

This is a repository copy of *From inter-group conflict to inter-group cooperation: insights from social insects*.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/182920/>

Version: Accepted Version

Article:

Rodrigues, Antonio M M, Barker, Jessica and Robinson, Elva Joan Hilda orcid.org/0000-0003-4914-9327 (2022) *From inter-group conflict to inter-group cooperation: insights from social insects*. *Philosophical Transactions of the Royal Society B: Biological Sciences*. ISSN 1471-2970

<https://doi.org/10.1098/rstb.2021.0466>

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

1 Author Accepted Manuscript DOI: 10.1098/rstb.2021.466
2 Philosophical Transactions of the Royal Society B - Biological Sciences Special issue
3 “Intergroup Conflict: Origins, Dynamics and Consequences across Taxa”, 2022.

4

5 From inter-group conflict to inter-group cooperation: insights from 6 social insects

7

8 António M. M. Rodrigues^{1*}, Jessica L. Barker², Elva J. H. Robinson^{3*}

9

10 1. Department of Ecology & Evolutionary Biology, Yale University, New Haven, US. antonio.rodrigues@yale.edu

11 2. Interacting Minds Centre, Aarhus University, Denmark; Alaska Department of Health & Social Services, US

12 3. Department of Biology, University of York, UK. elva.robinson@york.ac.uk

13 * To whom correspondence should be addressed

14 Abstract

15

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

30

31 Keywords

32

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

34 insects

35 Introduction

36

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

54

55 Inter-group Conflict

56

57 Highly social animals by definition exhibit high levels of within-group cooperation, and as a
58 result, can accumulate or generate valuable resources such as stores of food (Crane 1991, Karsai and
59 Schmickl 2019). Their very success in doing so increases the potential for inter-group conflict: large
60 groups need to continually acquire resources for maintenance and growth, and also the resources they
61 hold make them attractive targets to other groups, meaning that resource-driven conflict between
62 successful groups is likely (De Dreu et al. 2020). When groups are in conflict, increased within-group
63 cooperation is favoured, which can enable groups to increase their resources, and fuel further inter-group
64 conflict (Reeve and Hölldobler 2007, Korb and Foster 2010). Just as in humans, conflicts between
65 conspecific social insect colonies can involve the deaths of large numbers of participants (Mabelis 1979,

66 Salzemann and Jaffe 1990a, Grüter et al. 2016) and, as is frequently the case in human conflicts, when
67 social insect colonies fight, the individuals that stand to gain most from the conflict are not those engaged
68 in front line combat. Unlike in humans, in social insects, it is the colony's reproductive individuals (often
69 a queen or queens) who directly benefit from aggressive colony defence or the acquisition of additional
70 resources to fuel their brood production. The workers fighting on behalf of the colony are usually
71 daughters or sisters of the reproductive/s, and thus reap inclusive fitness benefits by promoting the
72 interests of the colony, even if they die in the process (Hamilton 1972). This applies particularly to
73 workers who have little scope for direct fitness gains if they survive, i.e. in species where workers are
74 sterile, or where fertility declines with age. In the latter case, we would expect colony defence to be the
75 province of physiologically senescent workers, and this is indeed the case across social insect taxa
76 (Cammaerts-Tricot 1975, Porter and Jorgensen 1981, Moore et al. 1987, O'Donnell 2001, Uematsu et al.
77 2010, Yanagihara et al. 2018). When workers are entirely sterile, their interests align strongly with those
78 of their reproductively active relatives: in these cases, fighting insect workers are better likened to somatic
79 tissue of a 'superorganism' than to individual combatants.

80
81 It is appealing to draw parallels between social insect workers and human soldiers, and the
82 impressive weaponry of many workers makes it easy to view an individual worker as a warrior. Social
83 insect workers have stings, jaws and chemical sprays with which to repel intruders, and specialist
84 defenders are often referred to as 'soldiers' as a result. The pitfalls of equating social insect workers and
85 human soldiers are illustrated by attempts to apply Lanchester's laws of human warfare strategy (relating
86 mortality to aspects of relative strength of opposing forces) to ant conflicts: across several species,
87 outcomes do not follow, or even run counter to the Lanchester predictions (Whitehouse and Jaffe 1996,
88 Plowes and Adams 2005, Clifton 2020). Indeed, the above examples notwithstanding, group-level combat
89 among conspecifics is relatively rare in the social insects. The weaponry borne by social insect workers is
90 primarily used to defend their resources (stored food and vulnerable protein-rich brood) from
91 heterospecific predators and kleptoparasites, rather than from conspecifics (Whitehouse and Jaffe 1996,
92 López-Incera et al. 2021). Many conspicuous colony-level conflicts are in fact attempts to withstand
93 heterospecific robbing (Whitehouse and Jaffe 1996, Powell and Clark 2004, Cunningham et al. 2014).

94

95 Inter-group Tolerance

96

97 The contrast between the fervent aggression with which social insect colonies will defend their nests from
98 heterospecific intruders, and the rarity of all-out conflicts with conspecifics, indicates that social insects
99 have evolved strategies to evade costly inter-group conflicts. Groups are mutually tolerant when their
100 members neither incur a net cost nor receive a net benefit as a result of interacting with other groups
101 (Robinson and Barker 2017). The simplest of such tolerance strategies is avoidance. This can sometimes
102 be achieved at the colony level. Army ants, for example, that live nomadically, actively avoid encounters
103 with conspecific colonies (Franks and Fletcher 1983), despite their warlike name and their voracious
104 attacks on other ant species (Hoenle et al. 2019). Other ant species relocate the colony in response to local
105 competition, but this is usually heterospecific, not conspecific competition (McGlynn 2012). For most
106 social insects, colony-level avoidance of conspecifics is no simple matter: depending on the level of
107 investment in the nest and their ability to transport their brood, once established a colony may effectively
108 be fixed in place. The consequence of this is seen in the patterns of regular spatial distribution
109 (overdispersion) common among ants: new nests cannot thrive close to existing nests (Ryti and Case
110 1986, Boulay et al. 2007, Franks et al. 2007, Eyer et al. 2019).

111

112 When avoidance at the colony level is impossible, individual-level avoidance can be employed.
113 The most familiar implementation of this approach is through the establishment of territories: static
114 colonies cannot entirely avoid their neighbours, but can reduce the likelihood of individual members of
115 different colonies encountering each other. A territorial strategy is particularly beneficial when the costs
116 of fighting are high (Morrell and Kokko 2005), as is likely for stinging and biting insects, and so
117 territories are used by many ant species (Hölldobler and Lumsden 1980, Adams 2016). Territorial
118 boundaries may be aggressively protected to prevent encroachment by neighbouring colonies, as seen in
119 arboreal ants *Azteca trigona* and *Oecophylla smaragdina* (Adams 1990, Newey et al. 2010), or once
120 established, may be maintained with little aggression, through mutual avoidance of the boundary zone as
121 in wood ants *Formica polyctena* (Mabelis 1979). Alternatively to maintaining discrete territories, ants
122 have evolved multiple ways to coexist within apparently overlapping space. They may avoid clashes by
123 temporally partitioning active foraging periods (Hölldobler and Lumsden 1980, Salzemann and Jaffe
124 1990b) or by avoiding each other's foraging trails (Hölldobler 1981, Ryti and Case 1986, Gordon 1992).
125 Other species show context-dependent aggression, where they actively defend their nest (Uematsu *et al.*
126 2019) and/or valuable resources (Boulay et al. 2007) but are non-aggressive if they encounter
127 conspecifics elsewhere in their foraging range.

128

129 In many group-living territorial species, a ‘dear enemy’ pattern can be observed, where
130 encounters with familiar neighbours are less aggressive than those with unknown intruders (Temeles
131 1994). This pattern is rarely seen in ants, indeed, the opposite is more frequent. This is likely because in
132 these central-place foragers with a relatively stable home base, encounters with members of distant
133 colonies are rare and unlikely to represent a significant threat, whereas workers from nearby colonies are
134 competitors who may attack, (Gordon 1989, Newey et al. 2010, Christensen and Radford 2018). An
135 advantage of the ‘dear enemy’ behaviour is that it avoids costly contests where the outcome is
136 predictable, but there are other ways to avoid contests without using familiarity as a heuristic. These
137 include signalling fighting ability before engaging (Parker 1974), and many social insect species employ
138 such behaviours to avoid encounters escalating to fights. Just as in many other animals, pre-conflict
139 posturing is common in social insects, and intruders will frequently retreat without engaging in a fight,
140 especially if not in their home territory (Bell and Hawkins 1974, Salzemann and Jaffe 1990a, Grüter et al.
141 2016). The most conspicuous example of signalling group strength is seen in ants that form lines of
142 workers along disputed territorial boundaries, as in *Tetramorium* pavement ants and *Myrmecocystus*
143 honeypot ants (Hölldobler 1981, Hoover et al. 2016, Adams and Plowes 2019). In the honeypot ants,
144 these ‘fighting’ lines are ritualistic, involving aggressive postures; in the pavement ants, pushing and
145 fighting does occur, but few fights escalate to actual injury or death. In these and other species, the
146 number of ants available to line the contested territory border is an honest signal of colony strength, and
147 the smaller colony may cede territory as a result (Hölldobler 1981, Adams 1990, Adams and Plowes
148 2019).

149

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

161 worker reproduction in a queenless fragment being outweighed by likely inclusive fitness gains of fusing
162 with a neighbour, who, due to population viscosity, is likely to be related (Kronauer et al. 2010).

163

164

165 Inter-group Cooperation

166

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

180

181 For some ant species, these conditions result in the establishment of cooperative social connections
182 between the occupants of spatially distinct nests. These nests form a network connected by non-
183 aggressive mutual exchange of workers, a phenomenon termed 'polydomy' (Debout et al. 2007, Robinson
184 2014). Within this network, inter-group cooperation in the form of resource exchange is possible, with
185 workers, brood and food being peacefully transferred between nests (Ellis et al. 2014, Ellis and Robinson
186 2016). In wood ants, sharing resources between groups subsidises nest establishment and can rebalance
187 resource heterogeneity (Ellis and Robinson 2015, Burns et al. 2020, Lecheval et al. 2021). In extreme
188 cases, polydomous colonies become 'unicolonial': lacking colony boundaries within a whole population,
189 for example as seen in the Argentine ant, *Linepithema humile* (Suarez et al. 2001). This status is most
190 common in invasive species, and may result in part from reduced genetic diversity in a population arising
191 from a single foundation event. Such huge cooperative units should be vulnerable to exploitation by
192 cheats, for example nests that produce only reproductives and rely on the wider workforce for support. As

193 such, they are predicted to be evolutionarily unstable (Helanterä et al. 2009). At more modest network
194 sizes however, this form of cooperation between groups in social insects appears to be a stable and
195 successful strategy (Robinson 2014).

196

197 **Modelling inter-group relationships**

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

206

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

223

224 Taylor's (1992) model assumes intra-group social interactions and a single group per patch, in
225 which each of the groups is equally spatially distant from any other group in the population, such that
226 individuals in different groups are unrelated (Box 1). These assumptions fail to capture the genetic,
227 ecological and demographic context of inter-group interactions in social insects. Consider for instance the
228 case of polydomous ants, in which colonies are composed of different nests with variable number of
229 reproductives, have variable movement between nests, variable relatedness both within and between
230 neighbouring nests, and range in size from pairs of nests to vast unicolonial populations (Debout et al.
231 2007, Helanterä et al. 2009, Robinson 2014). Here, we extend Taylor's (1992) viscous population model
232 to study the evolution of inter-group interactions among neighbouring groups in a multi-level society,
233 such as those seen in polydomous ants and other multi-level social systems (Grueter et al. 2020).

234
235 As in Taylor's model, we assume that the population is subdivided into patches connected by
236 long-distance dispersal (Figure 1 and Box 1). However, rather than assuming a single group per patch, we
237 consider a scenario in which patches are further subdivided into different groups connected by movement
238 of individuals among groups (i.e. short-distance dispersal), (see **Error! Reference source not found.**and
239 Box 2 for details). Thus any focal group in the population now has close neighbouring groups—i.e.
240 groups in the same patch—in addition to distant groups—i.e. groups located in other patches. In addition,
241 two key processes now contribute to the genetic structure of the population: (1) long-distance dispersal, d ,
242 which is defined as the fraction of offspring that leave the local patch; and (2) short-distance dispersal, m ,
243 which is defined as the movement of offspring between groups within the same patch, such that the total
244 fraction of offspring that remain in their native group is $(1 - d)(1 - m)$. We then perform a kin selection
245 analyses of the evolution of intra-group behaviour (c.f. Taylor 1992), and of the evolution of inter-group
246 behaviour, in which individuals in one group may help or harm individuals in other groups (see Electronic
247 Supplement for details).

248
249 The first important result of our model shows that Taylor's cancellation result for intra-group
250 behaviour extends to the evolution of inter-group social behaviour (**Error! Reference source not**
251 **found.**). Further, the cancellation result emerges independently of the level at which we consider
252 population viscosity. That is, the intensity of selection for inter-group social behaviour remains invariant
253 to the degree of both long-distance dispersal, d , and short-distance dispersal, m . First, we find that
254 reduced long-distance dispersal of offspring, i.e. lower d , increases average relatedness within a patch
255 (Figure 2d), which aligns the interests of the different groups within a patch and which favours the
256 evolution of inter-group helping behaviour. However, reduced long-distance dispersal also increases the
257 number of related offspring that compete locally for the same resources, which disfavors the evolution of

258 inter-group helping. These two opposing forces cancel each other out such that reduced long-distance
259 dispersal has no net effect on the evolution of inter-group helping and harming. Second, we find that
260 limited movement among groups (i.e. reduced short-distance dispersal or lower m) within a patch leads to
261 increased relatedness within groups but decreased relatedness among groups (Figure 2d), which reduces
262 the costs of inter-group harming. However, limited movement among groups also reduces the fraction of
263 offspring that obtain resources in neighbouring groups, which decreases the benefits of inter-group
264 harming. These two opposing forces cancel each other out such that limited movement between groups
265 within a patch does not influence the evolution of inter-group helping and harming.

266

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

277

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

291

292 Discussion and future directions

293

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

303

304 This modelling approach is applicable to a wide range of animal taxa, but fits particularly well
305 with some aspects of social insect ecology. If we view a ‘group’ in the model as the occupants of a social
306 insect nest, then the modelled ‘individuals’ represent the reproductives (usually queens). The presence of
307 multiple reproductives is widespread among social insects and can result from ‘primary polygyny’
308 whereby two or more mated females cooperate to establish a nest, or from ‘secondary polygyny’ where
309 one or more mated females join a nest that already has a reproductive present (Hölldobler and Wilson
310 1977). Interactions between these individuals can be negative, where one suppresses reproduction of the
311 other (common in the later stages of primary polygyny), neutral, where reproduction is tolerated, or
312 positive, where the resources produced by one reproductive (workers) are available to help rear the
313 offspring of the other reproductive. This latter process is a major advantage of secondary polygyny to the
314 newly joining reproductives. Relationships between the groups, i.e. nests, within a particular habitat patch
315 can also cover the full range of interaction types, as discussed in the review above, from aggressive
316 conflict, to tolerance, to active cooperation through resource sharing.

317

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

325 movement between some groups is more frequent than others, and how these heterogeneous patterns
326 impact inter-group relationships deserves future analyses.

327

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

334

335 Our model assumes an individual mode of dispersal, a factor that underlies the cancellation
336 between the kin-selected benefits and kin competition costs of inter-group helping and harming. As
337 described above, insect societies often adopt a budding mode of dispersal, in which one or more
338 reproductives disperse accompanied by workers to establish a new colony (Helanterä et al. 2009,
339 Hölldobler and Wilson, 1977). Theoretical and empirical studies of viscous populations show that
340 budding dispersal can uncouple within-group relatedness from the intensity of kin competition, such that
341 intra-group cooperation, in single-group patches, is favoured (Gardner and West 2006, Kümmerli et al.
342 2009, Rodrigues and Taylor 2018). We therefore expect budding dispersal to affect patterns of inter-group
343 conflict and cooperation. For instance, if the different groups within a patch are established through
344 competition between unrelated buds—following multiple long-distance budding dispersal events—we
345 expect high within-group relatedness, low between-group relatedness, and low kin competition, a
346 combination of factors that may drive the evolution of conflict. However, if each group emerges from a
347 single large bud after competition for patch ownership, then we expect high within and between group
348 relatedness, and low kin competition, a combination of factors that may favour the evolution of tolerance
349 and cooperation.

350

351 In natural populations, inter-group conflict is characterised by high cohesion, coordination and
352 some degree of unity of purpose among group members (Reeve and Hölldobler 2007, Korb and Foster
353 2010, Shen and Reeve 2010). High relatedness within a group is a key factor aligning the interests across
354 group members. Our model shows that population viscosity can increase within-group relatedness, but is
355 in itself insufficient to promote the evolution of inter-group conflict (or cooperation). More generally, our
356 model shows that in the simplest scenario, population viscosity processes that contribute to the genetic
357 structure of multi-level societies do not modulate the evolution of inter-group social behaviour. From this
358 perspective, our model can be seen as a null-model that provides a benchmark that facilitates the

359 development of future empirical and theoretical work. What additional ecological and demographic
360 conditions are needed to drive the evolution of within-group cooperation and between-group conflict
361 (cooperation) is still, to some degree, unknown. Exploring how these and other factors influence the
362 evolution of inter-group helping and harming can bring new insights into the nature of inter-group
363 conflict.

364

365 Conclusions

366 Our model demonstrates the benefits of a multilevel approach for investigating between and
367 within-group relationships. Multilevel social organisation is widespread among animals (Grueter et al.
368 2020), but among multilevel societies, organisational systems where groups interact with other groups
369 without fusing into a single larger group are relatively rare. Such networks of interacting groups provide
370 ideal conditions for investigating the ecology and evolution of inter-group processes. The social insects
371 thus make an ideal study system for addressing these relationships, because they exhibit such a wide
372 range of interaction types, both within and between spatially separate groups.

373

374

375 Authors' contributions

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

380

381

382 References

383 Adams, E. S. (1990). "Boundary disputes in the territorial ant *Azteca trigona*: effects of asymmetries in
384 colony size." *Animal Behaviour* 39(2): 321-328.

385 Adams, E. S. and N. J. R. Plowes (2019). "Self-organizing conflicts: Group assessment and the spatio-
386 temporal dynamics of ant territory battles." *Behavioural processes* 162: 119-129.

387 Adams, E. S. (2016). "Territoriality in ants (Hymenoptera: Formicidae): a review." *Myrmecological*
388 *News* 23 101-118.

389 Aureli, F., M. Cords and C. P. Van Schaik (2002). "Conflict resolution following aggression in gregarious
390 animals: a predictive framework." *Animal Behaviour* 64(3): 325-343.

391 Bell, W. J. and W. A. Hawkins (1974). "Patterns of intraspecific agonistic interactions involved in nest
392 defense of a primitively eusocial halictine bee." *Journal of Comparative Physiology* 93(3): 183-193.

393 Boulay, R., X. Cerdá, T. Simon, M. Roldan and A. Hefetz (2007). "Intraspecific competition in the ant
394 *Camponotus cruentatus*: should we expect the 'dear enemy' effect?" *Animal Behaviour* 74(4): 985-993.

395 Burns, D. D. R., D. W. Franks, C. L. Parr and E. J. H. Robinson (2020). "Ant colony nest networks adapt
396 to resource disruption." *Journal of Animal Ecology* 90: 143-152

397 Cammaerts-Tricot, M. C. (1975). "Ontogenesis of defence reactions in workers of *Myrmica rubra* L
398 (Hymenoptera-Formicidae)." *Animal Behaviour* 23: 124-130.

399 Christensen, C. and A. N. Radford (2018). "Dear enemies or nasty neighbors? Causes and consequences
400 of variation in the responses of group-living species to territorial intrusions." *Behavioral Ecology* 29(5):
401 1004-1013.

402 Clifton, E. (2020). "A brief review on the application of Lanchester's models of combat in nonhuman
403 animals." *Ecological Psychology* 32(4): 181-191.

404 Crane, E. (1991). "Honey from honeybees and other insects." *Ethology Ecology and Evolution* 3(sup1):
405 100-105.

406 Cunningham, J. P., J. P. Hereward, T. A. Heard, P. J. De Barro and S. A. West (2014). "Bees at war:
407 interspecific battles and nest usurpation in stingless bees." *The American Naturalist* 184(6): 777-786.

408 De Dreu, C. K. W., A. Fariña, J. Gross and A. Romano (2021). "Pro-sociality as a foundation for
409 intergroup conflict." *Current Opinion in Psychology*.

410 De Dreu, C. K. W., J. Gross, A. Fariña and Y. Ma (2020). "Group cooperation, carrying-capacity stress,
411 and intergroup conflict." *Trends in Cognitive Sciences*.

412 Debout, G., B. Schatz, M. Elias and D. McKey (2007). "Polydomy in ants: what we know, what we think
413 we know, and what remains to be done." *Biological Journal of the Linnean Society* 90(2): 319-348.

414 Ellis, S., D. W. Franks and E. J. H. Robinson (2014). "Resource redistribution in polydomous ant nest
415 networks: local or global?" *Behavioral Ecology* 25(5): 1183-1191.

416 Ellis, S. and E. J. H. Robinson (2015). "The role of non-foraging nests in polydomous wood ant colonies."
417 *PLoS One* 10(10): e0138321.

418 Ellis, S. and E. J. H. Robinson (2016). "Inter-nest food sharing in wood ant colonies: resource
419 redistribution behavior in a complex system." *Behavioral Ecology* 27(2): 660-668

420 Eyer, P.-A., E. M. Espinoza, A. J. Blumenfeld and E. L. Vargo (2019). "The underdog invader: Breeding
421 system and colony genetic structure of the dark rover ant (*Brachymyrmex patagonicus* Mayr)." *Ecology*
422 *and Evolution* 10(1): 493-505.

423 Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*, Clarendon Press.

424 Franks, N. R., A. Dornhaus, G. Hitchcock, R. Guillem, J. Hooper and C. Webb (2007). "Avoidance of
425 conspecific colonies during nest choice by ants." *Animal Behaviour* 73(3): 525-534.

426 Franks, N. R. and C. R. Fletcher (1983). "Spatial patterns in army ant foraging and migration: *Eciton*
427 *burchelli* on Barro Colorado Island, Panama." Behavioral Ecology and Sociobiology 12(4): 261-270.

428 Gardner, A. and S. A. West (2006). "Demography, altruism, and the benefits of budding." Journal of
429 Evolutionary Biology 19(5): 1707-1716.

430 Gardner, A. and S. A. West (2010). "Greenbeards." Evolution 64(1): 25-38

431 Gardner, A., S. A. West and G. Wild (2011). "The genetical theory of kin selection." Journal of
432 Evolutionary Biology 24(5): 1020-1043.

433 Gordon, D. M. (1989). "Ants distinguish neighbors from strangers." Oecologia 81(2): 198-200.

434 Gordon, D. (1992). "How colony growth affects forager intrusion in neighbouring harvester ant colonies."
435 Behavioral Ecology and Sociobiology 31: 417-427.

436 Grafen, A. (2006). "A theory of Fisher's reproductive value." Journal of Mathematical Biology 53(1): 15-
437 60.

438 Granato, E. T., T. A. Meiller-Legrand and K. R. Foster (2019). "The evolution and ecology of bacterial
439 warfare." Current Biology 29(11): R521-R537.

440 Grueter, C. C., X. Qi, D. Zinner, T. Bergman, M. Li, Z. Xiang, P. Zhu, A. B. Migliano, A. Miller, M.
441 Krützen, J. Fischer, D. I. Rubenstein, T. N. C. Vidya, B. Li, M. Cantor and L. Swedell (2020). "Multilevel
442 organisation of animal sociality." Trends in Ecology and Evolution 35(9): 834-847.

443 Grüter, C., L. G. Von Zuben, F. H. I. D. Segers and J. P. Cunningham (2016b). "Warfare in stingless
444 bees." Insectes Sociaux 63(2): 223-236.

445 Hamilton, W. D. (1964). "The genetical evolution of social behaviour." Journal of Theoretical Biology
446 7(1): 17-52.

447 Hamilton, W. D. (1972). "Altruism and related phenomena, mainly in social insects." Annual Review of
448 Ecology and systematics 3(1): 193-232.

449 Helanterä, H., J. E. Strassman, J. Carrillo and D. C. Queller (2009). "Unicolonial ants: where do they
450 come from, what are they and where are they going?" Trends in Ecology and Evolution 24(6): 341-349.

451 Hoenle, P. O., N. Blüthgen, A. Brückner, D. J. C. Kronauer, B. Fiala, D. A. Donoso, M. A. Smith, B.
452 Ospina Jara and C. von Beeren (2019). "Species-level predation network uncovers high prey specificity in
453 a Neotropical army ant community." Molecular Ecology 28(9): 2423-2440.

454 Hölldobler, B. (1981). "Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus*
455 Wheeler (Hymenoptera: Formicidae)." Behavioral Ecology and Sociobiology 9(4): 301-314.

456 Hölldobler, B. and C. J. Lumsden (1980). "Territorial strategies in ants." Science 210: 732-739.

457 Hölldobler, B. and E. O. Wilson (1977). "The number of queens: an important trait in ant evolution."
458 Naturwissenschaften 64: 8-15.

459 Hoover, K. M., A. N. Bubak, I. J. Law, J. D. W. Yaeger, K. J. Renner, J. G. Swallow and M. J. Greene
460 (2016). "The organization of societal conflicts by pavement ants *Tetramorium caespitum*: an agent-based
461 model of amine-mediated decision making." Current Zoology 62(3): 277-284.

462 Howard, K. J., P. M. Johns, N. L. Breisch and B. L. Thorne (2013). "Frequent colony fusions provide
463 opportunities for helpers to become reproductives in the termite *Zootermopsis nevadensis*." Behavioral
464 Ecology and Sociobiology 67(10): 1575-1585.

465 Karsai, I. and T. Schmickl (2019). Social Stomach. Encyclopedia of Social Insects. C. Starr. Cham,
466 Springer International Publishing: 1-4.

467 Korb, J. and K. R. Foster (2010). "Ecological competition favours cooperation in termite societies."
468 Ecology Letters 13(6): 754-760.

469 Korb, J. and E. A. Roux (2012). "Why join a neighbour: fitness consequences of colony fusions in
470 termites." Journal of Evolutionary Biology 25(11): 2161-2170.

471 Kronauer, D. J. C., C. Schöning, P. d'Ettorre and J. J. Boomsma (2010). "Colony fusion and worker
472 reproduction after queen loss in army ants." Proceedings of the Royal Society B: Biological Sciences
473 277(1682): 755-763.

474 Kümmerli, R., A. Gardner, S. A. West and A. S. Griffin (2009). "Limited dispersal, budding dispersal,
475 and cooperation: an experimental study." Evolution 63(4): 939-949

476 Lecheval, V., H. Larson, D. D. Burns, S. Ellis, S. Powell, M. C. Donaldson-Matasci and E. J. H.
477 Robinson (2021). "From foraging trails to transport networks: how the quality-distance trade-off shapes
478 network structure." Proceedings of the Royal Society B: Biological Sciences 288(1949).

479 López-Incera, A., M. Nouvian, K. Ried, T. Müller and H. J. Briegel (2021). "Honeybee communication
480 during collective defence is shaped by predation." BMC Biology 19(1): 1-16.

481 Mabelis, A. A. (1979). "Wood ant wars. The relationship between aggression and predation in the red
482 wood ant (*Formica polyctena* Först)." Netherlands Journal of Zoology 29(4): 451-620.

483 Markin, G. P., J. H. Dillier, S. O. Hill, M. S. Blum and H. R. Hermann (1971). "Nuptial flight and flight
484 ranges of the imported fire ant, *Solenopsis saevissima richteri* (Hymenoptera: Formicidae)." Journal of
485 the Georgia Entomological Society 6(3): 145-156.

486 McGlynn, T. P. (2012). "The ecology of nest movement in social insects." Annual Review of Entomology
487 57: 291-308.

488 Messenger, M. T. and A. J. Mullins (2005). "New flight distance recorded for *Coptotermes formosanus*
489 (Isoptera: Rhinotermitidae)." Florida Entomologist 88(1): 99-100.

490 Moore, A. J., M. D. Breed and M. J. Moore (1987). "The guard honey bee: ontogeny and behavioural
491 variability of workers performing a specialized task." Animal Behaviour 35: 1159-1167.

492 Morrell, L. J. and H. Kokko (2005). "Bridging the gap between mechanistic and adaptive explanations of
493 territory formation." Behavioral Ecology and Sociobiology 57(4): 381-390.

494 Newey, P. S., S. K. A. Robson and R. H. Crozier (2010). "Weaver ants *Oecophylla smaragdina* encounter
495 nasty neighbors rather than dear enemies." Ecology 91(8): 2366-2372.

496 O'Donnell, S. (2001). "Worker age, ovary development, and temporal polyethism in the swarm-founding
497 wasp *Polybia occidentalis* (Hymenoptera: Vespidae)." Journal of Insect Behavior 14(2): 201-213.

498 Parker, G. A. (1974). "Assessment strategy and the evolution of fighting behaviour." Journal of
499 Theoretical Biology 47(1): 223-243.

500 Pepper, J. W. (2000). "Relatedness in trait group models of social evolution." *Journal of Theoretical*
501 *Biology* 206(3): 355-368.

502 Plowes, N. J. R. and E. S. Adams (2005). "An empirical test of Lanchester's square law: mortality during
503 battles of the fire ant *Solenopsis invicta*." *Proceedings of the Royal Society B: Biological Sciences*
504 272(1574): 1809-1814.

505 Porter, S. D. and C. D. Jorgensen (1981). "Foragers of the harvester ant, *Pogonomyrmex owyheei* - a
506 disposable caste?" *Behavioral Ecology and Sociobiology* 9(4): 247-256.

507 Powell, S. and E. Clark (2004). "Combat between large derived societies: a subterranean army ant
508 established as a predator of mature leaf-cutting ant colonies." *Insectes Sociaux* 51(4): 342-351.

509 Price, G. R. (1970). "Selection and covariance." *Nature* 227: 520-521.

510 Reeve, H. K. and B. Hölldobler (2007). "The emergence of a superorganism through intergroup
511 competition." *Proceedings of the National Academy of Sciences* 104(23): 9736-9740.

512 Robinson, E. J. H. (2014). "Polydomy: the organisation and adaptive function of complex nest systems in
513 ants." *Current Opinion in Insect Science* 5: 37-43.

514 Robinson, E. J. H. and J. L. Barker (2017). "Inter-group cooperation in humans and other animals."
515 *Biology Letters* 13: 20160793.

516 Rodrigues, A. M. M. and A. Gardner (2013a). "Evolution of helping and harming in heterogeneous
517 groups." *Evolution* 67(8): 2284-2298.

518 Rodrigues, A. M. M. and A. Gardner (2013b). "Evolution of helping and harming in viscous populations
519 when group size varies." *The American Naturalist* 181(5): 609-622.

520 Rodrigues, A. M. M. and A. Gardner (2021). "Reproductive value and the evolution of altruism." *Trends*
521 *in Ecology and Evolution online early*. DOI: 10.1016/j.tree.2021.11.007

522 Rodrigues, A. M. M. and T. B. Taylor (2018). "Ecological and demographic correlates of cooperation
523 from individual to budding dispersal." *Journal of Evolutionary Biology* 31(7): 1058-1070.

524 Ryti, R. T. and T. J. Case (1986). "Overdispersion of ant colonies: a test of hypotheses." *Oecologia* 69(3):
525 446-453.

526 Salzemann, A. and K. Jaffe (1990a). "On the territorial behaviour of field colonies of the leaf-cutting ant
527 *Atta laevigata* (Hymenoptera: Myrmicinae)." *Journal of Insect Physiology* 36(2): 133-138.

528 Salzemann, A. and K. Jaffe (1990b). *Territorial ecology of the leaf-cutting ant, Atta laevigata* (Fr. Smith)
529 Hymenoptera: Myrmicinae. Boulder, Westview Press.

530 Shen, S.-F. and H. K. Reeve (2010). "Reproductive skew theory unified: The general bordered tug-of-war
531 model." *Journal of Theoretical Biology* 263(1): 1-12

532 Suarez, A. V., D. A. Holway and T. J. Case (2001). "Patterns of spread in biological invasions dominated
533 by long-distance jump dispersal: insights from Argentine ants." *Proceedings of the National Academy of*
534 *Sciences* 98: 1095-1100.

535 Sundström, L., P. Seppä and P. Pamilo (2005). Genetic population structure and dispersal patterns in
536 *Formica* ants—a review. *Annales Zoologici Fennici*, 163-177

537 Taylor, P. D. (1992). "Altruism in viscous populations - an inclusive fitness model." *Evolutionary*
538 *Ecology* 6(4): 352-356.

539 Taylor PD, Frank SA. (1996). "How to make a kin selection model." *Journal of Theoretical Biology*. 180,
540 27-37.

541 Taylor PD, Irwin AJ. (2000). "Overlapping generations can promote altruistic behavior." *Evolution* 54(4),
542 1135-1141.

543 Temeles, E. J. (1994). "The role of neighbours in territorial systems: when are they 'dear enemies'?"
544 *Animal Behaviour* 47(2): 339-350.

545 Uematsu, K., M. Kutsukake, T. Fukatsu, M. Shimada and H. Shibao (2010). "Altruistic colony defense by
546 menopausal female insects." *Current Biology* 20(13): 1182-1186.

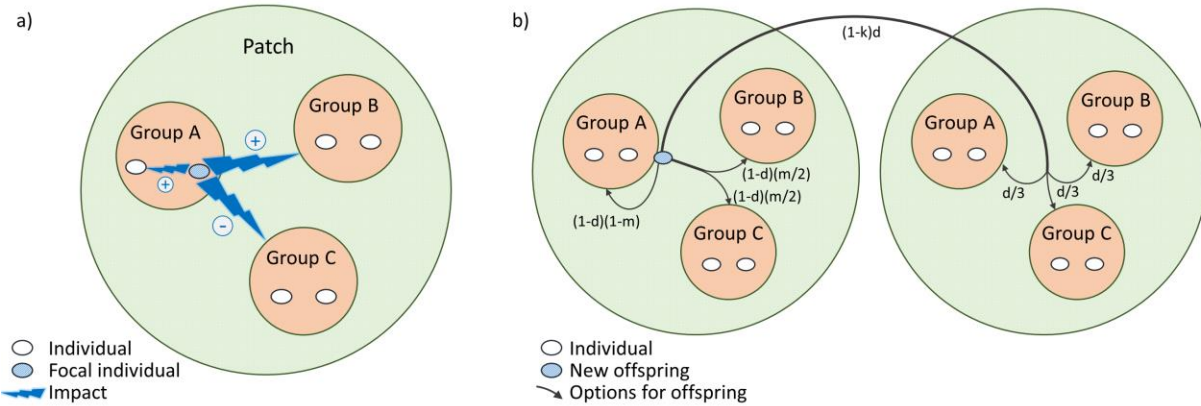
547 Uematsu, J., M. Hayashi, H. Shimoji, M.-O. Laurent Salazar and K. Tsuji (2019). "Context-dependent
548 aggression toward non-nestmates in the ant *Diacamma* sp. from Japan." *Journal of Ethology* 37(3): 259-
549 264.

550 Whitehouse, M. E. A. and K. Jaffe (1996). "Ant wars: combat strategies, territory and nest defence in the
551 leaf-cutting ant *Atta laevigata*." *Animal Behaviour* 51(6): 1207-1217.

552 Wright, S. (1931). "Evolution in Mendelian populations." *Genetics* 16(2): 97.

553 Yanagihara, S., W. Suehiro, Y. Mitaka and K. Matsuura (2018). "Age-based soldier polyethism: old
554 termite soldiers take more risks than young soldiers." *Biology Letters* 14(3): 20180025

555



556

557

558

559

560

561

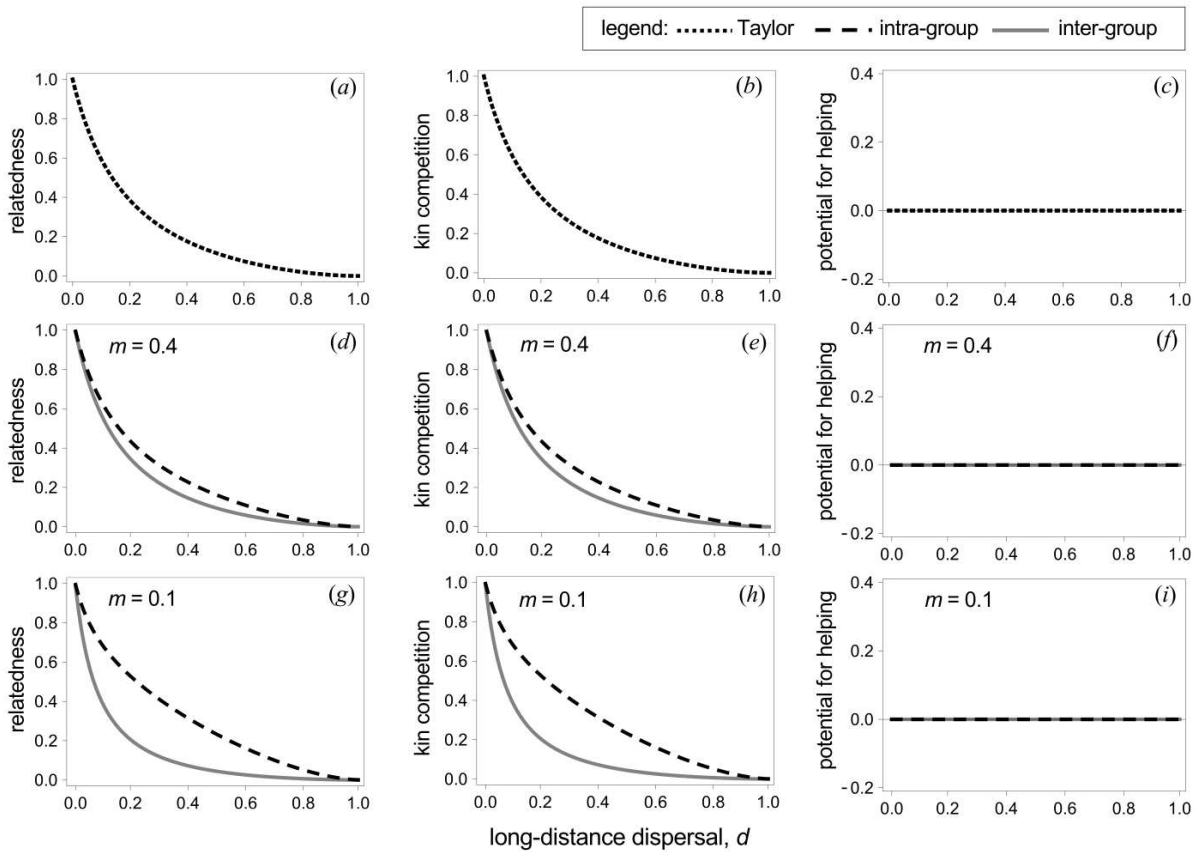
562

563

564

565

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).



566

567 **Figure 2.** Relatedness, kin competition, and the potential for helping (i.e. cooperation) as a function of
 568 long-distance dispersal, d . (a-c) Taylor's cancellation result: limited dispersal increases relatedness
 569 among group members, but it also increases the intensity of competition among related individuals; these
 570 two forces cancel each other out, such that population viscosity has no net effect on the evolution of
 571 helping or harming (negative interactions, i.e. conflict). (d-i) Taylor's cancellation result extends to higher
 572 levels of biological organisation when individuals form groups within patches, for both intra- and inter-
 573 group helping and harming, irrespective of the amount of movement, m , between groups within the focal
 574 patch, where m is the fraction of offspring that move to a different group among those offspring that
 575 remain in the local patch, i.e. $1 - d$. This cancellation result holds irrespective of the number of
 576 individuals within each group, n , the number of groups within a patch, N , and the long-distance dispersal
 577 mortality risk, k (see Electronic Supplement for details). Parameter values: (a-c) $k = 0.5$, $n_T = 6$; (d-i) $k =$
 578 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
 579 parameters)

580

581 **Box 1**

582

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

584

585 Taylor (1992) developed a formal model to study the impact of population viscosity on the evolution of
586 cooperation, in which a focal actor pays a cost c to provide a benefit b to social partners. The model is
587 based on Wright's (1931) infinite island model, which assumes a large population subdivided into patches
588 connected through "long-distance" dispersal. Generations are non-overlapping and each patch contains
589 exactly n_T asexually-reproducing individuals. Taylor (1992) originally used the inclusive-fitness method
590 to analyse his model. Here, we revisit his model using the neighbour-modulated method (Taylor and
591 Frank 1996, see Electronic Supplement for details). Each individual produces a very large number $f(x,y)$
592 of offspring, where x represents the focal individual's investment in helping (or harming), and y is the
593 average investment in the local patch (excluding the focal individual), in a population with an average
594 investment z . A fraction $1 - d$ of the offspring remain in the local patch, where they compete for the n_T
595 breeding sites, while a fraction d disperse to a random patch. Dispersal carries a cost k , such that only a
596 fraction $1 - k$ of the offspring survive dispersal. The neighbour-modulated fitness (Taylor and Frank 1996)
597 of a focal mother is then given by

598

599
$$\omega(x, y, Y, z) = \frac{f(x,y)(1-d)}{f(Y,Y)(1-d)+f(z,z)d(1-k)} + \frac{f(x,y)d(1-k)}{f(z,z)(1-d)+f(z,z)d(1-k)}, \quad (1)$$

600

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

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

607

$$608 \quad -c + br_T - (b - c)\varphi_T^2 R_T > 0, \quad (2)$$

609

610 where: $\varphi_T = (1-d)/(1-kd)$ is the probability of philopatry; r_T is the “other-only” relatedness between social
611 partners, which excludes the focal individual; and R_T the “whole-group” relatedness between social
612 partners, which includes the focal individual (Pepper 2000). The inclusive-fitness effect identifies three
613 selective pressures acting on helping: (1) the fertility cost c to the actor; (2) the benefit b provided to the
614 actor’s social partners; and (3) the kin competition cost due to the additional number of offspring
615 produced in the local patch, $b - c$, that remain in the local patch and displace other related offspring. The
616 behaviour evolves when $c/b < A_T$, where $A_T = (r_T - \varphi_T^2 R_T)/(1 - \varphi_T^2 R_T)$ is the potential for helping (Rodrigues
617 and Gardner 2013). At equilibrium, relatedness is such that the potential for helping is zero, i.e. $r_T = \varphi_T^2 R_T$
618 and $A_T = 0$. This recovers Taylor’s cancellation result: the positive effects of population viscosity on
619 helping, through increased relatedness, are fully offset by its negative effects, through increased kin
620 competition.

621

622 Box 2

623

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

625

626 Taylor’s (1992) model assumes that each patch is occupied by a single group equally distant from every
627 other group in the population, such that individuals in different groups are unrelated. Here, we extend
628 Taylor’s model by considering multiple groups per patch connected by movement of individuals among
629 groups, where individuals in different groups, and within the same patch, may be related (Figure 1). We

630 use the concept of “class” to model an arbitrary number of groups within each patch, with variable
631 distance between groups and variable relatedness within and between groups. Typically, classes have
632 been considered in relation to age (Fisher 1930, Grafen 2006) and sex (Fisher 1930, Price 1970). More
633 generally, classes are any features of individuals—including social and natural environment—that
634 influence their fitness, other than gene action (Rodrigues and Gardner 2021). Here, we define groups
635 within a patch as classes, such that an individual belongs to a single group, and each group is a separate
636 class. Each patch contains N groups and each group contains n_j breeding females, where the subscript j
637 denotes the group (cf. Rodrigues and Gardner 2013a). The fertility of females in group j is f_j , which may
638 vary across groups (cf. Rodrigues and Gardner 2012). As in Taylor (1992), we consider long-distance
639 dispersal, d , between patches. However, we also consider movement between groups, such that $m_{j \rightarrow l}$
640 represents the fraction of offspring born in group j and that move to group l for offspring that remain in
641 the local patch. Dispersed offspring compete for resources in a random group of their new patch. We
642 consider both intra- and inter-group helping and harming. Intra-group social behaviour occurs among
643 individuals that belong to the same group. Inter-group social behaviour occurs between individuals in
644 different groups within the same patch. We assume that social behaviour carries a fertility cost c to the
645 actor and a fertility benefit b to the recipients, in which the behaviour can be either helping ($b > 0$) or
646 harming ($b < 0$). We find that when groups are homogeneous, i.e. $n_j = n$ and $f_j = f$, and the movement of
647 offspring to other groups is random, i.e. $m_{j \rightarrow k} = m$ ($j \neq k$), the inclusive-fitness effect of the behaviour is
648 zero, for both intra-group and inter-group behaviour (see Electronic Supplement for details). Thus,
649 Taylor’s cancellation result extends to cases in which patches contain more than one homogenous group
650 per patch and random movement between groups, for both intra- and inter-group social behaviours.