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From inter-group conflict to inter-group cooperation: insights from social insects

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Abstract

Conflict between social groups is widespread, often imposing significant costs across multiple groups. The social insects make an ideal system for investigating inter-group relationships, because their interaction types span the full harming-helping continuum, from aggressive conflict, to mutual tolerance, to cooperation between spatially separate groups. Here we review inter-group conflict in the social insects, and the various means by which they reduce the costs of conflict, including individual or colony-level avoidance, ritualistic behaviours, and even group fusion. At the opposite extreme of the harming-helping continuum, social insect groups may peacefully exchange resources and thus cooperate between groups in a manner rare outside human societies. We discuss the role of population viscosity in favouring inter-group cooperation. We present a model encompassing intra- and inter-group interactions, and local and long-distance dispersal. We show that in this multi-level population structure, the increased likelihood of cooperative partners being kin is balanced by increased kin competition, such that neither cooperation (helping) nor conflict (harming) is favoured. This model provides a baseline context in which other intra- and inter-group processes act, tipping the balance towards or away from conflict. We discuss future directions for research into the ecological factors shaping the evolution of inter-group interactions.

Keywords

Class-structure, inclusive fitness, intergroup conflict, intergroup cooperation, population viscosity, social insects

Introduction

Relationships between separate social groups are typically structured around interactions that are competitive or actively hostile, and this pattern holds across a wide range of taxa, from bacteria to humans (Christensen and Radford 2018, Granato et al. 2019, De Dreu et al. 2021). In inter-group conflicts, costs are imposed by one group on one or more other groups of conspecifics (Robinson and Barker 2017); these costs can be substantial and incurred by both parties, favouring behavioural and physiological adaptations that reduce the likelihood of conflict escalation, such as changes in space use, or context-dependent affiliation with members of other groups (out-groups) (Aureli et al. 2002, Christensen and Radford 2018). In rare cases, inter-group relationships actually can switch from negative to positive, with groups engaging in active cooperation, for example by exchanging resources (Robinson and Barker 2017). The main groups in which inter-group cooperation is seen, primates and ants, are also known for extreme inter-group conflict, under certain circumstances. Here we review inter-group relationships in the social insects, covering inter-group conflict, strategies that promote inter-group tolerance, and the emergence of inter-group cooperation. We discuss the role of population viscosity in shaping intergroup relationships, from helping (cooperation) to harming (conflict) and introduce a model which provides a framework in which these relationships and their consequences can be explored. Finally, we suggest directions of future research, highlighting areas where a tight interplay between empirical and theoretical work can help clarify the nature of intergroup conflict and cooperation.

Inter-group Conflict

Highly social animals by definition exhibit high levels of within-group cooperation, and as a result, can accumulate or generate valuable resources such as stores of food (Crane 1991, Karsai and Schmickl 2019). Their very success in doing so increases the potential for inter-group conflict: large groups need to continually acquire resources for maintenance and growth, and also the resources they hold make them attractive targets to other groups, meaning that resource-driven conflict between successful groups is likely (De Dreu et al. 2020). When groups are in conflict, increased within-group cooperation is favoured, which can enable groups to increase their resources, and fuel further inter-group conflict (Reeve and Hölldobler 2007, Korb and Foster 2010). Just as in humans, conflicts between conspecific social insect colonies can involve the deaths of large numbers of participants (Mabelis 1979, Salzemann and Jaffe 1990a, Grüter et al. 2016) and, as is frequently the case in human conflicts, when social insect colonies fight, the individuals that stand to gain most from the conflict are not those engaged in front line combat. Unlike in humans, in social insects, it is the colony's reproductive individuals (often a queen or queens) who directly benefit from aggressive colony defence or the acquisition of additional resources to fuel their brood production. The workers fighting on behalf of the colony are usually daughters or sisters of the reproductive/s, and thus reap inclusive fitness benefits by promoting the interests of the colony, even if they die in the process (Hamilton 1972). This applies particularly to workers who have little scope for direct fitness gains if they survive, i.e. in species where workers are sterile, or where fertility declines with age. In the latter case, we would expect colony defence to be the province of physiologically senescent workers, and this is indeed the case across social insect taxa (Cammaerts-Tricot 1975, Porter and Jorgensen 1981, Moore et al. 1987, O'Donnell 2001, Uematsu et al. 2010, Yanagihara et al. 2018). When workers are entirely sterile, their interests align strongly with those of their reproductively active relatives: in these cases, fighting insect workers are better likened to somatic tissue of a 'superorganism' than to individual combatants.

It is appealing to draw parallels between social insect workers and human soldiers, and the impressive weaponry of many workers makes it easy to view an individual worker as a warrior. Social insect workers have stings, jaws and chemical sprays with which to repel intruders, and specialist defenders are often referred to as 'soldiers' as a result. The pitfalls of equating social insect workers and human soldiers are illustrated by attempts to apply Lanchester's laws of human warfare strategy (relating mortality to aspects of relative strength of opposing forces) to ant conflicts: across several species, outcomes do not follow, or even run counter to the Lanchester predictions (Whitehouse and Jaffe 1996, Plowes and Adams 2005, Clifton 2020). Indeed, the above examples notwithstanding, group-level combat among conspecifics is relatively rare in the social insects. The weaponry borne by social insect workers is primarily used to defend their resources (stored food and vulnerable protein-rich brood) from heterospecific predators and kleptoparasites, rather than from conspecifics (Whitehouse and Jaffe 1996, López-Incera et al. 2021). Many conspicuous colony-level conflicts are in fact attempts to withstand heterospecific robbing (Whitehouse and Jaffe 1996, Powell and Clark 2004, Cunningham et al. 2014).

Inter-group Tolerance

The contrast between the fervent aggression with which social insect colonies will defend their nests from heterospecific intruders, and the rarity of all-out conflicts with conspecifics, indicates that social insects have evolved strategies to evade costly inter-group conflicts. Groups are mutually tolerant when their members neither incur a net cost nor receive a net benefit as a result of interacting with other groups (Robinson and Barker 2017). The simplest of such tolerance strategies is avoidance. This can sometimes be achieved at the colony level. Army ants, for example, that live nomadically, actively avoid encounters with conspecific colonies (Franks and Fletcher 1983), despite their warlike name and their voracious attacks on other ant species (Hoenle et al. 2019). Other ant species relocate the colony in response to local competition, but this is usually heterospecific, not conspecific competition (McGlynn 2012). For most social insects, colony-level avoidance of conspecifics is no simple matter: depending on the level of investment in the nest and their ability to transport their brood, once established a colony may effectively be fixed in place. The consequence of this is seen in the patterns of regular spatial distribution (overdispersion) common among ants: new nests cannot thrive close to existing nests (Ryti and Case 1986, Boulay et al. 2007, Franks et al. 2007, Eyer et al. 2019).

When avoidance at the colony level is impossible, individual-level avoidance can be employed. The most familiar implementation of this approach is through the establishment of territories: static colonies cannot entirely avoid their neighbours, but can reduce the likelihood of individual members of different colonies encountering each other. A territorial strategy is particularly beneficial when the costs of fighting are high (Morrell and Kokko 2005), as is likely for stinging and biting insects, and so territories are used by many ant species (Hölldobler and Lumsden 1980, Adams 2016). Territorial boundaries may be aggressively protected to prevent encroachment by neighbouring colonies, as seen in arboreal ants *Azteca trigona* and *Oecophylla smaragdina* (Adams 1990, Newey et al. 2010), or once established, may be maintained with little aggression, through mutual avoidance of the boundary zone as in wood ants *Formica polyctena* (Mabelis 1979). Alternatively to maintaining discrete territories, ants have evolved multiple ways to coexist within apparently overlapping space. They may avoid clashes by temporally partitioning active foraging periods (Hölldobler and Lumsden 1980, Salzemann and Jaffe 1990b) or by avoiding each other's foraging trails (Hölldobler 1981, Ryti and Case 1986, Gordon 1992). Other species show context-dependent aggression, where they actively defend their nest (Uematsu *et al.* 2019) and/or valuable resources (Boulay et al. 2007) but are non-aggressive if they encounter conspecifics elsewhere in their foraging range.

In many group-living territorial species, a ‘dear enemy’ pattern can be observed, where encounters with familiar neighbours are less aggressive than those with unknown intruders (Temeles 1994). This pattern is rarely seen in ants, indeed, the opposite is more frequent. This is likely because in these central-place foragers with a relatively stable home base, encounters with members of distant colonies are rare and unlikely to represent a significant threat, whereas workers from nearby colonies are competitors who may attack, (Gordon 1989, Newey et al. 2010, Christensen and Radford 2018). An advantage of the ‘dear enemy’ behaviour is that it avoids costly contests where the outcome is predictable, but there are other ways to avoid contests without using familiarity as a heuristic. These include signalling fighting ability before engaging (Parker 1974), and many social insect species employ such behaviours to avoid encounters escalating to fights. Just as in many other animals, pre-conflict posturing is common in social insects, and intruders will frequently retreat without engaging in a fight, especially if not in their home territory (Bell and Hawkins 1974, Salzemann and Jaffe 1990a, Grüter et al. 2016). The most conspicuous example of signalling group strength is seen in ants that form lines of workers along disputed territorial boundaries, as in *Tetramorium* pavement ants and *Myrmecocystus* honeypot ants (Hölldobler 1981, Hoover et al. 2016, Adams and Plowes 2019). In the honeypot ants, these ‘fighting’ lines are ritualistic, involving aggressive postures; in the pavement ants, pushing and fighting does occur, but few fights escalate to actual injury or death. In these and other species, the number of ants available to line the contested territory border is an honest signal of colony strength, and the smaller colony may cede territory as a result (Hölldobler 1981, Adams 1990, Adams and Plowes 2019).

An approach to inter-group tolerance that falls at the opposite extreme to avoidance, is colony fusion. The fusion of genetically distinct mature social insect colonies is a rare phenomenon, but one that is seen in various termite genera (Korb and Roux 2012, Howard et al. 2013). If two similar-sized colonies encounter each other, such that one cannot simply annihilate the other, they may fuse. This is not an entirely peaceful option: usually one or more reproductives is killed, but nevertheless members of both original colonies may benefit: their increased group size makes them a superior competitive force, and workers from both colonies have the potential to develop into reproductive later (Howard et al. 2013). While there are still within-group conflicts of interest, a fused colony is now in effect a single group, and may contain reproductives from one or both original groups. Army ant colonies may also fuse, if one colony becomes queenless (Kronauer et al. 2010). Here, the queenless workers do not gain reproductive potential by fusing. Instead, this fusion is hypothesised to be driven by the low probability of success of worker reproduction in a queenless fragment being outweighed by likely inclusive fitness gains of fusing with a neighbour, who, due to population viscosity, is likely to be related (Kronauer et al. 2010).

Inter-group Cooperation

Population viscosity (local dispersal) is a common feature of social insect societies, and plays a role in the progression of some species beyond inter-group tolerance, to actively positive interactions between spatially separate stable groups. Such inter-group cooperation is characterised by the transfer of benefits from one group to one or more other groups, resulting in net benefits shared by members of the groups involved (Robinson and Barker 2017). How can such a state arise? When independent nest foundation is high risk, which it frequently is in social insects, it can be adaptive for mated queens to return to their natal nest rather than strike out alone, resulting in secondary polygyny: multiple closely related queens reproducing within a single nest (Hölldobler and Wilson 1977). Colony reproduction in such cases is often by budding, a local dispersal strategy in which a queen or queens found a new nest accompanied by workers. The combination of reduced within-nest relatedness due to multiple reproductives, and high population viscosity due to reproduction by budding, together reduces the relatedness differential between one's own and neighbouring colonies, providing conditions which favour reduction in inter-group aggression (Hamilton 1964, Hölldobler and Wilson 1977, Helanterä et al. 2009).

For some ant species, these conditions result in the establishment of cooperative social connections between the occupants of spatially distinct nests. These nests form a network connected by non-aggressive mutual exchange of workers, a phenomenon termed ‘polydomy’ (Debout et al. 2007, Robinson 2014). Within this network, inter-group cooperation in the form of resource exchange is possible, with workers, brood and food being peacefully transferred between nests (Ellis et al. 2014, Ellis and Robinson 2016). In wood ants, sharing resources between groups subsidises nest establishment and can rebalance resource heterogeneity (Ellis and Robinson 2015, Burns et al. 2020, Lecheval et al. 2021). In extreme cases, polydomous colonies become ‘unicolonial’: lacking colony boundaries within a whole population, for example as seen in the Argentine ant, *Linepithema humile* (Suarez *et al*. 2001). This status is most common in invasive species, and may result in part from reduced genetic diversity in a population arising from a single foundation event. Such huge cooperative units should be vulnerable to exploitation by cheats, for example nests that produce only reproductives and rely on the wider workforce for support. As such, they are predicted to be evolutionarily unstable (Helanterä et al. 2009). At more modest network sizes however, this form of cooperation between groups in social insects appears to be a stable and successful strategy (Robinson 2014).

Modelling inter-group relationships

Polydomous social insect colonies pose a challenge to many traditional models of social organisation and cooperation, because they comprise three levels of organisation: individuals interact within nests (their 'group') but members of these groups also interact locally with other groups through their social connections. This means that our understanding of an individual's social relationships is complete only if we look beyond what is happening in the nest and include inter-group relationships. A key influencer of these inter-group relationships is the local relatedness environment: as we have seen above, population viscosity caused by colonies reproducing through budding, can play an important role in the evolution of conflict, tolerance, and cooperation in social insects.

Hamilton (1964)—in his seminal work on inclusive fitness theory—was the first to suggest that population viscosity could be a key mechanism promoting the evolution of cooperation (helping). In viscous populations, a random neighbour is more related to the focal individual than a random individual in the population, and therefore population viscosity can even drive the evolution of indiscriminate cooperation. Because of its simplicity—unlike other mechanisms, such as kin discrimination and green-beard effects (Hamilton 1964, Gardner and West 2010)—this mechanism has the potential to drive the evolution of cooperation across a wide range of taxa. However, population viscosity can also inflate competition for resources among related individuals, a factor that works against cooperation, and instead promotes conflict (harming). In a theoretical model, Taylor (1992) showed that in the simplest case population viscosity generates relatedness among social partners—as suggested by Hamilton—but it also enhances competition among kin in such a way that population viscosity has no net effect on the evolution of cooperation (Box 1). This cancellation result has motivated a large body of work seeking to understand what ecological factors can break down the cancellation result and drive the evolution of intra-group cooperation (e.g. Taylor and Irwin 2000, Lehmann et al. 2006, Gardner and West 2006, Fernandes and Wild 2009). However, the role of different population viscosity processes in the genetic structure of multi-level societies and its consequences for the evolution of inter-group behaviour remains unclear.

Taylor’s (1992) model assumes intra-group social interactions and a single group per patch, in which each of the groups is equally spatially distant from any other group in the population, such that individuals in different groups are unrelated (Box 1). These assumptions fail to capture the genetic, ecological and demographic context of inter-group interactions in social insects. Consider for instance the case of polydomous ants, in which colonies are composed of different nests with variable number of reproductives, have variable movement between nests, variable relatedness both within and between neighbouring nests, and range in size from pairs of nests to vast unicolonial populations (Debout et al. 2007, Helanterä et al. 2009, Robinson 2014). Here, we extend Taylor’s (1992) viscous population model to study the evolution of inter-group interactions among neighbouring groups in a multi-level society, such as those seen in polydomous ants and other multi-level social systems (Grueter et al. 2020).

As in Taylor’s model, we assume that the population is subdivided into patches connected by long-distance dispersal (Figure 1 and Box 1). However, rather than assuming a single group per patch, we consider a scenario in which patches are further subdivided into different groups connected by movement of individuals among groups (i.e. short-distance dispersal), (see **Error! Reference source not found.**and Box 2 for details). Thus any focal group in the population now has close neighbouring groups—i.e. groups in the same patch—in addition to distant groups—i.e. groups located in other patches. In addition, two key processes now contribute to the genetic structure of the population: (1) long-distance dispersal, d, which is defined as the fraction of offspring that leave the local patch; and (2) short-distance dispersal, m, which is defined as the movement of offspring between groups within the same patch, such that the total fraction of offspring that remain in their native group is $(1 - d)(1 - m)$. We then perform a kin selection analyses of the evolution of intra-group behaviour (c.f. Taylor 1992), and of the evolution of inter-group behaviour, in which individuals in one group may help or harm individuals in other groups (see Electronic Supplement for details).

The first important result of our model shows that Taylor’s cancellation result for intra-group behaviour extends to the evolution of inter-group social behaviour (**Error! Reference source not found.**). Further, the cancellation result emerges independently of the level at which we consider population viscosity. That is, the intensity of selection for inter-group social behaviour remains invariant to the degree of both long-distance dispersal, d, and short-distance dispersal, m. First, we find that reduced long-distance dispersal of offspring, i.e. lower d, increases average relatedness within a patch (Figure 2d), which aligns the interests of the different groups within a patch and which favours the evolution of inter-group helping behaviour. However, reduced long-distance dispersal also increases the number of related offspring that compete locally for the same resources, which disfavours the evolution of inter-group helping. These two opposing forces cancel each other out such that reduced long-distance dispersal has no net effect on the evolution of inter-group helping and harming. Second, we find that limited movement among groups (i.e. reduced short-distance dispersal or lower *m*) within a patch leads to increased relatedness within groups but decreased relatedness among groups (Figure 2d), which reduces the costs of inter-group harming. However, limited movement among groups also reduces the fraction of offspring that obtain resources in neighbouring groups, which decreases the benefits of inter-group harming. These two opposing forces cancel each other out such that limited movement between groups within a patch does not influence the evolution of inter-group helping and harming.

Thus, while population viscosity at the patch level (i.e. lower *d*) may align the interests of all groups within a patch, population viscosity at the group level (i.e. lower *m*) may align the interest of individuals within a group, but not among groups. Both mechanisms however have no net effect on the evolution of inter-group helping and harming. On the one hand, reduced long-distance dispersal (i.e. lower *d*) increases the intensity of competition among related individuals, irrespective of the amount of short-distance dispersal, *m*. On the other hand, reduced short-distance dispersal (i.e. lower *m*) decreases between-group relatedness but it also decreases the intensity of competition among groups. These multiple opposing fitness-effects of population viscosity operating at different levels of biological organisation (both at the patch and group level), are such that they have no net effect on the evolution of helping and harming between groups.

The second key result of our model shows that population viscosity (both reduced long-distance dispersal, i.e. lower *d*, and reduced short-distance dispersal, i.e. lower *m*) has no net effect on the evolution of intra-group helping and harming in a multi-level society, and therefore we extend Taylor's cancellation result for cases in which patches contain an arbitrary number of groups. Intra-group behaviour affects both the intensity of competition for resources within the focal group and in neighbouring groups. Reduced long-distance dispersal (i.e. lower *d*) inflates relatedness within a group, but it also increases the intensity of kin competition both within the focal group and between the focal group and neighbouring groups. These two opposing forces cancel each other out such that long-distance dispersal does not impact the evolution of intra-group helping and harming. Similarly, reduced short-distance dispersal (i.e. lower *m*) increases relatedness within a group. However, it also increases the intensity of kin competition with the group. As in the previous cases, these two forces cancel each other out such that short-distance dispersal does not mediate the evolution of intra-group helping and harming in a multi-level society.

Discussion and future directions

Our review of the literature suggests that inter-group relationships in the social insects are highly diverse, including inter-group conflict, multiple strategies that promote inter-group tolerance, and cases of inter-group cooperation. We have highlighted the role of population viscosity in shaping inter-group relationships, from helping (cooperation) to neutral (tolerance) to harming (conflict), and its interaction with patterns of dispersal, and relatedness both within and between groups. While the theoretical underpinnings of the role of population viscosity in the evolution of intra-group relationships is well understood, how population viscosity mediates inter-group relationship is still relatively unclear. Here, we have introduced a model which provides a framework in which inter-group relationships and their consequences can be explored.

This modelling approach is applicable to a wide range of animal taxa, but fits particularly well with some aspects of social insect ecology. If we view a 'group' in the model as the occupants of a social insect nest, then the modelled 'individuals' represent the reproductives (usually queens). The presence of multiple reproductives is widespread among social insects and can result from 'primary polygyny' whereby two or more mated females cooperate to establish a nest, or from 'secondary polygyny' where one or more mated females join a nest that already has a reproductive present (Hölldobler and Wilson 1977). Interactions between these individuals can be negative, where one suppresses reproduction of the other (common in the later stages of primary polygyny), neutral, where reproduction is tolerated, or positive, where the resources produced by one reproductive (workers) are available to help rear the offspring of the other reproductive. This latter process is a major advantage of secondary polygyny to the newly joining reproductives. Relationships between the groups, i.e. nests, within a particular habitat patch can also cover the full range of interaction types, as discussed in the review above, from aggressive conflict, to tolerance, to active cooperation through resource sharing.

The options available to new reproductives in social insects also match well to the model options - for example in the wood ants, newly mated queens may return to their natal nest, move to a nearby nest of the same cooperative network, or disperse to a new area by flying (Sundström et al. 2005). Clearly real movement (*m*) and dispersal (*d*) processes are much more spatially heterogeneous than the specific case presented above. In cooperative networks, active trails along which local movement is possible are more likely between closer neighbours, but their nature is also shaped by the resource environment (Lecheval et al. 2021). Thus, while we assumed random movement between groups, exploring cases in which movement between some groups is more frequent than others, and how these heterogeneous patterns impact inter-group relationships deserves future analyses.

In our model, long-distance dispersal between patches is random. For many flying social insects wind-aided dispersal is somewhat undirected and can cover long distances (Markin et al. 1971, Messenger and Mullins 2005), and human-mediated jump dispersal commonly occurs in invasive ant species (Suarez et al. 2001) so the random dispersal model used here is not entirely unrealistic. In many cases, however, long-distance dispersal is more likely between nearby patches. Further model extensions will be required to analyse more complex patterns of dispersal and how these mediate inter-group interactions.

Our model assumes an individual mode of dispersal, a factor that underlies the cancellation between the kin-selected benefits and kin competition costs of inter-group helping and harming. As described above, insect societies often adopt a budding mode of dispersal, in which one or more reproductives disperse accompanied by workers to establish a new colony (Helanterä et al. 2009, Hölldobler and Wilson, 1977). Theoretical and empirical studies of viscous populations show that budding dispersal can uncouple within-group relatedness from the intensity of kin competition, such that intra-group cooperation, in single-group patches, is favoured (Gardner and West 2006, Kümmerli et al. 2009, Rodrigues and Taylor 2018). We therefore expect budding dispersal to affect patterns of inter-group conflict and cooperation. For instance, if the different groups within a patch are established through competition between unrelated buds—following multiple long-distance budding dispersal events—we expect high within-group relatedness, low between-group relatedness, and low kin competition, a combination of factors that may drive the evolution of conflict. However, if each group emerges from a single large bud after competition for patch ownership, then we expect high within and between group relatedness, and low kin competition, a combination of factors that may favour the evolution of tolerance and cooperation.

In natural populations, inter-group conflict is characterised by high cohesion, coordination and some degree of unity of purpose among group members (Reeve and Hölldobler 2007, Korb and Foster 2010, Shen and Reeve 2010). High relatedness within a group is a key factor aligning the interests across group members. Our model shows that population viscosity can increase within-group relatedness, but is in itself insufficient to promote the evolution of inter-group conflict (or cooperation). More generally, our model shows that in the simplest scenario, population viscosity processes that contribute to the genetic structure of multi-level societies do not modulate the evolution of inter-group social behaviour. From this perspective, our model can be seen as a null-model that provides a benchmark that facilitates the development of future empirical and theoretical work. What additional ecological and demographic conditions are needed to drive the evolution of within-group cooperation and between-group conflict (cooperation) is still, to some degree, unknown. Exploring how these and other factors influence the evolution of inter-group helping and harming can bring new insights into the nature of inter-group conflict.

Conclusions

Our model demonstrates the benefits of a multilevel approach for investigating between and within-group relationships. Multilevel social organisation is widespread among animals (Grueter et al. 2020), but among multilevel societies, organisational systems where groups interact with other groups without fusing into a single larger group are relatively rare. Such networks of interacting groups provide ideal conditions for investigating the ecology and evolution of inter-group processes. The social insects thus make an ideal study system for addressing these relationships, because they exhibit such a wide range of interaction types, both within and between spatially separate groups.

Authors' contributions

AMMR, JLB and EJHR conceptualized and planned the work. AMMR designed, implemented and analysed the model with input from JLB and EJHR. EJHR and AMMR wrote the paper with input from JLB. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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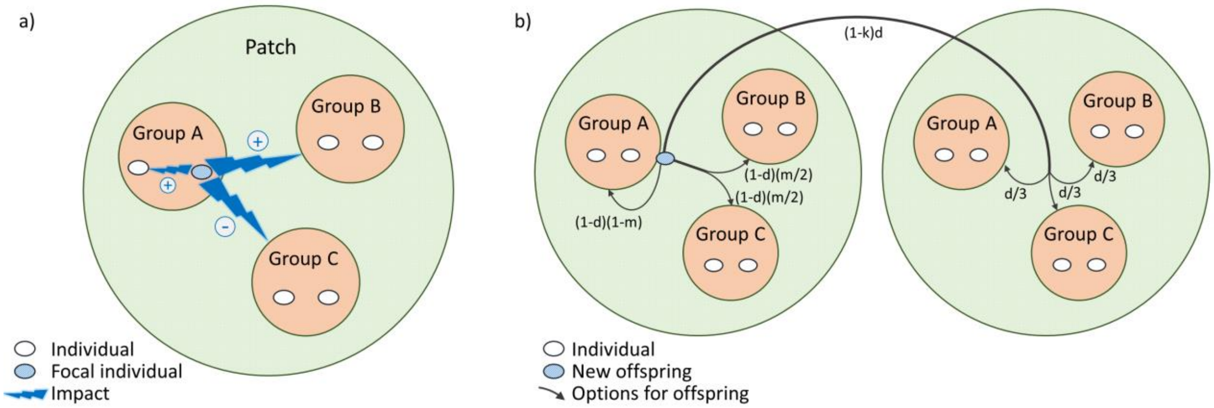

Figure 1. Conceptual schematic of model of intra- and inter-group relationships. We assume a large population composed of patches, each of which contains a fixed and equal number *N* of groups (here depicted as three). A group comprises two identical individuals (n=2). a) Each individual can have an impact on the members of its own group and on other groups within the patch. Impacts can be positive (cooperation = helping), neutral (tolerance), or negative (conflict = harming); as an example, here the individual has a positive impact on the other member of its own group and on Group B, but a negative impact on Group C. b) Offspring can stay in their own group, move (m) to another group in the same patch, or disperse (d) with long-distance dispersal-related mortality risk k, to a random group in a new patch (see Box 2 for more details).

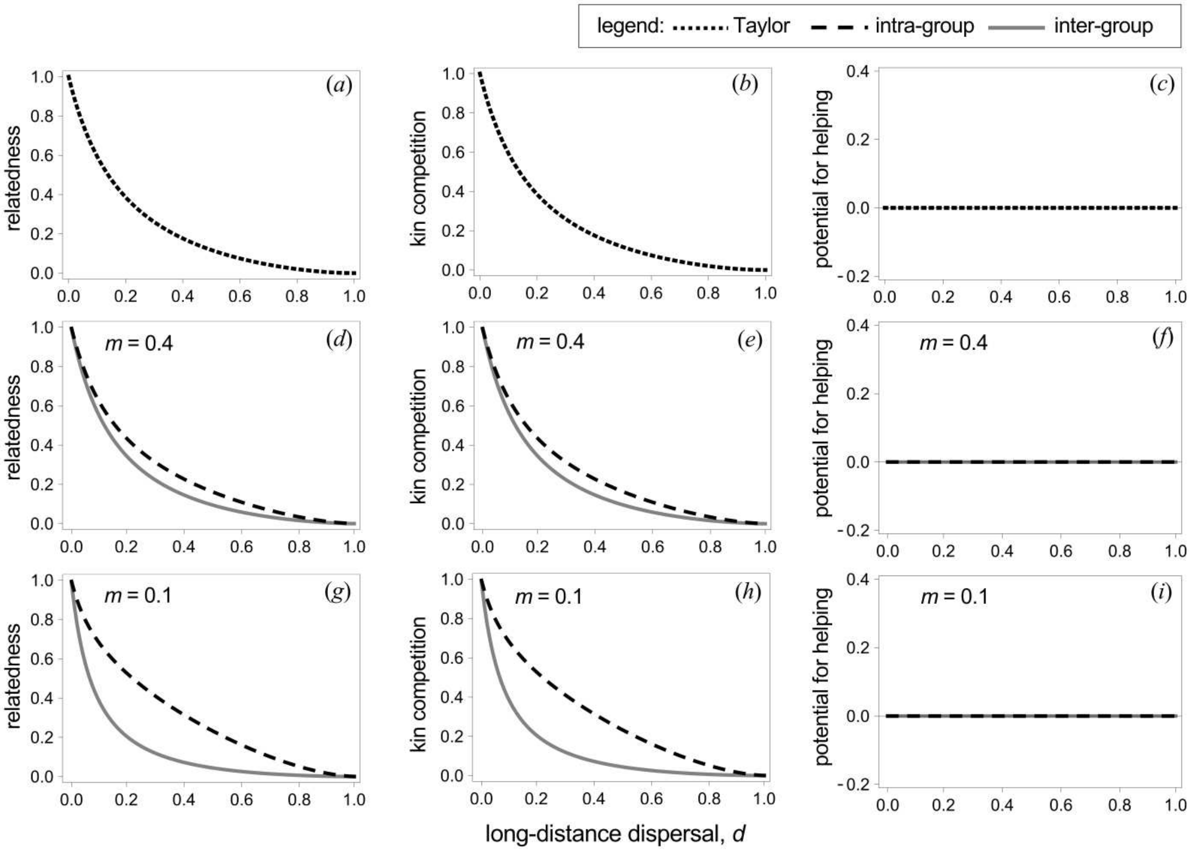

Figure 2. Relatedness, kin competition, and the potential for helping (i.e. cooperation) as a function of long-distance dispersal, *d*. (*a-c*) Taylor's cancellation result: limited dispersal increases relatedness among group members, but it also increases the intensity of competition among related individuals; these two forces cancel each other out, such that population viscosity has no net effect on the evolution of helping or harming (negative interactions, i.e. conflict). (*d-i*) Taylor's cancellation result extends to higher levels of biological organisation when individuals form groups within patches, for both intra- and inter-group helping and harming, irrespective of the amount of movement, *m*, between groups within the focal patch, where *m* is the fraction of offspring that move to a different group among those offspring that remain in the local patch, i.e. $1 - d$. This cancellation result holds irrespective of the number of individuals within each group, *n*, the number of groups within a patch, *N*, and the long-distance dispersal mortality risk, *k* (see Electronic Supplement for details). Parameter values: (*a-c*) $k = 0.5$, $n_T = 6$; (*d-i*) $k = 0.5$, $n = 2$, $N = 3$; (*d-f*) $m = 0.4$; (*g-i*) $m = 0.1$. (See Figure 1, Box 1 and Box 2 for definitions of parameters)

Box 1

Box 1. Population viscosity and intra-group conflict and cooperation

Taylor (1992) developed a formal model to study the impact of population viscosity on the evolution of cooperation, in which a focal actor pays a cost c to provide a benefit b to social partners. The model is based on Wright's (1931) infinite island model, which assumes a large population subdivided into patches connected through "long-distance" dispersal. Generations are non-overlapping and each patch contains exactly n_{T} asexually-reproducing individuals. Taylor (1992) originally used the inclusive-fitness method to analyse his model. Here, we revisit his model using the neighbour-modulated method (Taylor and Frank 1996, see Electronic Supplement for details). Each individual produces a very large number $f(x,y)$ of offspring, where x represents the focal individual's investment in helping (or harming), and y is the average investment in the local patch (excluding the focal individual), in a population with an average investment z. A fraction $1 - d$ of the offspring remain in the local patch, where they compete for the n_{T} breeding sites, while a fraction d disperse to a random patch. Dispersal carries a cost k, such that only a fraction $1 - k$ of the offspring survive dispersal. The neighbour-modulated fitness (Taylor and Frank 1996) of a focal mother is then given by

$$\omega(x,y,Y,z) = \frac{f(x,y)(1-d)}{f(Y,Y)(1-d)+f(z,z)d(1-k)} + \frac{f(x,y)d(1-k)}{f(z,z)(1-d)+f(z,z)d(1-k)}, \qquad (1)$$

where Y is the average phenotype in the focal patch (including the focal individual), and where the first term represents the fitness accrued from philopatric offspring, and the second from offspring who disperse. The selection gradient is the derivative of fitness ω with respect to breeding value g (the heritable component of the phenotype), $\mathrm{d}\omega(x,y,Y,z)/\mathrm{d}g$, evaluated at $x = y = Y = z$ (Frank & Taylor 1996).

We can express the selection gradient in terms of Hamilton's rule–which adopts the inclusive-fitness perspective (Gardner et al. 2011). This is given by

$$-c + br_{\mathrm{T}} - (b - c)\varphi_{\mathrm{T}}^{2}R_{\mathrm{T}} > 0, \tag{2}$$

where: $\varphi_{\mathrm{T}} = (1-d)/(1-kd)$ is the probability of philopatry; r_{T} is the "other-only" relatedness between social partners, which excludes the focal individual; and R_{T} the "whole-group" relatedness between social partners, which includes the focal individual (Pepper 2000). The inclusive-fitness effect identifies three selective pressures acting on helping: (1) the fertility cost c to the actor; (2) the benefit b provided to the actor's social partners; and (3) the kin competition cost due to the additional number of offspring produced in the local patch, $b - c$, that remain in the local patch and displace other related offspring. The behaviour evolves when $c/b < A_{\mathrm{T}}$, where $A_{\mathrm{T}} = (r_{\mathrm{T}}-\varphi_{\mathrm{T}}^{2}R_{\mathrm{T}})/(1-\varphi_{\mathrm{T}}^{2}R_{\mathrm{T}})$ is the potential for helping (Rodrigues and Gardner 2013). At equilibrium, relatedness is such that the potential for helping is zero, i.e. $r_{\mathrm{T}} = \varphi_{\mathrm{T}}^{2}R_{\mathrm{T}}$ and $A_{\mathrm{T}} = 0$. This recovers Taylor's cancellation result: the positive effects of population viscosity on helping, through increased relatedness, are fully offset by its negative effects, through increased kin competition.

Box 2

Box 2. Population viscosity and inter-group conflict and cooperation

Taylor's (1992) model assumes that each patch is occupied by a single group equally distant from every other group in the population, such that individuals in different groups are unrelated. Here, we extend Taylor's model by considering multiple groups per patch connected by movement of individuals among groups, where individuals in different groups, and within the same patch, may be related (Figure 1). We use the concept of "class" to model an arbitrary number of groups within each patch, with variable distance between groups and variable relatedness within and between groups. Typically, classes have been considered in relation to age (Fisher 1930, Grafen 2006) and sex (Fisher 1930, Price 1970). More generally, classes are any features of individuals—including social and natural environment—that influence their fitness, other than gene action (Rodrigues and Gardner 2021). Here, we define groups within a patch as classes, such that an individual belongs to a single group, and each group is a separate class. Each patch contains N groups and each group contains n_{j} breeding females, where the subscript j denotes the group (cf. Rodrigues and Gardner 2013a). The fertility of females in group j is f_{j}, which may vary across groups (cf. Rodrigues and Gardner 2012). As in Taylor (1992), we consider long-distance dispersal, d, between patches. However, we also consider movement between groups, such that $m_{\mathrm{j}\rightarrow\mathrm{l}}$ represents the fraction of offspring born in group j and that move to group l for offspring that remain in the local patch. Dispersed offspring compete for resources in a random group of their new patch. We consider both intra- and inter-group helping and harming. Intra-group social behaviour occurs among individuals that belong to the same group. Inter-group social behaviour occurs between individuals in different groups within the same patch. We assume that social behaviour carries a fertility cost c to the actor and a fertility benefit b to the recipients, in which the behaviour can be either helping ($b > 0$) or harming ($b < 0$). We find that when groups are homogeneous, i.e. $n_{\mathrm{j}} = n$ and $f_{\mathrm{j}} = f$, and the movement of offspring to other groups is random, i.e. $m_{\mathrm{j}\rightarrow\mathrm{k}} = m$ ($j \neq k$), the inclusive-fitness effect of the behaviour is zero, for both intra-group and inter-group behaviour (see Electronic Supplement for details). Thus, Taylor's cancellation result extends to cases in which patches contain more than one homogenous group per patch and random movement between groups, for both intra- and inter-group social behaviours.