

When is bigger better? The effects of group size on the evolution of helping behaviours

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ABSTRACT

Understanding the evolution of sociality in humans and other species requires understanding how selection on social behaviour varies with group size. However, the effects of group size are frequently obscured in the theoretical literature, which often makes assumptions that are at odds with empirical findings. In particular, mechanisms are suggested as supporting large-scale cooperation when they would in fact rapidly become ineffective with increasing group size. Here we review the literature on the evolution of helping behaviours (cooperation and altruism), and frame it using a simple synthetic model that allows us to delineate how the three main components of the selection pressure on helping must vary with increasing group size. The first component is the marginal benefit of helping to group members, which determines both direct fitness benefits to the actor and indirect fitness benefits to recipients. While this is often assumed to be independent of group size, marginal benefits are in practice likely to be maximal at intermediate group sizes for many types of collective action problems, and will eventually become very small in large groups due to the law of decreasing marginal returns. The second component is the response of social partners on the past play of an actor, which underlies conditional behaviour under repeated social interactions. We argue that under realistic conditions on the transmission of information in a population, this response on past play decreases rapidly with increasing group size so that reciprocity alone (whether direct, indirect, or generalised) cannot sustain cooperation in very large groups. The final component is the relatedness between actor and recipient, which, according to the rules of inheritance, again decreases rapidly with increasing group size. These results explain why helping behaviours in very large social groups are limited to cases where the number of reproducing individuals is small, as in social insects, or where there are social institutions that can promote (possibly through sanctioning) large-scale cooperation, as in human societies. Finally, we discuss how individually devised institutions can foster the transition from small-scale to large-scale cooperative groups in human evolution.

Key words: sociality, cooperation, altruism, reciprocity, punishment, relatedness, cultural evolution, group size, diminishing returns, institutions.

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I. INTRODUCTION

Throughout the biological world, individuals typically have social interactions with many other individuals. While obvious examples include mammalian social groups and eusocial insect colonies, even microbes secrete extracellular molecules that affect the material pay-off of other individuals close to them. Sociobiology has long been interested in understanding the evolution and stability of helping behaviours, those behaviours that provide a reproductive and/or survival benefit to other individuals, potentially at some cost to the actor (e.g. cooperation or altruism). Such behaviours are pivotal to social life, from the sterile somatic cells in metazoans that form a fortress for germ cells, to the contribution of individuals to defensive warfare in human societies. Since an ant colony or a human society can comprise interactions among millions of individuals, understanding the origin and stability of sociality involves understanding how helping behaviours can be evolutionarily stable in a population consisting of very large groups.

Consider an idealised case of such a population, where individuals interact in groups of fixed size N (like the island model of Wright, 1931). What is the selection pressure on a helping action that results in a marginal reproductive benefit B_N to the set of all group neighbours, but involves some fixed marginal reproductive cost C to the actor? There are essentially three pathways by which this kind of action can be selected for (Sachs *et al.*, 2004; Lehmann & Keller, 2006; West, Griffin & Gardner, 2007; Bourke, 2011; Van Cleve & Akçay, 2014).

The first pathway is an example of direct benefits, which refers to situations in which the helping action ultimately increases the reproduction and/or survival of the actor itself. In one-shot interactions, an action providing a benefit to group neighbours may not only result in some marginal cost to the actor, but also in some marginal benefit D_N to the actor. The action can then be favoured by selection when this benefit outweighs the costs (i.e. the net marginal effect is positive, such that $D_N - C > 0$). An example of this can occur when a meerkat performs sentinel behaviour. Sentinel behaviour carries an opportunity cost ($C > 0$), while providing a benefit to group neighbours ($B_N > 0$). Crucially,

sentinel behaviour also directly benefits the actor ($D_N > 0$), since the actor will be alerted to an approaching predator along with the rest of the group. This benefit to self, however, is likely to be greater in smaller groups, since in a small group if the individual does not perform sentinel duty then there may be no other group member available to do so, leaving the entire group including the actor unprotected.

The second pathway for the evolution of helping occurs when interactions are repeated (multimove interactions). If individuals can condition their behaviour on the outcome of past interactions, the marginal benefit B_N conferred to others during previous play may be reciprocated (either by a recipient of that act of help or by another group member). This returned benefit is usually discounted according to some factor ρ_N , which captures the responsiveness of others to the behaviour of the actor. Where the help given to others is reciprocated, this can provide direct benefits that outweigh the marginal cost (i.e. the net marginal effect is again positive, such that $\rho_N B_N - C > 0$). An example of this occurs in vampire bats, where a bat that has just had a blood meal may regurgitate some of the blood, and donate it to a group member that has been unsuccessful in feeding that night. The donation causes the actor to suffer an immediate loss of food (C), but may provide a greater marginal benefit to the recipient, in terms of increasing the time until death from starvation ($B_N > C$) (Wilkinson, 1984; Carter & Wilkinson, 2013). By donating, the actor increases the chances that the recipient will donate to the actor in future if the actor fails to feed ($\rho_N > 0$), and the benefit, discounted by the responsiveness of recipients, can outweigh the cost of donation (Carter & Wilkinson, 2013). However, responsiveness is likely to decrease with group size, since an individual will have to keep track of interactions between (or have information about) more and more individuals.

Finally, since by definition B_N affects the reproduction of others, the action of an individual can also result in indirect benefits. This then creates the third pathway by which helping can be favoured. An actor receives indirect benefits from helping other group members if these individuals are more likely themselves to be helpers than are individuals sampled at random from the global population. This entails that helping preferentially falls on other individuals carrying

the determinant (or predictor) of the action. This is measured by relatedness, κ_N , – the covariance between the trait of the actor and recipients (possibly scaled to account for local competition for resources; e.g. Queller, 1994). Given sufficient relatedness, the indirect marginal benefits of helping can outweigh the marginal cost ($\kappa_N B_N - C > 0$). An example of this occurs when a honeybee stings an intruder to its colony. This results in its own death ($C > 0$), but also the death of the intruder, which provides a marginal benefit to the rest of the colony ($B_N > 0$). Since the individuals in a colony are typically highly related ($\kappa_N \gg 0$), this suicidal helping provides an indirect fitness benefit to the actor, which can more than offset the cost, even in the absence of any direct benefit to helping. Importantly, relatedness between group members depends crucially upon group size. In eusocial colonies such as this, relatedness between workers decreases with the number of queens that found the colony, since the probability that two workers descend from the same queen decreases with queen number.

While it is, then, well understood how helping can in principle be favoured by selection, we have stressed above that all components of the selective pressures on helping in all pathways depend crucially upon group size N , and may actually decrease with it. Specifically, the following all depend upon group size: (i) the marginal reproductive benefits to self, D_N , and to others, B_N , (ii) the coefficient of responsiveness ρ_N , and (iii) κ_N the (scaled) coefficient of relatedness. Despite this, the effects of group size on the selective pressure in evolutionary models of cooperation and altruism are often sidelined. As a result, mechanisms are often suggested as supporting large-scale cooperation or altruism, when in fact they would rapidly become ineffective with increasing group size. Finally, there is often a mismatch between the implicit assumptions of the models concerning the effects of group size, as opposed to the actual effects of group size in the empirical world.

Our goal herein is twofold. First, it is to highlight the biological implications of assumptions about group size and their effect on the selection pressure in common models for the evolution of helping. Second, it is to delineate which mechanisms are likely to allow helping to evolve in very large groups. This is crucial to understanding the stability of sociality in general, as group size is perhaps the single most important limiting factor for its evolution. Importantly, our analysis implies that while social insect colonies are often compared with human societies in terms of sociality, the evolutionary mechanisms behind large-scale cooperation are in fact fundamentally different in these two cases.

In order to discuss the effect of group size on selection pressure in a quantitative way, we frame the literature on the evolution of helping into the simple selective pressures provided above, which can be summarized in a single synthetic evolutionary model [see online Supporting Information, Appendix S1 for a derivation and Sachs *et al.* (2004), Lehmann & Keller (2006), West *et al.* (2007), Bourke (2011), and Van Cleve & Akçay (2014) for more social evolution background on which our analysis builds].

This allows us to cover and discuss the role of group size in essentially all standard models of the evolution of cooperation and altruism. For example, through the direct benefits pathway we are able to cover the effects of group size in one-shot collective action problems, which may involve synergistic cooperation, punishment, or other incentive schemes. Through the responsiveness pathway, we cover the effects of group size under repeated interactions, which may involve direct, indirect, and generalised reciprocity (including partner choice and switching). Finally, through the relatedness pathway we are able to cover arbitrary spatial structure induced by limited dispersal, including patch-, lattice-, and network-structured populations.

II. HOW THE MARGINAL BENEFITS OF HELPING DEPEND ON GROUP SIZE

We start discussing the role of group size by assuming no responsiveness or relatedness between group members ($\rho_N = \kappa_N = 0$). This allows us to isolate the effects of group size on the benefits of helping. We consider the simplest case where a unit of investment into helping produces a public good that increases the number of offspring produced by all group members, which we refer to as group productivity, equally. That is, there is no dominance hierarchy or other class structure within a group that would create an unequal distribution of the benefits of help. This allows us to explore how the benefits of helping change with group size in the simplest way.

The marginal benefit to a focal individual of investing in a unit of help, D_N , is then its share ($1/N$) of the increased group productivity that its helping action creates. In turn, the marginal benefit to the rest of the group, B_N , is equal to $(N - 1)D_N$, since each of the other $N - 1$ group members also receives the same benefit (see online Supporting Information, Appendix S2). How, then, will these marginal effects of helping change with group size?

(1) The economics of helping

Production functions from microeconomics (Pindyck & Rubinfeld, 2001) provide a principled way to address this question. A production function maps factors of production into an output product. In our case the factors of production are the investment into helping of each individual in the group, as well as other biotic and abiotic factors such as space and food. The output product is group productivity. One can then ask: how does production change when a factor of production is altered? As in most models of the evolution of helping, we consider the effect of varying total investment into helping in the group (sum of the actions of all individuals), while holding all of the other biotic and abiotic factors of production constant (see online Supporting Information, Appendix S2 for specific examples).

The total investment into helping in a group is typically given by group size multiplied by the average individual

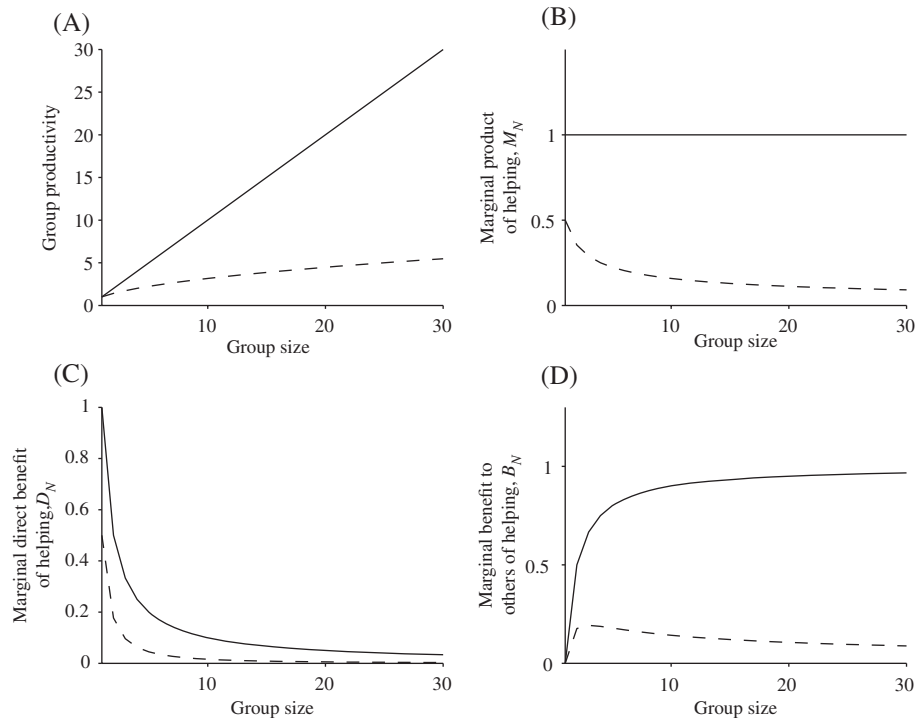


Fig. 1. Plots of group productivity (A), marginal product of helping M_N (B), marginal direct benefit D_N (C), and marginal benefit to others B_N (D), all as a function of group size for a public goods game (group productivity is given by Equation S14 in Appendix S2 with $\beta = 1 - (aN)^\gamma$ and $a = 1$; the marginal product of helping, M_N , is given by Equation S15; the direct benefit, D_N , is given by Equation S16; and the indirect benefit, B_N , is given by Equation S17). Solid lines display constant marginal returns ($\gamma = 1$), which represent investment into helping in the N -player Prisoner's Dilemma, and in many behavioural economics experiments on public goods production. Consequently, the direct benefit of helping decreases rapidly with group size. By contrast, dotted lines display diminishing marginal returns ($\gamma = 0.5$). In that case, the direct benefit decreases even more rapidly with group size.

investment into helping of the group members. We define the marginal product of helping, M_N , as the derivative of group productivity with respect to the investment into helping of the average group member (Equation S10 in Appendix S2, Supporting Information). The marginal product M_N is key because it gives the amount by which group productivity increases as a result of an individual's helping action, when all other factors are held constant. It therefore determines both the direct benefit of helping D_N (the actor's share of the marginal product, that is; $D_N = M_N/N$), and the benefit from helping conferred on the rest of the group B_N (each other group member's share of the marginal product, see Equations S11–S17 in Appendix S2, Supporting Information). We are then interested in how the marginal product of helping changes with group size.

Many theoretical models in evolutionary biology (e.g. Williams & Williams, 1957; Wilson, 1975; Wade, 1979; Nunney, 1985; Taylor, 1992; Boyd *et al.*, 2003; Gardner & West, 2006) assume that group productivity increases linearly with the total investment into helping by group members (Fig. 1A, solid line). The marginal product of helping is then constant for any amount of help, and hence across all group sizes (Fig. 1B, solid line). In this case, the marginal direct benefit of helping (D_N) will decrease with group size at a rate on the order of $1/N$ (Fig. 1C, solid line). The marginal

direct benefit of helping decreases rapidly (more formally, hyperbolically) when the marginal product of helping is a constant, because as group size increases each unit of help an individual produces provides the same increase in group productivity, but this constant amount is shared by more individuals. Consequently each individual, including the actor, benefits less from a single act of help as group size increases. The marginal benefit to the rest of the group (B_N) is then a concave function of group size (Fig. 1D, solid line).

This case of a linear production function corresponds to a linear public goods game, which is in standard use in behavioural economics experiments on cooperation (e.g. Güerke, Irlenbusch & Rockenbach, 2006; Kosfeld, Okada & Riedl, 2009; Putterman, Tyran & Kamei, 2011; Traulsen, Röhl & Milinski, 2012; Burton-Chellew & West, 2013). Crucially, however, it is hard to find actual empirical cases where group productivity increases linearly with total investment into helping. Indeed, it has been argued that constant marginal returns from helping never apply in biology (Archetti & Scheuring, 2012). Realistically, the benefits of helping must eventually saturate (Fig. 1A, dotted line), such that the marginal product of helping starts to decrease (Fig. 1B; dotted line). This is because of the fundamental fact that the other factors of production, apart from investment into helping, depend on limited resources

Table 1. Empirical examples of cases where helping behaviour has been demonstrated to have diminishing marginal returns on group productivity

Example	Reference
Reproductive efficiency is reduced in larger groups of Hymenoptera	Michener (1964)
The benefit of extra stalk cells to lift reproductive spores in <i>Dictyostelium discoideum</i> is reduced once the stalk is high enough to allow dispersal by invertebrates or water	Huss (1989) and Foster (2004)
Efficiency of cooperative hunting in social spiders decreases beyond a threshold colony size	Yip, Powers & Aviles (2008)
Group hunting success is a concave function of group size in falcons	Packer & Ruttan (1988)
The growth rate of yeast is a concave function of the amount of extracellular invertase enzyme produced	Gore, Youk & van Oudenaarden (2009)
<i>Pseudomonas aeruginosa</i> produce less iron-scavenging molecules <i>per capita</i> at higher cell densities	Kümmerli <i>et al.</i> (2009)
Colony productivity initially increases with queen number in <i>Solenopsis invicta</i> , but then decreases as further queens are added	Tschinkel (1993)
One sentinel is often sufficient to alert a group to approaching predators	Bednekoff (1997) and Clutton-Brock <i>et al.</i> (1999)
Investment in blood sharing gives decreasing returns in vampire bat groups	Wilkinson (1984) and Foster (2004)
Human problem-solving ability can increase with group size, but adding extra individuals also introduces problems of coordination and consensus making	Haleblan & Finkelstein (1993)

and so eventually limit group productivity. This is known in economics as the law of diminishing marginal returns. It is the principle that if only one factor of production is increased, while the others are held constant, then the increase in output from adding another unit of that factor will eventually become smaller. Table 1 provides empirically demonstrated examples of the law of diminishing marginal returns for various biological public goods.

While there must always be diminishing returns for very large group sizes, there are two different cases to consider for small or moderate group sizes. We develop these explicitly, and how they affect the marginal benefits D_N and B_N in standard evolutionary game theory models, in Appendix S2, Supporting Information.

In the first case, diminishing returns occur from the onset so that the production function is concave in the total investment into helping. This occurs when adding a second helper to a group increases group productivity by less than adding the first helper did. For example, adding a second sentinel to a group is unlikely to double the chances of detecting a predator (Clutton-Brock *et al.*, 1999). Similarly, yeast can cooperatively convert sucrose into glucose, but doubling the available glucose concentration does not double growth rate. Instead, an empirical study found that the growth rate depends on glucose concentration to the power 0.15 (Gore *et al.*, 2009), making for a highly concave production function. For a concave production function, the marginal benefit D_N generally decreases very rapidly with group size (Fig. 1C, dotted line), and the selection pressure on helping thus follows the same trend.

The second case is where there is an initial range of group sizes for which helping exhibits increasing marginal returns, which applies to many types of public good (Table 2). In biology this is commonly referred to as synergy (Sumpter, 2010, Chapter 10). In these cases the production function is likely to be sigmoidal (Fig. 2A), with an initial range of

group sizes over which it is convex. The marginal product of helping initially increases with group size (Fig. 2B), but then starts to decrease and eventually become zero as the benefits of helping saturate. Consequently, D_N and B_N are both humpback functions of group size (Fig. 2C and D), with an intermediate group size providing the largest individual benefit to investing in helping.

A common case of increasing marginal returns is where a threshold level of investment into a public good must be crossed before that good provides any benefit. For example, an attack by a large aggregation of bark beetles is required in order to overcome a host conifer's resin defences (Franceschi *et al.*, 2005). Below this threshold, increasing individual investment in helping group mates to attack has little effect, since the attack will fail regardless. But as the threshold group size is approached, an additional helper can have a large effect. Similarly, many microbial public goods only become effective at high cell densities. This is because at low cell densities the goods diffuse away before they can be used (Darch *et al.*, 2012).

In ecology, increased direct fitness with respect to group size is known as the Allee effect (Allee *et al.*, 1949). An important cause of this is synergistic helping (Courchamp, Clutton-Brock & Grenfell, 1999). For example, small colonies of Damaraland mole-rats *Cryptomys damarensis* may fail to locate and share food efficiently (Jarvis, Bennett & Spinks, 1998), while studies suggest that African wild dogs *Lycanox pictus* require a threshold group size for their cooperative hunting strategy to be energetically efficient (Courchamp *et al.*, 1999). Moreover, if the direct benefits of helping are to provide an incentive to forming social groups, then group productivity must have some initial increasing marginal returns (Avilés, 1999). This is because if group productivity increases only linearly with investment into helping, then the direct benefit of helping can only decrease with group size. Consequently, in the absence of indirect benefits ($\kappa_N = 0$)

Table 2. Empirical examples of cases where helping behaviour is synergistic, such that the marginal product of helping increases with group size for small- to medium-sized groups

Example	Reference
Large aggregations of bark beetles are required to overcome conifer resin defences	Franceschi <i>et al.</i> (2005)
Ant colonies founded by multiple queens are more effective at brood raiding	Bernasconi & Strassmann (1999)
Queen mortality is lower in colonies of <i>Solenopsis invicta</i> founded by four queens than one queen, but colonies founded by two queens have greater mortality than single-queen colonies	Adams & Tschinkel (1995)
In primates, physical contests are often won by the larger of two coalitions	Wrangham (1999)
Microbial public goods diffuse away too rapidly at low cell density, before they can be used	Darch <i>et al.</i> (2012)
<i>Myxococcus xanthus</i> social bacteria produce no spores below a critical density	Kadam & Velicer (2006)
Protective abilities of biofilms depend upon high cell density	Cui, Meng & Bhagwat (2001), Li <i>et al.</i> (2001) and Høiby <i>et al.</i> (2010)
<i>Per capita</i> food intake increases with pack size in cooperatively hunting African wild dogs (<i>Lycaon pictus</i>)	Creel & Creel (1995)
Prey biomass intake <i>per capita</i> increases with group size in cooperative social spiders (<i>Anelosimus eximius</i>)	Yip <i>et al.</i> (2008)
More than five dwarf mongooses (<i>Helogale parvula</i>) are required for continuous predator vigilance	Rasa (1989)
Groups of less than four white-winged choughs (<i>Corcorax melanorhamphos</i>) are incapable of cooperative breeding	Heinsohn (1992)
Predation rate decreases with group size in white-nosed coatis (<i>Nasua narica</i>)	Hass & Valenzuela (2002)
Net kJ per hunter increases more than linearly with group size when Tai chimpanzees hunt cooperatively	Boesch (1994)
Whale hunting in small-scale human groups requires cooperation between a minimum number of crew members	Alvard & Nolin (2002)
Human societies with larger initial population sizes have faster growth rates of technology	Kremer (1993)

or responsiveness to past behaviour in repeated interactions ($\rho_N = 0$), individuals would be better off as solitaries unless there were increasing marginal returns for some range of group sizes.

Increasing marginal returns also occur in between-group conflicts. For example, models of between-group warfare in humans often assume a sigmoidal production function (e.g. Bowles, Choi & Hopfensitz, 2003; Bowles, 2009; García & van den Bergh, 2011; Lehmann, 2011). Under the common assumption that losing groups are completely destroyed and repopulated by members of winning groups, this can cause D_N to become independent of group size, while B_N increases with group size (see online Supporting Information, Appendix S2, Section 2b). These assumptions can therefore produce a positive selection pressure for helping even in groups of arbitrarily large size (Lehmann, 2011). However, the extent to which these assumptions would have been met in human hunter–gatherer groups has been debated (for example, compare Bowles, 2009, with Fry & Söderberg, 2013).

(2) Direct benefits through enforcement

So far, we have considered helping traits that evolve because the benefit from the actor's share of the public good it produces outweighs the cost. But direct benefits to helping can also arise when helping is enforced through punishment, even when the actor receives none of the good that it

produces (Clutton-Brock & Parker, 1995). This happens when the cost of being punished is greater than the cost of helping. We can write the cost to an individual of being punished for not helping as P_N . Not being punished then provides a direct marginal benefit of $D_N = P_N$ to the individual (equal to the cost of being punished), so helping is selected for if $P_N > C$. Punishment can therefore convert helping into a stable equilibrium when it otherwise would not be.

Crucially, for a given level of investment into punishment, P_N must decrease with the number of non-helpers that need to be punished. Intuitively this is because the *per capita* effect of being punished is likely to be proportional to the total investment into punishment, divided by the number of individuals that need to be punished. This means that the effect of punishment decreases with group size when helpers are rare. In addition, as group size increases then problems arise in monitoring the actions of more and more group members (Carpenter, 2007; Fischer *et al.*, 2014).

Despite this, the effects of group size on the efficacy of punishment have been glossed over in studies of human pool punishment (Sigmund *et al.*, 2010, 2011; Traulsen *et al.*, 2012; Schoenmakers *et al.*, 2014). Under pool punishment each individual decides whether to invest resources into a centralised punishment pool, and then decides whether to help or not. The resources in the punishment pool are subsequently used to punish each non-helper. In a realistic setting, P_N should be the total amount in the punishment pool

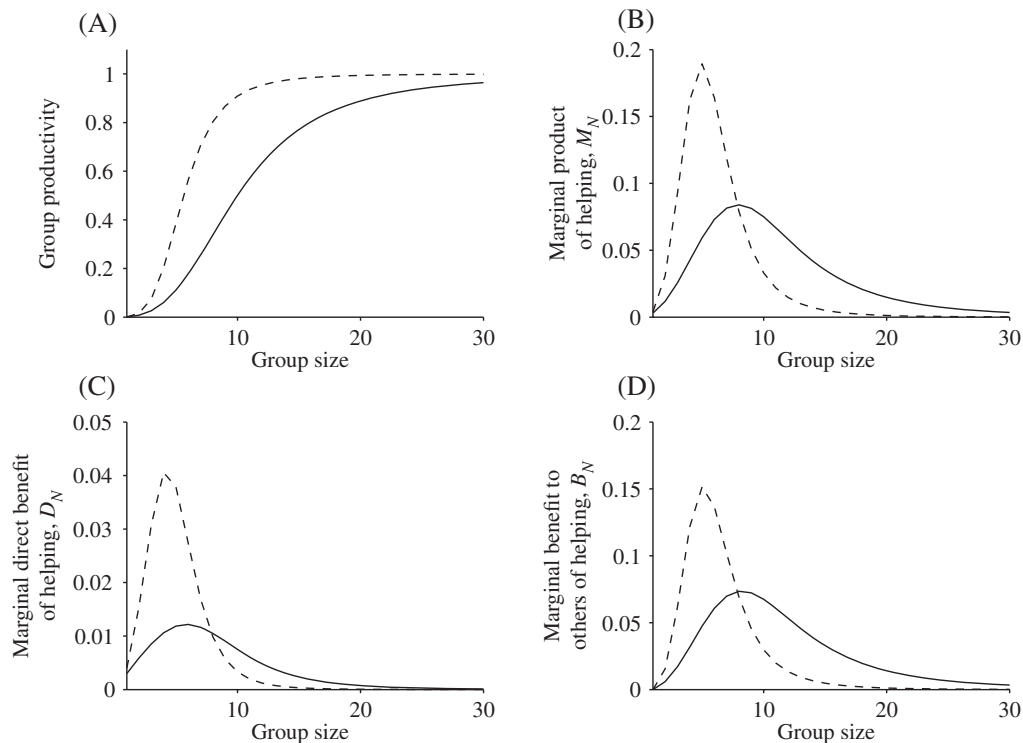


Fig. 2. Same plots as in Fig. 1 except that $\beta = 1000$ in the production function is now a constant, where solid lines are for $\gamma = 3$ and dotted lines for $\gamma = 4$. Group productivity is a sigmoidal function of group size (A), so that the marginal product (B), marginal direct benefit (C), and the marginal benefit to others (D) are all humpback functions of group size. This means that intermediate group sizes are most favourable for the evolution of helping.

divided by the number of non-helpers. However, both theoretical models and experiments on pool punishment have concealed this by assuming that each non-helper is punished by the entire contents of the pool (Sigmund *et al.*, 2010, 2011; Traulsen *et al.*, 2012; Schoenmakers *et al.*, 2014). This assumption means that the only factor that matters is the total amount of resources in the punishment pool, and not group size. But in a more realistic setting, the number of non-helpers in the group should also matter – the greater the number of non-helpers, the less each will be punished by. Explicitly taking account of group size in this way makes the models more complicated. Nevertheless, realism with respect to group size is important given that pool punishment is suggested as an explanation for large-scale human cooperation.

So far we have discussed the effect of group size on the effect of being punished, P_N . But group size also effects selection pressure on investment into punishment itself. This is because a threshold level of punishment must be reached before it pays non-helpers to become helpers (Boyd & Richerson, 1992; Lehmann *et al.*, 2007). If a group is initially fixed for non-helpers, then a single mutant punisher will have little effect. Consequently, individuals that invest into punishment must cross a threshold frequency before their investment has any effect. While this threshold frequency may stay the same as group size increases, an increase in group size means that a larger absolute number of individuals that invest into punishment will be needed in order to cross it. The result

is that it becomes more difficult for punishment to invade as group size increases. In addition, problems of second-order free-riding become greater in larger groups (Boyd *et al.*, 2003; Lehmann *et al.*, 2007). This is where individuals that help in order to avoid being punished, but that do not themselves invest into punishment, obtain a larger pay-off than helpers that do invest into punishment. If punishment and helping are not perfectly linked traits, then this can lead to the breakdown of sanctioning systems in large groups.

(3) Summary

Group productivity is often assumed in models of helping to be a linear function of the total amount of help. In that case, the direct fitness benefit of helping tends to decline rapidly with group size, on the order of $1/N$. However, in reality group productivity is often likely to be a sigmoidal function of the total amount of help (Fig. 2A). As a result, the marginal product of helping (M_N) then initially increases with group size (Table 2), but must eventually start to decline as group size continues to increase, due to the law of decreasing marginal returns. In such cases the direct fitness benefits of helping are strongest in intermediate sized groups (Fig. 2C). Punishment of non-helpers can also select for helping, even when helpers receive none of the benefits of their own helping acts. However, realistically the *per capita* effect of punishment must decrease with the absolute number of non-helpers in the group.

III. HOW RESPONSIVENESS DEPENDS ON GROUP SIZE

We now turn to consider situations in which individuals engage in repeated (or multimove) interactions, so that they can condition actions on the previous actions of their partners. In terms of our model, this means that the selection pressure on helping takes the form $\rho_N B_N - C > 0$ (see online Supporting Information, Appendix S1, we assume that the population is not spatially structured and there are no direct benefits, so that $D_N = \kappa_N = 0$). Our aim is to make clear how the coefficient of responsiveness ρ_N must depend upon group size.

(1) The interdependency of helping

The coefficient of responsiveness, ρ_N , gives the degree to which other group members adjust their action in response to that of the actor in a group of N interacting individuals (see online Supporting Information, Appendix S1). This quantifies the extent to which the current partner of a focal individual will change its investment into helping when the focal does (this coefficient can also be thought as the regression of a partner's action on the focal's action; Van Cleve & Akçay, 2014). For example, primates adjust the amount of time they spend grooming other individuals based on how much the recipient has groomed them in the past (Schino & Aureli, 2010). The extent to which they adjust this is then captured by ρ_N .

In general, the coefficient of responsiveness ρ_N must decrease with increasing group size. This follows simply from the cognitive demands of tracking the behaviour of more and more individuals. Consequently, the evolution of helping through reciprocation becomes less likely as group size increases. As we now discuss, this applies to direct, indirect, and generalised forms of reciprocity.

(2) Direct reciprocity

Under direct reciprocity (Trivers, 1971; Axelrod & Hamilton, 1981), individuals are assumed to have interactions with the same partners repeatedly. We consider first dyadic social interactions. The coefficient ρ_N then measures the degree to which the partner changes its action based on the action of the focal individual during their previous interaction. In biologically realistic settings, individuals are likely to interact with many partners during their lifetime. This means that a memory large enough to store the outcomes of previous personal interactions (and monitor more or less noisy signals) with N individuals is required in order for a large value of ρ_N to be obtained with each interaction partner (Stevens & Hauser, 2004; Brosnan, Salwiczek & Bshary, 2010; Connor, 2010; Moreira *et al.*, 2013).

One line of empirical support that memory size constrains reciprocal helping in large groups comes from the fact that social group size covaries positively with the size of the neocortex in non-human primates. This suggests that neocortex size limits the number of reciprocal relationships

that an individual can keep track of (Dunbar, 1992). Indeed, the need to track social relationships in larger and more complex groups has been argued to be a key driver of the relatively large brains seen in primates (Byrne & Whiten, 1988; Dunbar, 1998). Yet even with a large neocortex size, ρ_N should still be expected to decline rapidly with group size under dyadic direct reciprocity. For example, a study has shown that when humans have to remember whether the last actions of 15 group members were cooperative or not, they exhibit a high mean error rate of 24% (Stevens *et al.*, 2011). This suggests that individuals were having to guess whether half of their group members had cooperated or not, even when they had been directly provided with this information at an earlier point in time.

Direct reciprocity can also occur in repeated public goods games. These are situations where N individuals simultaneously decide whether to invest in helping that will benefit all of them, and this is repeated between the same players for a number of times during their life. In such cases, individuals can condition their decision to contribute to the public good on how their group members have behaved in the past. In this case ρ_N is diluted compared to a pairwise interaction, even in the absence of memory constraints. This is because the focal individual cannot directly respond to the action of any one individual group member, but only to some aggregate of the action of all of the N group members. This diluting effect is on the order of $1/N$.

A concrete example of the diluting effect is given by models of the evolution of response rules of the form: 'help if at least x other group members helped in the previous round'. When group composition is random, then the only such rule that is evolutionarily stable is 'help if all of the other $N - 1$ group members helped in the last round' (Joshi, 1987; Boyd & Richerson, 1988). However, although this rule is stable when common in a population, the conditions for it to invade a population of unconditional non-helpers becomes very stringent as group size increases. Specifically, the spread of the rule relies on the formation of at least one group where all individuals use it (Boyd & Richerson, 1988), and the probability of this happening is very unlikely in groups of even moderate size.

(3) Indirect reciprocity

In models of indirect reciprocity (Sugden, 1986; Kandori, 1992; Nowak & Sigmund, 1998; Leimar & Hammerstein, 2001; Ohtsuki & Iwasa, 2006; Roberts, 2008), individuals are assumed to be repeatedly rematched in a pairwise way with partners that they have not interacted with before. Individuals cannot then condition their behaviour on how their partner has behaved towards them in the past. Instead, individuals are assumed to be able to condition their behaviour on some information characterising the behaviour of their current partner towards other group members in past interactions (usually called 'reputation' or 'condition').

To highlight the effects of group size in such cases, let us first consider again dyadic interactions. The fate of helping then depends upon the extent to which an

individual accurately knows the reputation of its partner. A simple model of indirect reciprocity can be used to make this point. The model considers competition between only two strategies: discriminator *versus* always-defect. The discriminator strategy cooperates only with an individual that helped another individual in its previous interaction. The always-defect strategy never cooperates. A population of discriminators is stable against invasion by always-defect only if the probability of correctly knowing whether the partner previously helped another individual or not (its reputation) is greater than the cost-to-benefit ratio of helping (Nowak & Sigmund, 1998). We argue that from an empirical point of view, the probability of correctly knowing a partner's reputation should be expected to decrease with group size.

Knowledge of a current partner's reputation can come from one of two sources: either from direct observation of its behaviour in previous interactions with other individuals, or through communication (such as gossip) with other group members. Clearly, the number of interactions which an individual can directly observe is limited, which has a detrimental effect on cooperation in large groups. For example, simulations have looked at the case where an interaction can only be observed by ten randomly chosen group members. In this case, while helping was stable in groups of 20, it became increasingly unstable as group size increased, with helping actions becoming very rare in groups of 100 (Nowak & Sigmund, 1998). This implies that limits on what can be observed will limit the evolution of helping through indirect reciprocity in large groups. Empirical evidence also suggests that observing other group members becomes more difficult as group size increases (Fox & Guyer, 1977; Kollock, 1998; Alencar, Deoliveirasiqueira & Yamamoto, 2008). Moreover, if interactions are dyadic and private, which many undoubtedly are, then it is hard to see how they could reliably be observed by a third party at all. As such, even assuming that individuals can directly observe the dyadic interactions of 10 other group members may be an unrealistic assumption.

The same problem is likely to apply if knowledge of reputation is spread through communication. This is because as group size becomes larger, then the reputation of a new partner is likely to have to be passed through a larger chain of individuals to reach the actor. Errors in the communication channel are then likely to become greater with every individual in the chain. Moreover, in larger groups a chain of individuals linking the partners may not even exist at all. Finally, individuals may be dishonest when communicating the reputation of others. Thus while experiments have shown that communication can successfully transmit reputational information in small groups (Sommerfeld *et al.*, 2007; Sommerfeld, Krambeck & Milinski, 2008), on the order of 10 individuals, it is a pressing issue for future empirical work to investigate the reliability of communicating reputation between individuals in larger groups.

However, the quality of information received by an individual may actually initially increase with group size when groups are small. Evidence for this comes from experiments which have shown that individuals tend to discriminate

more accurately between helpers and non-helpers when they receive multiple gossip statements about a partner's past behaviour (Sommerfeld *et al.*, 2008). In other words, receiving reputational information from multiple individuals increased the accuracy with which reputations were formed. Intuitively, this is because multiple sources of correct information drown out a small number of incorrect ones, and indeed individuals tended to believe the majority assessment of whether a partner had helped or not in the past (Sommerfeld *et al.*, 2008). This suggests that up to a point, the benefits of having multiple information sources in larger groups may partly offset the errors created by increased chain length. Nevertheless, this effect must eventually tail off in large groups. Moreover, as well as there needing to be a chain of individuals to pass along information, psychology experiments also suggest that knowledge of reputation, by either observation or communication, requires explicit person memories (Wilkowski & Chai, 2012). This implies that, as with direct reciprocity, indirect reciprocity is also constrained by memory size in large groups.

Unfortunately, the direct dependence of reputational knowledge on group size has often been obscured in models of indirect reciprocity, which assume a constant error rate in knowing the reputation of a partner (e.g. Panchanathan & Boyd, 2003; Roberts, 2008; dos Santos, Rankin & Wedekind, 2011; Nakamura & Masuda, 2011). This assumption leads to a ρ_N that is constant and thus independent of group size, which then implies that indirect reciprocity has no difficulty in scaling with group size. Indeed, it has been established long ago that in this case helping can be favoured in groups of any size under indirect reciprocity (Kandori, 1992). However, while common, the assumption that the responsiveness coefficient is independent of group size is not supported empirically. If a per interaction error rate is used, then a more plausible assumption would be for it to scale positively with group size.

The same issues apply in models of biological markets, in which individuals can choose their interaction partner based upon the amount of help the potential partner offers (Noë & Hammerstein, 1995). For partner choice to favour helping, individuals must be able to evaluate the cooperative propensity of a potential partner. This may be done by direct, first-hand evaluation of the partner. For example, when a plant makes an offer of food to ants in return for the ants guarding the plant, this offer of food cannot be retracted by the plant and so serves as an honest signal of cooperation (Noë & Hammerstein, 1995). But as group size increases, such direct evaluation between a large number of potential partners becomes unfeasible. In such cases individuals must indirectly evaluate the degree of help offered by a partner, which then relies on the spread of reputation (André & Baumard, 2011), for example through communication (Enquist & Leimar, 1993). Consequently, biological market models where individuals actively choose their interaction partner (instead of being randomly matched) face the same problems of the reliable transmission of information.

If interactions are not pairwise, but instead take place between many individuals simultaneously, then the decline

of ρ_N with group size under indirect reciprocity becomes even more acute. This is because, as with direct reciprocity, in a collective action problem an individual can no longer respond to the action of any one particular group member. Instead, an individual can only respond to the aggregate reputation of the other individuals taking part. This then leads to a rapid decline in helping as group size increases, even when the reputation of all group members is known perfectly (Suzuki & Akiyama, 2005, 2007, provide explicit models of this effect). Combining this effect with reputational errors draws into question the prospect of classic indirect reciprocity models providing a satisfactory explanation for the evolution of human cooperation in large groups (Fowler, 2005).

(4) Generalised reciprocity

In generalised (or ‘upstream’) reciprocity, individuals are also repeatedly matched with new partners from a group of size N . However, unlike indirect reciprocity, they do not use information about the past actions of their new partner. Instead, they condition their behaviour towards a new partner based on how their own previous partner behaved towards them (Boyd & Richerson, 1989; Pfeiffer *et al.*, 2005). If an individual was helped during its previous interaction with any group member, then it will help the next group member that it interacts with. Conversely, if it did not receive help during its last interaction, then the individual will not help whichever group member it interacts with next. The idea is that generalised reciprocators will establish chains of helping. For example, in the three-individual case, individual A helps individual B, in the expectation that individual B will then go on to help C, who will in turn help A. By investing in helping, an individual thus increases the likelihood that it will be helped in the future by some other individual.

As opposed to both direct and indirect reciprocity, this is cognitively less demanding, with individuals only ever needing to remember the outcome of their previous interaction, regardless of who that interaction was with. As such, it has been argued to apply to a wider range of taxa than indirect reciprocity. For example, some experimental evidence has suggested that it occurs in rats (Rutte & Taborsky, 2007).

However, the price of this cognitive simplicity is that for a given group size, ρ_N becomes much more diluted as compared to direct or indirect reciprocity. This is because an act of helping has to flow through many other individuals before its effects return to the actor. If one individual in the chain does not help after being helped, then the original actor’s investment into helping will not make it more likely to receive help itself. In that case, a generalised reciprocator will have paid the cost of helping without receiving a benefit in return. This could happen, for example, if the group contains an unconditional non-helper, or if a generalised reciprocator makes an error. As group size increases, the chain of individuals becomes larger before helping returns to the actor, making this breakdown of helping more likely. In fact, ρ_N decreases with group size on the order of $1/N$ in this case (see online Supporting Information, Appendix

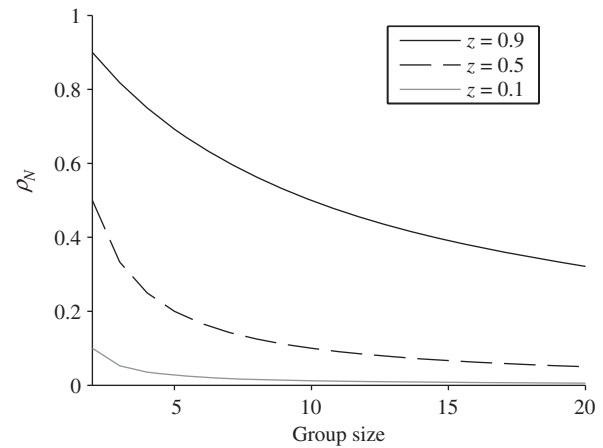


Fig. 3. Plot of the coefficient of responsiveness, ρ_N , with respect to group size under generalised reciprocity (Equation S22 in Appendix S3). An individual’s phenotype, z , is here a linear response slope to the partner’s previous action – the marginal change in the focal individual’s investment into cooperation when its partner makes a marginal change in their investment. Note that in a population where reciprocity has not yet evolved the phenotype z takes very low values or can even be zero.

S3; Fig. 3). Because of this, generalised reciprocity can only invade in very small groups (Boyd & Richerson, 1989; Pfeiffer *et al.*, 2005), or equivalently, in networks created in behavioural time where individuals have only a small number of links (Sander & Taborsky, 2012).

(5) Summary

Under direct reciprocity, ρ_N declines rapidly with group size because of the memory constraints of keeping track of the past behaviour of N individuals. Under indirect reciprocity, ρ_N must also decline rapidly with group size because of the additional problem of obtaining reliable information about the past behaviour of N individuals, either by observation or gossip. Under generalised reciprocity, ρ_N again declines rapidly with group size. This is because as group size increases then the result of an individual’s previous interaction becomes less informative of how that individual should behave with a randomly sampled partner from the population.

IV. HOW (SCALED) RELATEDNESS DEPENDS ON GROUP SIZE

Up to this point, we have discussed the role of group size in situations in which individuals interact in randomly formed groups of size N , ruling out relatedness between interacting individuals. However, most natural populations are not well mixed, and so interaction groups are not formed at random in each generation. Rather, populations are often viscous such that individuals do not tend to disperse far from their parents, creating spatial or family structure. This means that individuals with the helping phenotype can tend to interact

with others also carrying the gene or cultural trait that induces helping, leading to indirect fitness benefits. In terms of our model, we now focus on the case where the action is selected for when $\kappa_N B_N - C > 0$ (only one-shot interactions occur, see online Supporting Information, Appendix S1), and our aim is to discuss how the coefficient of (scaled) relatedness depends on group size. This can be written as

$$\kappa_N = s_N r_N \quad (1)$$

where r_N is the usual relatedness between patch members (e.g. Rousset, 2004), and $s_N \leq 1$ is a scale factor, which when < 1 reduces relatedness. The values of both variables depends upon the demographic assumptions of the model (Lehmann & Rousset, 2010), and are thus endogenously determined.

(1) The genealogy of helping

In a group-structured population with a very large number of groups, relatedness (r_N) can be thought of as the probability that the gene lineages at the helping locus in the actor and the recipient coalesce in a common ancestor who lived in that group in some previous generation (see e.g. Rousset, 2004). This in turn depends on the probability that over a single generation, the ancestral lineages of the genes in actor and recipient descend from the same individual, and will thus be identical-by-descent. It is a standard result in population genetics that the probability of this event is inversely proportional to the (effective) number of reproducing individuals in a group, since each such individual could be the common ancestor of actor or recipient in the next generation (Ewens, 2004). As such, relatedness will decrease rapidly with N (Fig. 4; see online Supporting Information, Appendix S3, Section 2, for an example of how to calculate relatedness).

A complication is that relatedness, measured in terms of the probability of identity-by-descent, must be scaled (or compensated) to take into account the effects of local competition (Queller, 1994; Lehmann & Rousset, 2010). This is important, because if helping is to spread then the extra offspring that individuals receiving help produce must not go on to compete with the actor's own offspring, or those of related group members. Otherwise, the benefits of helping can be partially offset (West, Pen & Griffin, 2002), or even completely cancelled out (Taylor, 1992; Wilson, Pollock & Dugatkin, 1992). The exact consequence of local competition on scaled relatedness κ_N depends on the precise demographic assumptions under scrutiny. But because of the fact that scaled relatedness still depends upon the probability of identity-by-descent, it will generally tend to decline rapidly with group size (see Table 2 in Lehmann & Rousset, 2010).

Importantly, relatedness need not necessarily decrease as the absolute number of interacting individuals increases, since it depends on the effective number of reproducing individuals. In the case of eusocial insects, relatedness remains more or less constant as their colony size expands into the thousands, since all individuals are offspring of one or a few queens. That is, the number of reproducing individuals, N , remains very small even as group size expands. Likewise,

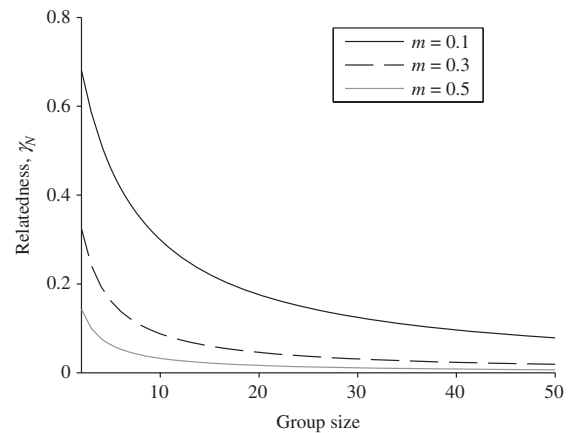


Fig. 4. Plot of the coefficient of relatedness with respect to group size, in an infinite island model with Wright–Fisher reproduction (r_N as given by Equation S24 in Appendix S3). The parameter m here represents the migration rate between groups. Relatedness depends on the probability that two randomly sampled individuals share gene copies that are identical-by-descent. It is a basic result from population genetics that this coalescent probability must decrease rapidly with increasing group size, on the order $1/N$ (see Appendix S3). This applies to all forms of spatial structure, including lattice and network models.

microbial colonies can show helping between thousands of individuals, but many individuals in the colony will be genetic clones, so the number of genetically distinct reproducing individuals is very low ($N = 1$ if all individuals are clones). An analogous situation applies in family-structured populations (Williams & Williams, 1957; Wade, 1979). In the classic case a mated female leaves a clutch of offspring, who then interact with each other in the nest before they all disperse and mate at random in the global population to form the next generation. In this case the probability of identity-by-descent, and hence relatedness, is constant in the sibling group regardless of the clutch size.

Finally, although we have not discussed it here, and it does not affect our main argument, it is worth noting that in a repeated interaction setting there can be an interaction between reciprocal helping and population structure, and that this interaction is non-linear (e.g. Van Cleve & Akçay, 2014; see online Supporting Information, Appendix S1).

(2) Lattice models and other variations of the baseline group-structured model

The first models of social evolution looked at cases where individuals disperse to a random group in the population with some fixed probability (e.g. Eshel, 1972). In essence, this is the island model of dispersal (Wright, 1931), which leads to the genealogical interpretation of (scaled) relatedness given above, and to the build up of relatedness if dispersal is limited. In this standard model the role of various demographic, ecological, environmental, and genetic factors for the selection pressure on helping has been analysed in an extensive and consistent analytical literature. These

analyses demonstrate that scaled relatedness will in general decrease with group size (e.g. Aoki, 1982; Taylor, 1992; Taylor & Irwin, 2000; Roze & Rousset, 2004; Gardner & West, 2006; Lehmann, Perrin & Rousset, 2006; Rousset & Roze, 2007; Johnstone & Cant, 2008; Sozou, 2009; Gardner, 2010; Ohtsuki, 2010; Van Dyken, 2010; Bao & Wild, 2012; Kuijper & Johnstone, 2012; Rodrigues & Gardner, 2012; Van Dyken & Wade, 2012). It is worth noting here that the size of the breeding group (deme) in island models may not be the same as the size of the social group in which helping interactions occur. For example, the subset of the population with which an individual can exchange help may be smaller than the subset of the population with which it can mate (Wilson, 1975). In these cases, it is the size of the group in which exchange of help occurs that matters.

Exactly the same concepts apply in models of isolation by distance, where space is cartesian (Comins, 1982). Here, relatedness between interacting individuals must still depend on the probability of identity-by-descent at the helping locus, which again results from coalescence of ancestral gene lineages taken in actor and recipients. Consequently, this still decreases rapidly with the number of reproducing individuals that contribute to interacting pairs of individuals in subsequent generations (Rousset, 2004). Likewise, neighbours from the same or nearby groups are likely to compete locally for resources (Wilson *et al.*, 1992) and so relatedness needs to be scaled (κ_N) in order to assess the net selection pressure on an action when dispersal is limited (Taylor, 1992; Queller, 1994; Lehmann & Rousset, 2010).

As an example, under iteroparous reproduction modelled by the Moran death–birth process, with dispersal completely localised to the neighbourhood where interactions occur, corresponding to a network or lattice structure, $\kappa_N = 1/(N - 1)$ (Ohtsuki *et al.*, 2006). This says that for helping to be selectively favoured, the benefit-to-cost ratio of helping must exceed the average number of neighbours that an individual has. Interestingly, this situation corresponds approximately to the island model where dispersal is very low (so that dispersal is in a sense spatially localised), in which case κ_N is asymptotically equal to $1/(N + 1)$ (Equation 11 in Mullan & Lehmann, 2014). This displays exactly the same qualitative features but is higher because, unlike in a lattice model, dispersing individuals in an infinite island model never compete with relatives. This illustrates the well-established fact that spatial patterns of dispersal, in which individuals tend to disperse to neighbouring patches, are qualitatively well approximated analytically by the classic island model where dispersal is to a random patch (Comins, 1982).

In spatially explicit demographic models of isolation by distance, each site is either empty or contains a single individual (e.g. van Baalen & Rand, 1998; Le Galliard, Ferrière & Dieckmann, 2003; Lion & van Baalen, 2007; Lion & Gandon, 2009). The actual number of neighbours any one individual has is then determined endogenously as a result of birth, death, and migration processes, making these models particularly suitable to capture cases where groups arise dynamically as a result of feedbacks between

evolution, ecology, and demography. However, the selection pressure on helping is still affected by relatedness and local competition in the same way as discussed above (Rousset & Ronce, 2004), where N in our framework can be thought as the upper bound on the number of neighbours an individual can exchange help with.

(3) Summary

Under limited dispersal, the laws of inheritance imply that (scaled) relatedness, κ_N , decreases rapidly with group size, on the order of $1/N$ (Fig. 4). This result applies to classic group-structured populations such as Wright's island model, and equally to lattice- and network-structured populations with and without explicit demography.

V. ENDOGENOUS GROUP SIZES

So far we have largely discussed group size as if it were an endogenous parameter, separate from evolutionary, ecological, and behavioural dynamics. But in practice group size is affected by both demography, and by individual decisions about whether to join or leave groups or with whom to interact.

As already alluded to in the last paragraph of Section IV.2, the number of neighbours an individual has may depend on local birth and death rates, which in turn depend on the level of helping (see e.g. Lion & van Baalen, 2007, for a review). Such dependence of birth and death rates is either direct or is mediated through environmental conditions, since the environment can itself be affected by the level of helping. For example, helping may allow access to new resources (niche expansion), or may allow existing resources to be used more efficiently (Wilson, 1987; Lehmann *et al.*, 2006; Powers & Lehmann, 2013). In structured populations, the selection pressure on helping traits that increase group carrying capacity can be markedly increased when compared to other helping traits that do not increase carrying capacity. Essentially, this is because an action that increases a group's carrying capacity increases the representation of the group members' gene lineages in the global population, without simultaneously increasing local competition (Lehmann *et al.*, 2006). Consequently, helping that increases carrying capacity increases the scaled relatedness, κ_N , compared to a helping trait that does not do so.

Group size is also often affected by individual decisions to join or leave groups. These decisions can be influenced by heritable traits, and can hence evolve. For example, group size preference has been shown to be a genetically inherited trait in cliff swallows, *Petrochelidon pyrrhonota* (Brown & Brown, 2000), with individuals actively choosing to join colonies of a similar size to their birth colony. Similarly, individuals may have genetically encoded strategies to disperse once group size becomes too large or too small. It is plausible that a heritable group size preference could co-evolve with helping (Avilés, 2002; Avilés, Fletcher & Cutter, 2004; van Veelen,

García & Avilés, 2010; Powers, Penn & Watson, 2011). This can even lead to a runaway process where selection results in decreased group size, since this increases the indirect benefits of helping, which then further favours a reduction of group size (Powers *et al.*, 2011). Hence, a population can evolve from large-group living with little helping, to small groups with substantial helping, as for example in the evolution of a reproductive bottleneck during the transition to multicellularity (where founding cell groups from a single cell makes the effective group size very small; Roze & Michod, 2001). Likewise, in a situation of repeated interactions, the social network of an individual is not necessarily static but may be the result of behavioural dynamics, such as when partner-switching and partner choice evolve along with helping (e.g. Noë & Hammerstein, 1994; McNamara *et al.*, 2008; Izquierdo, Izquierdo & Vega-Redondo, 2010; Schwagmeyer, 2014).

In summary, group size will often be determined endogenously, as a result of a coupling between evolutionary, ecological, and behavioural dynamics, and where all of these interacting features can sometimes depend directly on the level of helping. Crucially though, whenever group size changes endogenously, this will not change the qualitative features of the selection pressure on helping, which is still affected by D_N , B_N , ρ_N , and κ_N in the way that we have described.

VI. LARGE-SCALE HUMAN COOPERATION

For hundreds of thousands of years, early humans adopted a hunter–gatherer lifestyle in which they lived and interacted in small groups, where relatedness is likely to have been positive and altruistic behaviours towards group members plausible (e.g. Bowles, 2009). However, the origin of agriculture around 10000 years ago produced a demographic expansion that led humans to live in much larger social groups. This ultimately resulted in states comprising millions of individuals, where many interactions occur among unrelated individuals.

We stress that large-scale post-hunter–gatherer human helping involves essentially cooperative rather than altruistic behaviour, since altruism is unlikely to occur among unrelated individuals (or only maladaptively; Johnson, Stopka & Knights, 2003; Trivers, 2004; Hagen & Hammerstein, 2006). We now turn to discuss mechanisms of cultural evolution that have been proposed to account for the evolution of this large-scale cooperation. In doing so, we will distinguish between two hypotheses about what drove this transition: we refer to these as the ‘biased-cultural-transmission’ hypothesis, and the ‘institutional-path’ hypothesis. These hypotheses make different assumptions about the cognition of individuals, especially their abilities to communicate and plan.

(1) The biased-cultural-transmission hypothesis

Under a variety of decision processes involving the individual and/or social learning of behaviours, the learned actions (or

strategies) taken by individuals can be regarded as replicators, whose dynamics are very similar to those considered in population genetics (Börger & Rajiv, 1997; Hopkins, 2002). Treating cultural traits as replicators therefore allows methods analogous to population genetics to be used to model their evolution (Cavalli-Sforza & Feldman, 1981; Lumsden & Wilson, 1981; Boyd & Richerson, 1985). The idea of the biased-cultural-transmission hypothesis is that compared to genetic transmission, some of the ways in which cultural traits are transmitted between individuals can lead to a greater (cultural) relatedness κ_N in large groups (Boyd, Richerson & Henrich, 2011). We will discuss the role of group size for three types of biased-cultural-transmission modes that have been invoked in cultural transmission models: pay-off-biased, conformist-biased, and prestige-biased.

Under pay-off-biased transmission, individuals tend preferentially to imitate behaviours of other group members that have produced above-average pay-offs. This parallels fitter individuals leaving a greater fraction of offspring in a genetic model. Consequently, κ_N should be expected to scale the same way with group size as in a genetic model, i.e. to decrease rapidly with the number of individuals that can be imitated. Importantly, local competition tends to be stronger under pay-off-biased transmission than under genetic transmission if individuals copy the behaviour of others in their group. This means that κ_N can be equal to zero or even be negative in situations where it would be positive under genetic transmission (Lehmann, Feldman & Foster, 2008; Mullon & Lehmann, 2014). As a result, pay-off-biased transmission is unlikely to help explain the evolution of cooperation in groups of a larger size than genetic transmission can support.

The second type of biased cultural transmission is conformist-biased transmission (Boyd & Richerson, 1985; Henrich, 2001). In conformist-biased transmission, individuals are more likely to imitate the most common behaviour in their group. This can create multiple stable equilibria, such that different groups will reach different stable frequencies of helping depending upon the initial frequency of helping in the group. Conformity can thus help to maintain variation between groups, since a new migrant or mutant individual coming into a group will tend to adopt the most common type. If conformity is strong enough, this can overcome selection against helping behaviour within groups (Guzman, Rodriguezsickert & Rowthorn, 2007; Boyd *et al.*, 2011). In such cases, κ_N will decrease less rapidly with group size, allowing helping to be maintained in larger groups, or when groups expand in size.

There are two issues with this, however. The first concerns the origin of the helping trait. Conformist-biased transmission, by its very nature, cannot explain the origin of helping when rare in large groups (Lehmann & Feldman, 2008; Molleman, Pen & Weissing, 2013a; Molleman, Quiñones & Weissing, 2013b), as any rare trait is strongly selected against. Models that use conformist-biased transmission must therefore rely on the assumption that at least one group is somehow initially fixed for helping behaviour. The second issue is that even if helping becomes common in a

single group, how can it then spread to other groups? This is a problem because conformity will select against helper migrants that arrive into non-helper groups. Essentially, if helping is to spread between groups under conformist-biased transmission, then groups with fewer helpers need to be more prone to extinction. This is because extinction of a whole group produces vacant sites that helper migrants can colonise, and so be in the majority where conformity will not select against them. One mechanism for this is group warfare in which losing groups are driven extinct (e.g. Boyd *et al.*, 2003; García & van den Bergh, 2011). Another is if the environment periodically deteriorates, causing groups with fewer helpers to become extinct and so leave territory for helper groups to expand into (Peck, 2004; Peck & Welch, 2004).

But how relevant are these scenarios empirically? While conformity has been demonstrated in some laboratory settings, the extent to which it occurs outside of these artificial contexts remains an open question. Indeed, while a recent field experiment did demonstrate conformity, this effect scaled only weakly with the frequency of the behaviour in the group (Claidière, Bowler & Whiten, 2012). In fact, work in social psychology has instead tended to support an anti-conformity bias, where rare behaviours are likely to be more influential to others in a large group (Eriksson & Coultas, 2009). Such an anti-conformity bias has been shown theoretically to favour the spread of a rare helping trait (Lehmann & Feldman, 2008). Overall, this means that while conformity-biased transmission has played an important role theoretically, more work is needed to address its empirical relevance.

The last form of biased cultural transmission that we discuss is one-to-many or leader transmission (Cavalli-Sforza & Feldman, 1981), also known as prestige-biased transmission (Henrich & Gil-White, 2001). With this type of social learning, all individuals in a group tend to copy the traits of a popular model individual, i.e. a leader. If leaders have already gained prestige, and hence are already being imitated, then they may be able to introduce a helping trait into their group that will spread rapidly, even if the trait would be disadvantageous under pay-off-biased transmission. If all individuals copy the trait of the leader, then κ_N is effectively independent of group size (Lehmann *et al.*, 2008). This can then explain both the emergence of helping when rare, and its stability when common in large groups.

From a purely theoretical and dynamic perspective then, one-to-many transmission is the form of biased cultural transmission that is the most likely to explain helping in large groups (Lehmann *et al.*, 2008; Molleman *et al.*, 2013*b*). However, empirically it is naive to assume that human group members, who have sophisticated cognitive skills, would systematically blindly copy the trait of a leader. Indeed, there tend to be marked interpersonal differences in the social learning strategies that different individuals use in the same setting (Molleman, van den Berg & Weissing, 2014). As such, unlike in the models, individuals are unlikely to base their decision to help or not purely on prestige- or conformist-biased social learning. Rather, they are

likely to make some computation based on the perceived costs and benefits of helping in a particular environmental context (Lamba & Mace, 2011). This decision process will incorporate individual learning, as well as various forms of social learning.

Another major simplifying assumption of the biased-cultural-transmission hypothesis (in both models and experiments) is that the choice of actions by group members is uncoordinated. That is, each individual decides in isolation whether to help or not, whether and who to punish, etc. However, this is a worst-case scenario for the evolution of helping. In reality, human social interactions are typically constrained and coordinated by pay-off structures (or incentives) that are determined by the interacting individuals themselves. Consequently, we now turn to discuss the institutional-path hypothesis, and how institution formation can drive a transition from small- to large-scale cooperation.

(2) The institutional-path hypothesis

(a) *Institutions as mechanisms that generate the rules of the game*

The key idea behind institutions is that individuals are not merely passive recipients of their social environment. Rather, they can communicate with each other and negotiate the 'rules of the game' (North, 1990; Ostrom, 1990; Greif, 2006) to create a different pay-off structure (or social organisation) than that given by the default environment (Gardner & Ostrom, 1991, p. 127). More formally, an institution is a set of possible game forms (Hurwicz, 1996); that is, an institution is a (communication) mechanism whose outcomes are rules for social interactions (Hurwicz, 1996, p. 128). As an example, an institution could correspond to a group deciding to allocate a fraction of its common resources to sanction individuals who do not contribute to the production of public goods. The set of all possible allocations then corresponds to the set of game forms, as it specifies the rules of social interactions. The realised allocation of a group in this example, and hence the particular rules of the game, may be decided by various means, such as discussion between group members, or imposition by a group leader (Conradt & Roper, 2003; Conradt & List, 2009).

The formation of institutions has long been studied in economics (Ostrom, 1990; Okada, 1993; Casari & Plott, 2003; Greif, 2006; Ertan, Page & Putterman, 2009; Kosfeld *et al.*, 2009; Putterman *et al.*, 2011), but has remained outside of the scope of the traditional literature on cultural evolution discussed in Section VI.1. This is because evolutionary models generally make the simplifying assumption that the pay-off structure of social interactions is fixed and outside of individual control. Evolutionary biologists, however, are starting to become interested in understanding how institutional rules change the selection pressure on helping (Sasaki *et al.*, 2012; Sasaki, 2013; Schoenmakers *et al.*, 2014), and in how the individual behavioural traits that create institutional rules themselves evolve (van den Bergh & Gowdy, 2009; Safarzyńska & van den Bergh, 2010; Powers & Lehmann, 2013).

Why can institutions encourage helping in large groups? Essentially, institutional rules transform the game the

individuals play, by changing any of the non-genetic components of the selection pressure on helping (D_N , B_N , P_N , or ρ_N). As an illustration, one issue that limits impersonal exchange, such as indirect reciprocity, in large groups is reliable knowledge of the reputation of other individuals. But institutional rules can help to alleviate this by facilitating the reliable spread of reputational information. One example of this is if individuals that are caught cheating are forced to apologise in public to the rest of the group, as happens in modern institutions governing the use of common forests in the Himalayas (Ostrom, Gardner & Walker, 1994). Another example is the system of the Law Merchant for trade in medieval Europe, where judges adjudicated and stored the reputation of international merchants (Milgrom, North & Weingast, 1990). The implementation of these institutional rules (*sensu* Hurwicz, 1996) shares reputational information about cheaters in an organised way that is not dependent upon gossip (and the informational errors that can introduce), and so they create a social network structure where past actions can become known to all. As a result, they cause the response coefficient ρ_N to decline less severely with group size. Consequently, they change the social environment into one in which it pays to help in large groups.

Likewise, institutional rules can increase the *per capita* effect of being sanctioned for cheating, P_N , for a given N . Empirical surveys have shown that institutionally coordinated monitoring and sanctioning is fundamental to securing cooperation in situations where individuals share a common pool resource, such as a forest or fishing water (Gibson, Williams & Ostrom, 2005). In classic peer-punishment models, P_N is limited by the opportunity for second-order free-riding (Fowler, 2005), because the game structure is such that each individual must unilaterally decide whether or not to invest into sanctioning, at a cost to itself. This favours defection in the long run in large groups. One might then wonder, are institutions also vulnerable to second-order free-riding?

Institutional rules that are successful in promoting cooperation take away the incentive of second-order free-riding (Ostrom, 1990; Ostrom *et al.*, 1994; Greif, 2006). An example is given by the institutions that manage the use of common land in the Hirano, Nagaike, and Yamanoka villages in Japan. This common land was potentially vulnerable to exploitation by cheats harvesting too much of a communal resource, such as timber (Ostrom, 1990). To prevent this, institutional rules were put in place to regulate how much and at what times each household was allowed to harvest. The villagers then used a proportion of their common resources to hire monitors – individuals that were rewarded for patrolling the commons and monitoring rule violations. But why did these monitors not themselves cheat by taking payment but then shirking during monitoring, as would be predicted from peer-punishment models? The answer is that they were incentivised to monitor actively, by being allowed to take a supply of money and saké from any rule violator that they personally found. Similarly, in the building and running of the Spanish *huerta* irrigation systems, monitors were incentivised by being permitted to keep a third

of any fine imposed on a defector that they found (Ostrom, 1990). Successful institutions therefore create individual benefits to monitoring and sanctioning, changing the game from one where second-order free-riding pays to one where it does not (Ostrom, 1990; Baumard, 2010; Guala, 2012).

Crucially, such institutions do not have to be externally imposed but can be self-enforcing (Ostrom, 1990; Greif, 2006). Prior work has often thought of sanctioning institutions as analogous to modern police forces (e.g. Sigmund *et al.*, 2010; Sasaki *et al.*, 2012). But individuals can devise rules where sanctioning for not complying, and the benefits from helping, are provided endogenously as an equilibrium outcome without the need for an external arbiter. This can be achieved by individuals having forward-looking preferences over institutional rules (Milgrom *et al.*, 1990; Greif, 2006), or by the cultural evolution of preferences for specific rules (Powers & Lehmann, 2013). Consequently, sanctioning institutions are not inventions of modern societies.

Since institutions that incentivise cooperative behaviour through coordinated sanctioning seem to be universal, understanding their cultural evolution is key to explaining large-scale human cooperation. A key question is then how these institutions evolved to produce a transition from small- to large-scale cooperative groups with the Neolithic origin of agriculture (see Powers, van Schaik & Lehmann, 2016 for further developments of the institutional-path hypothesis).

(b) Demographic transition from small- to large-scale cooperative groups

Provided there are high benefits from helping, institutionally coordinated sanctioning can produce a stable equilibrium level of helping in large groups (as long as the condition $P_N > C$ holds). But, the problem is that it is difficult for individuals that create sanctioning institutions to invade unless group size is small. As we have seen, for a given investment into sanctioning, P_N decreases with the number of non-helpers that must be sanctioned. Consequently, when non-helpers are common in a group, it becomes harder for sanctioning institutions to become established as group size increases.

Conversely, it is easier for sanctioning institutions to invade in small groups, since a smaller total investment into sanctioning is required to make the condition $P_N > C$ hold. This means that institutions which promote helping may initially evolve quite easily in small groups. Crucially, once helping is established in a small group, it may lead to demographic expansion that increases group size, for instance by producing surplus resources that increase local carrying capacity. A concrete example of this is where helping involves contributing to construction and maintenance of an irrigation system (Spencer, 1993; Carballo, Roscoe & Feinman, 2014). Groups with institutions that allow them successfully to manage the collective action problem of irrigation will receive surplus resources and so grow to a larger size.

Once a sanctioning institution is established in a group, it can maintain helping even as the group expands to a much larger size. This is because when helping is common,

the investment into sanctioning is directed towards only a handful of non-helpers. As such, in groups where helping is already common, P_N will be large even for a large group size. In this way, co-evolution of institutions, helping, and demography can produce a coherent transition from small- to large-scale cooperation, which overcomes the conundrum of how helping and sanctioning can invade into large groups (Powers & Lehmann, 2013). This explanation crucially relies on a transient process – the dynamic explicit transition from small-scale to large-scale groups, which provides a linkage between behavioural equilibria in small and large groups.

This explanation relies on the empirically plausible assumption that humans can communicate and create institutional rules that change the outcome of their social actions. However, it does not require conformity, anti-conformity, or prestige-biased social learning rules. Instead, individuals need to be forward-looking and have shared intentionality (shared goals; Tomasello & Carpenter, 2007).

(3) Summary

The biased-cultural-transmission hypothesis proposes that simple conformity- or prestige-biased learning heuristics select for large-scale human cooperation, since they decelerate the decline of cultural relatedness, κ_N , with group size. However, it may be unrealistic to assume that humans cannot reason their way to the fact that cheating or shirking may pay, despite what a leader or other group members do. If they can work this out, then they may stop copying the behaviour of the leader or the majority, leading to a decline in κ_N and hence a decline in investment into helping.

The institutional-path hypothesis proposes that the formation of social institutions selected for large-scale human cooperation. Institutions can affect any of D_N , B_N , P_N , or ρ_N even under pay-off-biased social learning. This requires a higher level of cognition than the biased-cultural-transmission hypothesis, since in order to create institutions individuals need to communicate, be innovative, and have planning abilities. This fits well, though, with the propensity of humans to have shared intentionality, planning, and language.

VII. CONCLUSIONS

(1) Our theoretical analysis alongside the empirical evidence reviewed here implies that in most cases, both relatedness (κ_N) and the responsiveness of other group members behaviour to the actor's own helping (ρ_N) are expected to decrease rapidly with increasing group size. The marginal benefits of helping must also eventually decrease with increasing group size (Table 1), due to the law of diminishing marginal returns. Consequently, both the benefits to self (D_N) and to other group members (B_N) of helping will eventually decrease with group size. Together, these provide convincing explanations for why very large cooperative groups are relatively rare in nature. Nevertheless they do sometimes occur, for example in social insects and human societies.

(2) Parallels are often drawn between large-scale helping in social insects and humans. However, the mechanisms promoting helping behaviours in these taxa are very different. At the risk of oversimplifying, social insect societies essentially rely on indirect benefits of helping, driven by high relatedness, while human societies essentially have low relatedness and so must rely on direct benefits.

(3) Humans are capable of creating social institutions that promote cooperation through direct benefits. Successful institutions change the social environment to one where our predispositions to reciprocity and sanctioning, which are likely to have evolved in small groups in our evolutionary past (e.g. Johnson *et al.*, 2003; Trivers, 2004; Hagen & Hammerstein, 2006), are still advantageous and can be made self-enforcing (Milgrom *et al.*, 1990; Ostrom, 1990; Greif, 2006; Guala, 2012).

(4) Both relatedness and institutions are the product of individual heritable behavioural traits, and so can themselves evolve by processes of 'social' niche construction (Odling-Smee, Laland & Feldman, 2003; Ryan, Powers & Watson, 2016). A promising avenue for future theory is to determine the conditions under which evolution favours individual behaviours that create high cultural relatedness, or cooperation-promoting institutions.

VIII. ACKNOWLEDGEMENTS

We thank Charles Mullon and Miguel dos Santos for helpful discussions, and two anonymous reviewers for their helpful feedback. This work was funded by Swiss NSF grant PP00P3-146340 to Laurent Lehmann.

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X. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. A synthetic evolutionary model.

Appendix S2. Marginal returns of helping.

Appendix S3. Assortation coefficients.

(Received 3 May 2015; revised 3 February 2016; accepted 11 February 2016)

Supporting Information for

**When is bigger better? The effects of group
size on the evolution of helping behaviours**

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This file includes:

Appendices S1-S3

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Appendix S1: A synthetic evolutionary model

We here derive the selection pressures presented in the main text, which are expressed in terms of the marginal costs (C) and marginal benefits to self (D_N) and other group members (B_N), and in terms of the coefficient of responsiveness (ρ_N), and the coefficient of (scaled) relatedness (κ_N). We use a synthetic evolutionary model that is fully detailed in Van Cleve & Akçay (2014). We consider a group-structured population of constant and very large size, which is homogeneous and without class structure (e.g. there are no dominance hierarchies or age or class structure), but that can otherwise have an arbitrary spatial structure (e.g. family structure, group structure, lattice model). The main assumption about social interactions is that the expected number of offspring produced by a focal individual, f_N , which performs a stationary level of helping a_f , depends on the stationary level of helping a_j of its $j = 1, 2, \dots, N - 1$ symmetric social partners and can be written as

$$f_N(a_f, a_1, \dots, a_{N-1}). \tag{S1}$$

This can be thought as a long-term average pay-off (after many interactions have taken place, see Van Cleve & Akçay, 2014). We assume throughout for simplicity that all functions are continuous and differentiable, and use the subscript N to emphasise the functional dependence of fecundity on interacting group size N [an alternative interpretation of the model is that all forthcoming derivatives are replaced by regression coefficients (McGlothlin *et al.*, 2010), in which case neither continuity nor weak selection is required]. With this, the partial derivative $\partial f_N / \partial a_f$ represents the change in pay-off to the focal individual stemming from it changing its own level of helping by an infinitesimal amount (marginal change). Because of the fact that its $N - 1$ partners are symmetric, the effect of any such partner on the focal's pay-off resulting from a change in behaviour is $\partial f_N / \partial a_{N-1}$ (i.e. $\partial f_N / \partial a_j$ are equal for all $j = 1, 2, \dots, N - 1$ since f_N is invariant under permutation of the actions of neighbours).

We assume that increasing the level of helping results in some cost to the focal individual,

but can also generate some benefits that may depend on group size, and so set

$$\frac{\partial f_N}{\partial a_f} = D_N - C, \quad (\text{S2})$$

where C is the fixed cost of helping, and D_N is the benefit that may depend in a complex way on interacting individuals' actions. We also denote the total marginal benefit conferred by partners as

$$(N - 1) \frac{\partial f_N}{\partial a_{N-1}} = B_N. \quad (\text{S3})$$

Actions themselves are assumed to be under the indirect control of an evolving phenotype (see fig. 1 in Van Cleve & Akçay, 2014) and we write $a_f(z_f, z_1, \dots, z_{N-1})$ and $a_j(z_f, z_1, \dots, z_{N-1})$, where z_f is the phenotype of the focal individual and z_j its value in partner j . With this, we can define the response coefficient

$$\rho_N = \frac{\partial a_{N-1}}{\partial z_f} \bigg/ \frac{\partial a_f}{\partial z_f} \quad (\text{S4})$$

which can be thought of as a measure of the extent to which the actions of its partners change when the focal changes its own action (see Van Cleve & Akçay, 2014 for more details). Using this definition and equations S2–S3, it then follows directly from equation 7 of Van Cleve & Akçay, 2014 that a mutant with a small phenotypic deviation from a resident value z (weak selection) will be selected for in the resident population when

$$(D_N - C) + \rho_N B_N + \kappa_N [\rho_N (N - 1) (D_N - C) + B_N (1 + \rho_N \{N - 2\})] > 0, \quad (\text{S5})$$

where all terms are evaluated at the phenotypic value z of the resident population, and κ_N is a demographically scaled relatedness coefficient (Queller, 1994; Lehmann & Rousset, 2010; Van Cleve & Akçay, 2014).

This selection pressure (equation S5) captures three pathways to helping behaviour: (i) when $\rho_N = \kappa_N = 0$, it reduces to $D_N - C > 0$, (ii) when $\rho_N = D_N = 0$, we recover $\kappa_N B_N - C > 0$, and (iii) when $\kappa_N = D_N = 0$, we have $\rho_N B_N - C > 0$. These are the three invasion conditions in the main text. More generally, equation S5 shows that there can be interactions between reciprocity and spatial or family structure when both ρ_N and κ_N are non-zero (when $N = 2$, equation S5 is analogous to equation 5 of Lehmann & Keller 2006).

Appendix S2: Marginal returns of helping

(1) Group productivity

Here, we express the marginal costs, C , and benefits, D_N and B_N , in terms of marginal changes to group productivity. To that end, we write group productivity as $g(a_f, a_1, \dots, a_{N-1})$ and assume that this function is invariant under the permutation of the actions of all group members (i.e. $\partial f_N / \partial a_f = \partial f_N / \partial a_j$ are equal for all $j = 1, 2, \dots, N$, and consequently $\partial g / \partial a_f = \partial g / \partial a_j$ are equal for all $j = 1, 2, \dots, N$). Because we assume that group members are undifferentiated, then it is standard to assume that each group member receives an equal share of the productivity of its group (e.g. Williams & Williams, 1957; Wilson, 1975; Wade, 1979; Nunney, 1985; Taylor, 1992; Boyd *et al.*, 2003; Gardner & West, 2006). We can then write the fecundity of the focal individual as

$$f_N(a_f, a_1, \dots, a_{N-1}) = \frac{g(a_f, a_1, \dots, a_{N-1})}{N} - C a_f. \quad (\text{S6})$$

Then from equation S2, the marginal direct benefit to an individual of investing into helping is

$$D_N = \frac{1}{N} \cdot \frac{\partial g(a_f, a_1, \dots, a_{N-1})}{\partial a_f}, \quad (\text{S7})$$

and where all derivatives throughout are evaluated at $a_f = a_1 = \dots = a_{N-1} = a$. This is the actor's share of the marginal increase in group productivity that its investment into helping produces. Similarly, from equation S3 and the permutation invariance of group productivity, the marginal effect of the focal individual's help on the rest of the group (excluding itself) is

$$\begin{aligned} B_N &= \frac{N-1}{N} \cdot \frac{\partial g(a_f, a_1, \dots, a_{N-1})}{\partial a_f} \\ &= (N-1)D_N. \end{aligned} \quad (\text{S8})$$

We will now consider explicit examples of the group production function, and for simplicity we make a standard assumption that this function depends only on the total investment

into helping of all group members (Sumpter, 2010, chapter 10), which we can write as $\bar{a}N$, where \bar{a} is the average investment into helping by individuals in the focal group:

$$\bar{a} = \frac{1}{N} \sum_{j \in \{f, 1, \dots, N-1\}} a_j. \quad (\text{S9})$$

According to this assumption $g(a_f, a_1, \dots, a_{N-1}) = g(\bar{a}N)$. Note that we can graph group productivity as a function of N by taking \bar{a} as a constant. We define the marginal product of helping, M_N , as

$$M_N = \frac{\partial g(\bar{a}N)}{\partial \bar{a}}, \quad (\text{S10})$$

that is, how group productivity changes with respect to the investment into helping of the average group member. Since $\partial g(\bar{a}N) / \partial a_f = [\partial g(\bar{a}N) / \partial \bar{a}] \times [\partial \bar{a} / \partial a_f] = [\partial g(\bar{a}N) / \partial \bar{a}] / N$, we have that

$$D_N = \frac{M_N}{N}. \quad (\text{S11})$$

(2) Contest success functions

A general way to model how group productivity changes with respect to total investment into helping $\bar{a}N$, and hence with group size, is to use the concept of a contest success function (Hirshleifer, 1989). This models a “contest” between the individuals in the focal group against another entity. We can consider two types of contest: a contest against “nature” or the environment, and a contest against another group of individuals. We will consider both in turn.

(a) Contests against nature

Although a contest success function can take several forms, one type commonly used in economics is the additive form (Skaperdas, 1996), in which the amount of resource obtained (or the probability of obtaining the resource) depends upon the relative strength of both entities involved in the contest (Hirshleifer, 1989). This gives the following production

function for group productivity when the contest is against nature

$$g(\bar{a}N) = \frac{F(\bar{a}N)}{F(\bar{a}N) + \beta}, \quad (\text{S12})$$

where the function F maps investment into helping of group members into “strength” (or ability to solve a problem) and β is the strength of the environment. That is, it controls how much total investment into helping is required to reach a given group productivity, and so represents the degree of hostility of the environment. Substituting equation S12 into equation S10 yields the following expression for the marginal product of investing into helping:

$$M_N = \frac{\partial g(\bar{a}N)}{\partial \bar{a}} = \frac{\beta}{[F(\bar{a}N) + \beta]^2} \frac{\partial F(\bar{a}N)}{\partial \bar{a}}. \quad (\text{S13})$$

To evaluate the marginal product explicitly we need an explicit expression for F . A standard form for the contest success function is to take $F(x) = x^\gamma$, where the parameter γ measures the decisiveness of increasing investment into helping in “defeating” the environment (Hirshleifer, 1989). Then, group productivity, evaluated at $\bar{a} = a$ is

$$g(aN) = \frac{(aN)^\gamma}{(aN)^\gamma + \beta}. \quad (\text{S14})$$

The marginal product of helping, evaluated at $a_f = a_1 = \dots = a_{N-1} = \bar{a} = a$, is given by substitution into equation S13:

$$M_N = \frac{(aN)^{\gamma-1} \beta \gamma}{[(aN)^\gamma + \beta]^2}. \quad (\text{S15})$$

The direct benefit to helping, D_N (equation S7), evaluated at $a_f = a_1 = \dots = a_{N-1} = \bar{a} = a$ is then

$$D_N = \frac{a (aN)^{\gamma-2} \beta \gamma}{[(aN)^\gamma + \beta]^2}. \quad (\text{S16})$$

A necessary condition for this to increase with group size is that $\gamma > 2$. This means that there must be a range where group productivity increases by more than the square of total investment into helping. The marginal benefit given to other group members from helping, B_N , evaluated at $a_f = a_1 = \dots = a_{N-1} = \bar{a} = a$, is given by substitution into equation S8:

$$B_N = \frac{a(N-1)(aN)^{\gamma-2} \beta \gamma}{[(aN)^\gamma + \beta]^2}. \quad (\text{S17})$$

For $\beta = 1 - (aN)^\gamma$, the production function reduces to $g(aN) = (aN)^\gamma$. Then if $\gamma = 1$, production is linear with investment into helping across all group sizes (Fig. 1A), in which case D_N (Fig. 1C) corresponds to the selection pressure on helping under a linear public goods game or N -player Prisoner's Dilemma. If $\gamma < 1$, the production function increases less than linearly (the production function is concave), and so displays decreasing marginal returns across all group sizes (Fig. 1). This produces results that correspond to an N -player Snowdrift game [although in the classic formulation of the Snowdrift game it is the cost rather than the benefit function that decreases with total investment into helping (Zheng *et al.*, 2007), but both cases can produce a coexistence of helpers and non-helpers Archetti & Scheuring, 2012)]. Finally, if $\gamma > 1$ then group productivity continues to increase with investment into helping without limit, such that there are increasing marginal returns across all group sizes. This results in two stable equilibria, with either zero or full investment into helping (Motro, 1991). However, because of the law of diminishing marginal returns, unbounded increasing returns is not biologically plausible.

When $\beta > 0$ and $\gamma > 1$, the production function can take sigmoidal shapes (Fig. 2A). Situations where the marginal returns of helping follow a sigmoidal function as given in equation S12 have been modelled as a Volunteer's Dilemma game (Motro, 1991; Archetti & Scheuring, 2011). In the most basic version of this model, a threshold number of helpers are required in order to produce any benefit, but once produced this benefit does not increase with the addition of extra helpers. This can lead to a stable coexistence of helpers and non-helpers. However, sigmoidal benefits can make the invasion of helping more difficult, since a certain number of helpers must be present before direct benefits select for helping, i.e. before $D_N - C > 0$ is satisfied (compare Fig. 2C with Fig. 1C). This same threshold problem is also faced by the origin of punishment, or by the origin of helping under conformity-biased social learning in cultural evolution models.

(b) Contests against other groups

We can obtain from equation S12 a contest success function that gives the probability that the focal group wins a war against another group by setting the strength of environment to

$$\beta = F(N\bar{a}_o), \tag{S18}$$

where \bar{a}_o is the average investment into helping by individuals of the other group (assumed to be of the same size). In this case, F maps investment into helping into combat strength, i.e., it increases a group's chances of winning the contest, and relative combat strength determines group productivity.

One could use as before $F(x) = x^\gamma$, which when substituted into equations S12–S18 means that the probability of winning the war depends upon the *ratio* of the two groups' investments into helping. Another form is $F(x) = \exp(\gamma x)$, so that contest success depends upon the *difference* between the groups' investments into helping (Hirshleifer, 1989; Cant, 2012). This results in increasing marginal returns right up until the point that both groups invest equally, and means that a small increase in investment into helping can produce a large increase in the probability of victory.

If the losing group is completely destroyed and repopulated by the winning group and all group members contribute equally to this repopulation (as per e.g. Boyd *et al.*, 2003; Bowles, Choi & Hopfensitz, 2003; Bowles & Gintis, 2004; Choi & Bowles, 2007; Lehmann, Feldman & Foster, 2008; García & van den Bergh, 2011; Lehmann, 2011), then an individual's share of group productivity may become independent of N . This is because the losing group effectively yields N breeding slots to the winning group. Consequently, the fecundity of an individual is given by $f_N(a_f, a_1, \dots, a_{N-1}) = g(a_f, a_1, \dots, a_{N-1}) - Ca_f$ (instead of g being divided by N as in equation S6). An alternative scenario is that the losing group cedes a proportion of its resources to the winning group, in which case an individual's share of this resource will decrease with the size of its group, giving the fecundity function in equation S6.

We can compute the benefits to helping in these four cases by calculating $\partial f_N / \partial a_f$ (by

using equation S18 in equation S12 and evaluating the derivatives at $a_f = a_1 = \dots = a_{N-1} = \bar{a}_o = a$). Under the ratio form with whole-group replacement, then D_N is proportional to $1/N$ [and B_N to $(N-1)/N$], while without whole-group replacement D_N is proportional to $1/N^2$ [and B_N to $(N-1)/N^2$]. However, under the difference form with whole-group replacement, we have $D_N = \gamma/4$, which is a constant [while $B_N = (N-1)\gamma/4$]. This means that the direct benefit of helping is independent of group size in such a case, and so helping can potentially evolve in very large groups (Lehmann, 2011). On the other hand, under the difference form *without* whole-group replacement, the direct benefit is proportional to $1/N$ and so rapidly decreases with group size.

Appendix S3: Assortation coefficients

We here exemplify how both the response coefficient ρ_N , and the relatedness coefficient r_N , decrease hyperbolically with group size.

(1) Responsiveness under generalised reciprocity

Generalised reciprocity is the least cognitively demanding form of reciprocity, since individuals condition their behaviour only on what happened to them in their previous interaction, without regard to who that interaction was with. Nevertheless, even in this case the responsiveness of individuals must decrease with group size. This in turn means that selection pressure favouring reciprocal helping must decrease with group size, even in this most simplest form of reciprocity.

To see this, we can consider the following simple model of generalised reciprocity, which is a particular instance of the general model described in Appendix S1. Individuals have an evolving phenotypic trait, z , which represents the gradient of a linear response slope to their partner's action. We consider invasion of a focal mutant individual with rare phenotype z_f into a population monomorphic for phenotype z_n . Individuals live in randomly formed

groups of size N . We write fecundity at the equilibrium of the behavioural dynamics as

$$f(z_f, z_n) = 1 + Ba_n - Ca_f, \quad (\text{S19})$$

where a_f is the equilibrium investment into helping of the mutant focal individual, and a_n the equilibrium investment into helping of its partner. The helping actions of generalised reciprocators are determined as follows

$$\begin{aligned} a_f(h+1) &= \alpha + z_f a_n(h), \\ a_n(h+1) &= \alpha + z_n \left(\frac{1}{N-1} a_f(h) + \frac{N-2}{N-1} a_n(h) \right), \end{aligned} \quad (\text{S20})$$

where $h = 1, 2, 3, \dots$ is the number of rounds of interactions, α is a constant baseline investment into helping, and where we solve for the equilibrium to substitute into equation S19.

In order to compute the response slope ρ_N , we note that from equation S4 we can write for this model

$$\rho_N = \frac{\partial a_n}{\partial z_f} \bigg/ \frac{\partial a_f}{\partial z_f} = \frac{\partial a_n}{\partial a_f} \quad (\text{S21})$$

(Van Cleve & Akçay, 2014). Computing the last derivative by using the steady solution of equation S20 for the actions, which we evaluate at $z_f = z_n = z$, yields

$$\rho_N = \frac{z}{N(1-z) + 2z - 1}. \quad (\text{S22})$$

This thus decreases very rapidly with group size under generalised reciprocity (Fig. 3), and is positive only if $z > 0$. For example, if $z = 0.5$, then in a group of size two an individual will return half the investment of its partner. However, if the group size increases to 20 then an individual will return only one twentieth of it. This occurs because the benefit of an act of helping has to pass through a chain of recipients to return to the actor, and the length of this chain is proportional to group size. The conclusion is that although generalised reciprocity escapes the cognitive demands of other forms of reciprocity, the selection pressure favouring reciprocal helping nevertheless decreases rapidly with group size.

(2) Relatedness under limited dispersal

Relatedness measures the effect of limited dispersal (which can arise from spatial or network structure, for example) on genetic variance. It is calculated from the probability that a pair of genes sampled from two different individuals in a subpopulation are identical by descent. Here, we show how to perform this calculation in Wright's infinite island model (Wright, 1931). The principles, however, apply to all other forms of population structure, and to other life cycles, such as those with overlapping generations.

Consider a population of haploid individuals that live in an infinite number of discrete groups of size N . Each adult asexually produces a very large number of juveniles. Each juvenile remains philopatric with probability $1 - m$, or disperses to a random group with probability m . After dispersal, N juveniles in each group, chosen at random, survive to adulthood and reproduce, completing the life cycle.

We can calculate the probability that two gene copies, sampled from a random pair of individuals in a group, are identical by descent. In other words, the probability that two randomly sampled gene lineages share a common ancestor in the same group (coalesce). The probability that the genes of two randomly sampled adults descend from a common ancestor in the previous generation, i.e. that the individuals have the same parent, depends upon two factors. The first is that it is necessary that both adults are philopatric, i.e. that they were both born in the same group. This is because as the number of groups become large, then the probability that an immigrant and a philopatric individual (or two immigrants) descend from the same parent tends to zero. Therefore, both individuals must be philopatric if the probability of them descending from the same parent is to be non-negligible.

The second factor that determines the probability of identity-by-descent is the number of possible parents in the group in the previous generation. This is given by the group size, N . The larger the number of possible parents, the less likely that two philopatric individuals in the group will share the same one. In fact, the probability that two individuals descend from the same parent is $1/N$. This means that the probability that the gene lineages of two

individuals coalesce in an ancestor in the previous generation decreases hyperbolically with group size.

These two factors, probability of philopatry and group size, determine the probability that the gene copies in two randomly chosen individuals descend from the same parent in the previous generation. If they do not descend from the same parent, then they may nevertheless share a common ancestor in a previous generation. We can therefore apply the same logic backwards through the generations, leading to the following recursion for relatedness:

$$r_N(t+1) = (1-m)^2 \left[\frac{1}{N} + \left(1 - \frac{1}{N}\right) r_N(t) \right]. \quad (\text{S23})$$

The term $(1-m)^2$ is the probability that the two individuals are both philopatric. They must both be philopatric if they are to share a common ancestor back through the generations. Given that they are both philopatric, the probability that they share a common ancestor directly in the previous generation is $1/N$. If they do not, which occurs with probability $(1 - \frac{1}{N})$, then the probability they share a common ancestor in the generation before this (i.e. two generations ago) is given by $r_N(t)$.

We can solve this recursion for $r_N(t+1) = r_N(t) = r_N$ to give the following equation for relatedness at steady state:

$$r_N = \frac{(1-m)^2}{1 + m(2-m)(N-1)}. \quad (\text{S24})$$

This shows that relatedness decreases with both group size and migration rate. Although this example is specific it illustrates a very general feature that follows from the laws of genetic inheritance (Rousset, 2004), which in turn entails that the scaled relatedness coefficient κ_N generally decreases very rapidly with group size (see Table 2 in Lehmann & Rousset, 2010).