than the origins of cooperation per se. For the same reason, in our main analysis, we also ignore complications brought about by kin recognition and preferential helping among kin; we thus do not track relatedness of the individuals (but see additional simulations in electronic supplementary material, figures S1 and S2).

Cooperative traits, $A_i$ and $G_i$, jointly determine to what extent individuals focus versus diversify cooperative investments. We focus on the implications of the volatility of the social environment on the evolution of those cooperative traits. We explicitly implement four sources of volatility. First, memory of past interactions between each pair of individuals can become erased with probability $p_{\text{erase}}$, making the individuals strangers to each other. Second, individuals may be unsuccessful during foraging with probability $p_{\text{unsuccessful}}$. Third, successful individuals may be unavailable with probability $p_{\text{unavailable}}$, not being able to give any resources. Fourth, individuals may randomly die with probability $p_{\text{die}}$. Increasing each of these probabilities associates with an increased volatility of the social environment, with strong social bonds being lost temporarily or permanently.

(b) Social bonds

(i) Basic properties

We model the strength of a social bond between each pair of individuals as a continuous variable ($r \in [0,1]$) that changes when individuals interact with each other. We list here the properties of social bonds as we have modelled them (mathematical definitions are provided in electronic supplementary material, appendix). Social bonds are strong if individuals have helped each others reciprocally in the past (allowing us to call them ‘partners’; without however implying that the relationship excludes having outside options). Strong bonds mean that an individual that has helped another individual is predisposed to ask resources from its partner should the need arise. Conversely, an individual that has been helped by another individual will tend to return the favour. As a flipside, an individual refusing to help another individual is less tempted to ask resources from this same individual, who, as a mirror image of the argument, will be little inclined to help.

(ii) Perspective dependence of the strength of social bonds

Each individual uses Bayesian updating to formulate its own estimate of the social bond. Individuals with different trait
values, $A_i$ and $G_i$ have different estimates of the strength of the same social bond. In particular, individuals with high $A_i$ and $G_i$ trait values have high estimate values of the baseline strength of social bonds with strangers and are therefore more inclined to interact with them than individuals with low $A_i$ and $G_i$ trait values do. Hence, we define the strength of social bonds from the perspective of each individual, with $\Pi(i,j)$ representing the estimate by individual $i$ of the strength of the social bond between individuals $i$ and $j$, and $\Pi'(i,j)$ representing the estimate by individual $j$ of this same quantity (see electronic supplementary material, appendix for mathematical definitions). These estimates directly determine the cooperative behaviour of individuals (see §2c(ii) below). To describe the properties of the emerging social network, however, we act as an unbiased external observer who gives the same weight to the perspective of each actor, as detailed later.

(c) Processes
At each time step, foraging is followed by resource donations, social bond updating, mortality and reproduction.

(i) Foraging
Each time step begins with independent foraging, which ends with each individual in an unsuccessful state with probability $p_{unav}$. We assume that foraging success ($= 1 - p_{unav}$) is independent of each individual’s previous foraging successes or previous interactions with group members.

(ii) Resource donations
If available with probability $1 - p_{unav}$ each successful individual, regardless of her trait $A_i$ and $G_i$, set aside a total of $R$ resources for donating to others (while consuming the rest of foraged resources individually; we do not model this consumption explicitly, but assume that it allows successful individuals to survive without needing help from others). This total amount $R$ is divided into $n_{give}$ resource ‘packages’ of magnitude $r_{give}$ each (thus $R = n_{give} \times r_{give}$). Each of the $n_{give}$ packages are set aside to be donated to a specific individual. The probability that any given individual is assigned by the focal individual to be the intended recipient is proportional to the strength of the social bond as estimated by the focal successful individual (schematized in electronic supplementary material, figure S3).

Individuals by definition do not have an interaction history with strangers. Nevertheless, the social bond with a stranger is estimated based on a prior belief (based on $G_i$ when assigning resource packages). Depending on the value of $G_i$ of the successful individual, the above rules therefore make it possible that one (or more) of the $n_{give}$ packages is set aside to be donated to a particular stranger. Whether an interaction history is existing or not, a focal individual may set aside resources in a targeted fashion, unsuccessful individuals can target several or even all of their $n_{ask}$ requests in the direction of the same individual in the network.

Note that the above decisions of setting aside resources, or placing requests for resources, are done without information on anyone else’s most recent success, or on their decisions to set aside resources or to request them. This means that some of the resources set aside for donation by the successful individual will not be matched by a request from the intended recipient (who may be successful and thus not needy, or may be unsuccessful but direct requests in some other direction). Likewise, some of the help requests are not matched by willingness to donate, either because there is nothing to donate as both the requester and the target of the request were unsuccessful or because the target of the help request did not set aside any packages for the requester. If there is a match, all matching resource packages are transferred. Note that the limited number of interaction per time step (controlled by parameters $n_{give}$ and $n_{ask}$) is at the origin of a trade-off between quantity and quality of social relationships.

(iii) Social bond updating
Resource donations associate with social bond updating. We assume that the total numbers of requests and donations ($n_{ask}$, $n_{give}$, $d_{i\rightarrow j}$ and $d_{j\rightarrow i}$ for all pairs of individuals $i$ and $j$, as defined in electronic supplementary material, appendix) are updated among pairs of individuals only if (i) one individual is successful and the other is unsuccessful and (ii) if the successful individual is available and able to give resources. Individuals refine their estimates of the strengths of social bonds with individuals with whom an interaction took place or could have taken place. The total numbers of requests and donations are updated, leading to new estimate values of the strengths of social bonds, $\Pi(i,j)$ and $\Pi'(i,j)$, for all individuals $i$ and $j$. We also specify a parameter (identical for all individuals) $F$, which describes the strength of prior belief (i.e. high values of $F$ make it more difficult to shift away from prior belief). The above rules imply that there is no social bond updating when both partners are unsuccessful. Likewise, not being able to give resources (with probability $p_{unav}$) does not harm relationships.

As another source of volatility of the social environment, we assume that any interaction history can be erased with probability $p_{erase}$ leading to a state as if individuals had never interacted with each other. This differs from death in two ways: the two individuals’ other social bonds are kept intact, and they can also begin rebuilding their mutual social bond. This source of volatility is by far the most unrealistic one we implement and may not be found in nature. Nonetheless, we believe it is important to implement it in our model because erasing the history of past interactions is the most parsimonious way to increase social volatility. In particular, this does not change directly age structure (contrary to a direct increase in mortality for instance).

(iv) Mortality
Mortality has two components. The first, resource-independent component causes each individual, regardless of success and
social interactions, to die with probability \( p_{\text{die}} \). The second, resource-dependent component is only applied to unsuccessful individuals (thus, successful ones always have sufficient resources to survive the second step, regardless of how many resource packages they donated).

Unsuccessful individuals die of starvation during the second round of mortality with a probability that depends on the amount \( r \) of resources received during the ‘resource donation’ phase:

\[
p_{\text{starv}}(r) = \frac{2\exp(-(r + \gamma_i)/R_i)}{1 + \exp(-(r + \gamma_i)/R_i)}
\]

Parameters \( \gamma_i \) and \( R_i \) adjust the risk of death due to starvation. Functions implemented in simulations are shown in figure 1.

(v) Reproduction

Reproduction is clonal. Each vacancy, created by death, is filled with an offspring, whose mother is a randomly chosen living individual (thus selection acts via differential survival; there is no differential success among the living potential parents). The offspring traits \( A_i \) and \( G_i \) are drawn from truncated normal distributions with means equal to the corresponding parental trait value (reflecting inheritance), with standard deviation \( \sigma \) (reflecting mutation), and with \( A_i \) and \( G_i \) constrained to be in the interval \([0, 1]\).

In our main simulations, individuals must build their social network from scratch. By contrast, we assumed in supplementary simulations that newborn individuals initially have strong social bonds with their mother, their sisters or their mother’s partners (social inheritance). Although deviating patterns occur in special cases (that are biologically not likely scenarios, see electronic supplementary material, figure S1), as a whole our main message remains robust whether the initial network of a newborn is zero (the network has to be built from scratch) or non-zero (electronic supplementary material, figures S1 and S2).

(d) Simulation experiments

We aim at investigating how the volatility of the social environment affects the evolution of ‘social bet-hedging strategies’, i.e. strategies that diversify cooperative investments. In particular, we test whether changing volatility from low to high favours a shift from a focused to a diversifying approach to social relationships, following the intuition that focusing investments in a single most-profitable partnership is risky if partners often disappear. More precisely, we vary the values of four parameters that determine the volatility of the social environment: the probability \( p_{\text{erase}} \) of forgetting all information about past interactions with any given individual, the probability \( p_{\text{die}} \) of dying by chance (i.e. irrespective of foraging success), the probability \( p_{\text{unav}} \) of being unsuccessful, and the probability \( p_{\text{unav}} \) of being unavailable when successful. The intuitive prediction is confirmed if high values of these parameters lead to the evolution of high trait values \( A_i \) and \( G_i \).

We run the model for 5 million time steps. We assume that \( A_i = G_i = 0.02 \) for all individuals \( i \) initially (but note that initial variation in trait values does not change qualitatively our results; electronic supplementary material, figure S4), and we consider mutations of small effect size (\( \sigma = 10^{-4} \)). And, unless stated otherwise, we implement a group size of \( N = 500 \), a baseline resource-dependent mortality function as shown in figure 1, a maximum amount of resources given by each successful individuals \( R = 1 \), numbers of interactions \( n_{\text{inter}} = 100 \), and the strength of the prior belief \( F = 1 \). A stable social environment is defined by parameters \( p_{\text{erase}} = 0, p_{\text{die}} = 0, p_{\text{unav}} = 0 \), and with the only source of mortality determined by cooperative relationships such that \( p_{\text{unav}} = 0.1 \). Any simulation characterized by higher values of \( p_{\text{erase}} \), \( p_{\text{die}} \), \( p_{\text{unav}} \) and \( p_{\text{unav}} \) is referred to as simulations modelling a volatile social environment. For each combination of parameters tested, we run 30 simulation replicates.

To describe simulation outputs, we assume that a partnership has been built as soon as an individual is ten times more likely to interact with this individual rather than with a stranger. The quality of partnership refers to the exact likelihood of interacting with a partner relative to that with a stranger. As noted above, we give the same weight to the perspective of each individual within a pair, and we define the quality of partnership between individuals \( i \) and \( j \) as:

\[
Q(i, j) = \frac{\langle \prod_i (i/j) A_i^2 \rangle + \langle \prod_j (i/j) A_j^2 \rangle}{2},
\]

reflecting the degree to which individuals are more likely to interact with each other than with a stranger. Note that we get qualitatively the same result with \( \prod_i (i/j) \) (resp. \( \prod_j (i/j) \)) relative to \( G_j^2 \) (resp. \( G_i^2 \)). As noted above, we assume that a partnership has been built as soon as \( Q(i, j) > 10 \), with individuals being ten times more likely to interact with each other than with a stranger. This assumption is made for the purpose of describing the outcome of our simulations and does not affect the simulation. In our simulations, low traits values \( A_i \) and \( G_i \) leads to more focused cooperative investments than high traits values \( A_i \) and \( G_i \), regardless of the definition we use to define partnership establishment (electronic supplementary material, figure S5).

Figure 1. Probability of dying of starvation depending on the amount of resources received by the unsuccessful individual. Baseline function: \((\gamma_i, R_i) = (0.3, 0.2)\). Other functions implemented in supplementary analyses: \((\gamma_i, R_i) = (0.3, 0.15)\) (low mortality) and \((\gamma_i, R_i) = (0.3, 0.3)\) (high mortality).
3. Results

(a) Evolutionary outcome under stable versus volatile social environments

In accordance with the definition of a ‘social bet-hedging strategy’, individuals with higher propensities to interact with strangers (high $A_i$ and high $G_i$) ultimately diversify cooperative investments across more partners while building weaker social bonds with each partner (see examples of emerging social network in figure 2 and electronic supplementary material, figures S5 and S6).

Contrary to what we expected, a volatile social environment does not favour such diversifying cooperative strategy. Regardless of the type of volatility ($p_{\text{erase}} > 0$, $p_{\text{die}} > 0$, $p_{\text{unsucc}} > 0.1$ and $p_{\text{unav}} > 0$), higher volatility selects for lower, not higher, values of $A_i$ and $G_i$ (figure 3). In other words, the tendency to diversify cooperative investments is the lowest in the most volatile environments. Our findings (figure 3) are not anomalous special cases; we find similar evolutionary outcomes when we change the group size (but note that in a very large group, individuals have to focus investment on few individuals to build partnerships, leading to low trait values $A_i$ and $G_i$ i.e. the opposite of social bet-hedging). (Online version in colour.)
social environments, as detailed in electronic supplementary material, figure S1). Interestingly, we show that a focused cooperative strategy translate into a higher proportion of partnership between relative versus unrelative individuals when partnership between kins occurs but into a lower proportion of partnership between relative versus unrelative individuals when social inheritance takes place (electronic supplementary material, figure S2).

(b) Demographic feedback under a volatile social environment

It is clearly necessary to explain why a volatile social environment leads to the evolution of a strategy focusing cooperative investment on few partners. We illustrate this with an example, where we trace the life of a single mutant individual i with deviating traits A_i, G_i when all other population members j have trait values A_j = 0.035 and G_j = 0.035. For the mutant i, we consider traits values A_i, G_i ∈ {0.02, 0.035, 0.05}. We then assess the characteristics of the social relationships and the survivorship of this mutant as it ages. Age is defined based on time steps at unsuccessful state; note that this quantification of age is strongly correlated with the true age of the individual based on all time steps (electronic supplementary material, figure S12).

Individuals with high A_i and G_i values ultimately have many partnerships of poor quality (first and second rows in figure 4). Nonetheless, at early age, these individuals have fewer partnerships than individuals focusing on few partnerships (with low A_i and G_i values). Focusing on few partnerships speeds up social bonding and increases the exploitation of the benefits associated with the existing partnerships, ultimately increasing survival at early age (third and fourth rows in figure 4). Although the focused approach carries some risk, they are smaller than the reduction in early performance if attempting to diversify when one’s own network is still in the first stages of being built. This occurs even if newborn individuals do not need to build their social network from scratch; exploiting the benefits associated with the pre-existing social bonds (e.g. with the mother; electronic supplementary material, figure S13) at the expense of diversifying cooperative investments increases survival at early age.

In other words, focusing on few partnerships appears necessary at early age, whereas building many partnerships proves beneficial at older ages once the many partnerships have been built.

Under a volatile social environment (when p_{dis} = 5 \times 10^{-3} in figure 4; but this is also true for high p_{es}, p_{success} and p_{unav} as shown in electronic supplementary material, figures S14–S16), diversifying cooperative investment benefits old but not young individuals (old individuals with high A_i and G_i trait values have a higher survivorship than old individuals with low A_i and G_i trait; last row in figure 4). In that sense, the premises on the benefits associated with a ‘social bet-hedging strategy’ hold: in volatile social environments such diversifying cooperative strategy proves beneficial late in life because is reduces the temporal variance in cooperative returns caused by unpredictable changes in partner availability [11]. Nevertheless, the evolution of such a cooperative strategy does not depend only on the performance of individuals belonging to a certain age group. Here, a key question is how much of one’s life one will spend being ‘young’ versus ‘old’. As a whole, the selection gradient changes as the age distribution changes (electronic supplementary material, figure S17).

Overall, high mortality increases the proportion of young individuals relative to old individuals. As a result, under a volatile social environment, fewer individuals reach old ages where they can reap the benefits of diversifying cooperative investment. The details differ between settings: a volatile social environment may associate with high mortality directly (high p_{die}), indirectly (high p_{base} and high p_{unav}) or both directly and indirectly (high p_{success} via resource-dependent mortality and via a lower pool of helpers). Regardless of the specific route to short lives, volatility means that relatively few individuals reach sufficiently old age to reap the benefits of a diversified approach to network building. Instead, speeding up the socializing process and exploiting existing partnerships at an early age matters the most (see percentage in last row of figure 4), even if this proves deleterious later in life (should the individual still be alive, which is relatively unlikely under high volatility). This explains why a ‘focused’ rather than diversifying approach to cooperative investment is beneficial under a volatile social environment.

4. Discussion

Our model shows the fragility of the intuitive prediction that stable social environments should favour individuals that develop few but strong relationships, while volatile social environments favour those whose social networks end up ‘broad but shallow’. Our model shows that the premises on the benefits associated with a diversifying cooperative strategy hold: ‘broad and shallow’ social networks can prove beneficial because they reduce the temporal variance in cooperative returns caused by unpredictable changes in partner availability (as argued by [11]). Nevertheless, our model also highlights that the evolution of cooperative strategies does not depend solely on the performance of the social networks once they are built. When accounting for the costs associated with the build-up of such social networks, selection can lead to the precise opposite outcome: volatility selects for focused network building.

The reason is clear once reciprocity theory is linked to theories of senescence, specifically antagonistic pleiotropy that hypothesizes that alleles that enhance fitness early in life but are detrimental later can be favoured because selection is stronger early in life than late in life [36,37]. Diversifying cooperative investments can be beneficial late in life (once the individual has built its social network), but this is preceded by a substantial cost early in life while the network has to be built. Since the probability to reach a sufficiently old age is low in volatile environments, the negative effect early in life predominates, and the successful strategy is one that focuses cooperative investments on few partners. Focusing allows individuals to build strong partnerships more quickly while also exploiting existing social bonds (including those with relatives, and inherited ones). It is notable that a strategy that focuses reciprocal interactions on few individuals is able to spread in a population, even though it clearly has the potential to lead to a disastrous loss of all ‘friends’ for some individuals. Our model accounts for this cost, and simply shows that the beneficial effects of a focused strategy are on average better than those of a diversifying one.

Pleiotropic effects are also discussed in the field of social behaviour, where it has been suggested as a mechanism stabilizing cooperation in slime moulds and bacteria [38] (but...
These cases, however, do not have the same pleiotropic structure as the one we consider. We focus on a situation where pleiotropy is clearly age-dependent, and our question is also different: we do not consider whether cheats can spread and destroy cooperation, instead we ask how reciprocal cooperation deals with the quantity-quality trade-off ‘beyond the dyad’ (as advocated by Connor [19]).

It is of interest to note that the field of social behaviour is generally starting to realize that the social environment is very likely different for individuals differing in their age; Croft et al. [40] discuss this with respect to kinship (see also [41]). Our work shows that the social state, i.e. the position of an individual within its network of social partners and the properties of this network, can be age-dependent in a manner that can switch selection from favouring narrowing this network down or broadening it further.

In our model, pleiotropy arises from differences in the exploitation of existing social bonds but also from differences in the speed at which social bonding takes place. What is known as ‘social bet-hedging strategy’ refers to a diversifying approach to social relationships and via the quality–quantity trade-off, we have shown it associates with slow social bonding. Cooperation typically relies on some form of assortment [42,43], which involves individual recognition and social bond formation (at least in the type of organisms that our model is inspired from). We know very little on how social bonds initially form, especially when they entail investments of time and energy. Social bonding may be characterized by a
raise in cooperative investments over time, as long as reciprocal cooperation takes place [44,45]. In our knowledge, however, the speed at which social bonding takes place has rarely been assessed (but see [45]). Our model shows that the speed at which social bonding takes place is likely to have a strong impact on the evolution of cooperative strategies because most of social bondings occur early in life.

It is interesting to reflect on the pitfalls of intuition. Intuition often involves ‘putting oneself in another organism’s shoes’—in sometimes fallible ways [46]. In the current context, intuition may be based on imagining what one should ideally have done, given the sudden death of a social partner. Clearly, having built a broad network helps to recover future fitness prospects, mitigating the current loss. Strangely, intuition does not prompt us to reflect equally much on the possibility that death might target ‘oneself’ (the focal individual). Yet volatility obviously also strikes, with some regularity, this way, and now the hope is that one did whatever one could to maximize performance until that age; death made performance at later ages unmeasurable and irrelevant. If intuition only considers actions and their benefits among those who keep avoiding death themselves, it falls victim to the well-known effects of survivorship bias.

Survivorship bias also is a tough problem for the empirical aspects of the question, as data collection on behavioural details can, logically, only be based on observations involving current survivors. While frustrating, this also helps to understand apparent discrepancies between data and our model. Losses of individuals whose networks did not help them avoid death create a process of selective disappearance within each cohort. This makes it exceedingly hard to collect unbiased data: unless one traces social bonds longitudinally and records every death, any analysis among living individuals will pay disproportionate attention to the successful subset of individuals who are presently observable by virtue of being alive—a problem which applies to a wide range of taxa (beyond bats), whenever aiming to document effects of the quantity versus quality of social relationships [11,28–34]. Whenever disappearance is selective (not random), the problem is exacerbated by the fact that situations where selection is at its strongest also produce the most severe data collection biases. To help solve this conundrum, future empirical studies paying particular attention to the longitudinal aspect of individual lives (and the age-dependent dynamics of their networks) could shed new light onto the question of well performing networks and their temporal trade-offs.

One notable study with a temporal aspect is the one by Testard et al. [47], where the authors showed that macaques diversified their social relationships after their population was devastated by a hurricane. We believe that the discrepancies between this result and our theoretical predictions can be explained. First, such a dramatic event is far from the level of instability we modelled, and second, the observed changes in cooperative behaviours in those macaques were an example of plasticity, not an evolutionary response to permanent volatility that would select for a different type of behaviour due to individuals routinely dying young. Testard et al.’s [47] study therefore highlights some limits of our modelling approach. It is a clear avenue for future work to consider plasticity, as expression of behaviours is often remarkably sensitive to environmental conditions [48].

Plasticity could also make traits age-dependent and also perhaps dependent on the state of one’s own network: cooperative behaviours could change through life. If one’s social network is already broad enough, one may change its cooperative strategy and stop expanding it further. Such age-dependent and/or network state-dependent plasticity has received some empirical support in rhesus macaques, where older females engage less in the social environment compared to younger ones [49], and should therefore be investigated in future theoretical studies. Based on our predictions, a strategy focusing cooperative investment on few partners at early age and diversifying cooperative investment on many partners at old age could conceivably be optimal. However, note that a social network of an individual at any point in its life is an accumulation of an entire ‘career’ of work towards it. Even if behavioural changes are possible, it is not clear that an adjustment schedule is able to choose performance in early life such that two goals are simultaneously optimized: to have as good as possible fitness should death happen at a relatively young age, and, should early death not occur, to ‘prepare’ the individual’s social network to allow best possible capitalization of the gains that follow from a switch in strategy (since any attempt to broaden the network must start from where early-age efforts ended). Since it is never clear how long an individual life will last, antagonistic pleiotropy may be unavoidable even under plastic social traits.

As a whole, our model highlights the importance of population age structure for the evolution of social traits such as cooperative behaviours. The evolution of social traits has been traditionally studied using evolutionary game theory [50] and quantitative genetics [51], without much emphasis on the implication of demography. Recent studies have started to uncover the role of spatial structure for the evolution of social traits (e.g. [52–54]), but little is known on the role of age structure (but see [41] for an age-dependent kin-selection model). We appreciate that our individual-based modelling approach comes with its limits, including the absence of analytical insights; we hope however that the predictions of our model will stimulate further theoretical and empirical investigations assessing the role of population age structure for the evolution of social traits.

Data accessibility. All code needed to reproduce the analyses is available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k6djh9w87 [55]. The data are provided in electronic supplementary material [56].

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