



Ten recent insights for our understanding of cooperation

Stuart A. West  , Guy A. Cooper, Melanie B. Ghoull and Ashleigh S. Griffin 

Since Hamilton published his seminal papers in 1964, our understanding of the importance of cooperation for life on Earth has evolved beyond recognition. Early research was focused on altruism in the social insects, where the problem of cooperation was easy to see. In more recent years, research into cooperation has expanded across the entire tree of life, and has been revolutionized by advances in genetic, microbiological and analytical techniques. We highlight ten insights that have arisen from these advances, which have illuminated generalizations across different taxa, making the world simpler to explain. Furthermore, progress in these areas has opened up numerous new problems to solve, suggesting exciting directions for future research.

Complex life is built by cooperation. Genes cooperate to produce organisms, cells cooperate to produce multicellular organisms and multicellular animals cooperate to form complex social groups¹. This cooperation poses an evolutionary problem. Cooperation provides a benefit to other individuals, and so, all else being equal, should reduce the relative fitness of individuals that cooperate².

From a theoretical perspective, the evolutionary problem of ‘why cooperate?’ has long been solved^{3–5}. Inclusive fitness theory showed how cooperation can be favoured when it provides either a direct benefit to the individual performing the cooperation, or an indirect benefit to their relatives^{2,6} (kin selection; Box 1).

The major outstanding problem is not to explain ‘why cooperate?’ at an abstract level, but rather to explain the distribution and diversity of cooperation across the natural world. Research has started to address this problem by asking more precise or nuanced questions. For example, how can we explain why only some species cooperate, the amount that particular individuals cooperate, or sex differences in cooperation (Box 2)?

Methodological and analytical advances have revolutionized how we study cooperation. Genetic manipulations have been used to identify and manipulate cooperation in bacteria and other microorganisms⁷. Genomic analyses have elucidated mechanisms of cooperation, identified new forms of cooperation and revealed social dynamics in natural populations^{8–10}. Analytical advances have allowed cross-species comparative studies to better investigate evolutionary causality, and phylogenetically based meta-analyses^{11–13}.

Taxonomically, the study of cooperation has expanded across the tree of life (Fig. 1). Major insights have arisen from previously neglected groups of animals, such as termites, beetles and shrimps^{14–17}. Research on cooperation in microorganisms has exploded, following the demonstration of cooperation in slime moulds, bacteria and viruses^{7,14–16}. This contrasts with the situation only 15 years ago, when the suggestion of cooperation in bacteria could cause a microbiologist to spit out their drink.

Our aim is to examine the impact of these recent advances in how we study cooperation. What biological insights have they provided? In addition, while we clearly know more about particular species, can we also identify big picture generalities?

Ten recent insights

We focus on identifying the main insights over approximately the past 15 years of research on cooperation. We focus on this time period because there has been a revolution in how we study cooperation. Inclusive fitness has provided a unifying framework for studying all forms of cooperation across the tree of life (Box 1). Methodological advances have allowed us to study cooperation in species and ways where this was not previously possible. The advantage of examining cooperation, with a single framework, across the entire tree of life, is that we can move from anecdotes of what happens in particular species to identifying general patterns. Progress prior to the past 15 years is reviewed elsewhere^{1,3–5,17–19}.

Insights 1–7

Our first seven insights are about the factors that favour cooperation, and how organisms respond to their variation.

1. Relatedness and broad generalizations. Inclusive fitness theory shows how cooperation can be favoured by kin selection if it is directed towards relatives, who carry the gene for cooperation (relatives²; Box 1). But how widespread is the importance of kin selection? And if it is important, how do we explain variation between individuals in the level of cooperation, or explain why cooperation is favoured in some species and not others?

Recent research has shown that the relatedness (R) between interacting individuals has a clear and consistent influence on the evolution of cooperation, with both theory and data suggesting that the same factors play analogous roles at all levels of biology, from simple replicators and viruses, to complex animal groups (see below; Supplementary Tables 1 and 2). When relatedness is higher, individuals are more likely to cooperate, and cooperate at greater levels. This role of relatedness has been demonstrated with a combination of methodologies, including observational, experimental, experimental evolution, across-species comparisons and genomic.

1a. Group formation. Consistent with kin selection favouring cooperation, there is considerable evidence that population structure and how groups form is a major determinant of whether cooperation is favoured² (Fig. 2). Cooperation is more likely when group formation leads to a relatively high relatedness.

Box 1 | Inclusive fitness and why cooperate?

A behaviour or trait is cooperative if it provides a benefit for another individual, and has evolved at least partially because of this benefit. Inclusive fitness theory provides two broad categories of theoretical explanation for cooperation: direct fitness benefits and indirect fitness benefits (kin selection)^{3–5}.

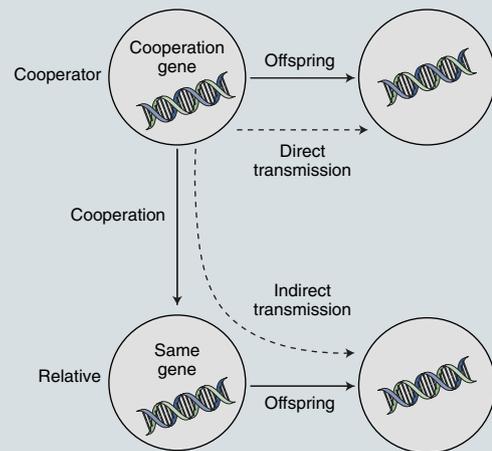
Direct fitness benefits arise when cooperation increases the reproductive success of the actor that performs the cooperation^{6,142}. In such a case, cooperation is ‘mutually beneficial’, benefiting both the actor and the recipient¹⁷. Direct benefits could arise as a simple consequence of cooperation. For example, the fitness of a symbiont could depend on host reproduction, favouring cooperation with its host. Alternatively, direct benefits may depend on mechanisms that enforce cooperation, such as rewarding cooperators, or punishing non-cooperators.

Indirect benefits arise when cooperation is directed towards other individuals that carry the gene for cooperation². This is usually termed ‘kin selection’ because the simplest and most common way this could occur is if cooperation is directed at relatives that share genes from a common ancestor. Genes don’t care where copies in future generations come from—so copies in the offspring of relatives are equally as valuable as copies in direct descendants. Indirect benefits provide the only possible explanation for altruism: cooperative behaviours that are costly to the actor and beneficial to the recipient.

These explanations for cooperation are encapsulated in a simple way by Hamilton’s rule, which states that a behaviour or trait will be favoured by selection when $RB - C > 0$, where C is the fitness cost to the actor in terms of number of offspring, B is the fitness benefit to the recipient, and R is the genetic relatedness of the recipient to the actor^{2,210}. Indirect fitness benefits can explain cooperation when the benefits to the recipient, weighted by relatedness (BR), outweigh the costs to the actor (C). Direct benefits can explain cooperation when the actor gains a direct benefit (C is negative).

The advantage of applying inclusive fitness to understand adaptations such as cooperation is that it has three complementary

properties²¹¹. First, it provides a method for calculating the direction and potential endpoints of evolution^{2,212}. Second, it provides a property that we expect natural selection to evolve towards maximizing^{2,213}. This provides a clear and simple link from evolutionary gene dynamics to the behaviour of individuals, and facilitates the identification of conflicts between individuals²¹⁴. Third, it emphasizes the special importance of common ancestry (kinship), because it leads to appreciable relatedness across the entire genome^{180,211}. This unites the interest of genes across the genome, allowing complex multi-gene social adaptations to be constructed.



Direct benefits and kin selection. A gene can influence its transmission to the next generation by influencing the reproductive success of the individual carrier (direct), or by influencing the reproductive success of other individuals that carry copies (indirect). Hamilton’s rule provides an elegantly simple way of formalizing this².

- (1) Individuals are more cooperative in species where social groups form by staying together (with kin), compared with species where social groups form by aggregation (with potential non-kin), across a range of taxa, including bacteria, fungi, slime moulds, insects and birds^{19–23}.
- (2) Individuals are more cooperative in species where females mate monogamously or with few males, in birds, mammals, insects and shrimps^{13,19,21,24–26}.
- (3) When population structure is manipulated experimentally, in a range of microorganisms, including bacteria, fungi and viruses, the conditions that lead to high relatedness favour greater cooperation^{15,27–32}.
- (4) The role of group formation has also been supported by sequence data. If a trait is favoured by kin selection, then lower relatedness will lead to weaker selection for that trait, and so the removal of deleterious mutations will be slower and less likely^{33–36}. Consistent with kin selection playing an important role, ant and bee species with either multiple mating or multiple queens, and hence reduced relatedness within family groups, showed greater polymorphism in genes upregulated in the worker caste (kin selected) compared with genes upregulated in the reproductive caste (directly selected)^{35,37–39}. Furthermore, cooperative traits in bacteria and slime moulds show enhanced polymorphism^{10,34,40,41}.

A number of other factors can help maintain high relatedness between interacting individuals. For example, in bacteria, clonal

growth and limited movement will mean that clone mates will often be clustered⁴², and viscous mediums, biofilms and fibres can keep secreted public goods local, to be shared with clone mates^{43–46}.

1b. Kin discrimination. Inclusive fitness theory predicts that individuals can be favoured to preferentially seek out closer relatives to cooperate with, and/or cooperate at higher levels when interacting with closer relatives. There is considerable evidence of such kin discrimination across a range of organisms, including slime moulds, ants, mice and birds^{47–54}. In some cases, kin discrimination is based on genetic cues, with individuals adjusting cooperation depending on whether they match genotype at a ‘tag’ loci⁴⁹. In other cases, environmental cues are used to recognize kin. For example, long-tailed tits seem to assess kinship on the basis of both vocal similarity and prior association⁵⁵.

Inclusive fitness theory can also explain when kin discrimination is not observed. Across cooperative breeding vertebrates, the extent of kin discrimination is lower in species where the mean relatedness in groups is higher and shows less variation⁵⁶. This pattern reflects that kin discrimination is not required when individuals tend to be highly related to all group members anyway⁵⁷.

Kin selection theory has even explained situations when closer relatives are preferentially discriminated against (negative kin discrimination). In banded mongooses, dominant individuals are more likely to harass and evict subordinates in the group when they are closer relatives⁵⁸. Resisting eviction is costly to

Box 2 | New questions and future directions

Research on cooperation has advanced by asking more precise or nuanced questions about the distribution and form that cooperation takes in the natural world. For example:

- Why does cooperation occur in some species, but not others?
- Why does the effort or resources put into cooperation vary across species? For example, in birds, the amount of food provided by helpers varies across species from 20 to 160% of the rate at which parents feed²⁶.
- Within a species or group, why do some individuals cooperate, but not others? Considering individuals that cooperate, why does the effort put into cooperation vary? For example, within groups of meerkats, different helpers give away between 0 and 58% of their food to pups⁷⁷.
- Which sex cooperates? Across different species, both the likelihood of helping and the effort put into helping varies between the sexes^{74,139}.
- Why do individuals preferentially direct help towards relatives (kin discrimination) in some species, such as long-tailed tits, but not others, such as superb fairywrens⁵⁵?
- Should cooperating individuals specialize to perform different tasks (division of labour)? For example, in the bacteria *Bacillus subtilis*, only a fraction of cells produce and release proteases to break down proteins²¹⁵.

These questions have been addressed at all levels, from genes to individuals, to species and across the entire tree of life, from bacteria to birds, and in viruses. By examining the same questions at different levels, this research has illuminated several repeating or consistent patterns. Nonetheless, we have only just begun to explain the distribution and diversity of cooperation in the natural world. There are many outstanding problems and opportunities—here, we provide a few examples that follow from the insights we have discussed.

Kin selection and kin discrimination

- Relatedness is determined by the mechanism of group formation. What determines how groups form and why?
- The importance of kin discrimination remains to be tested in a variety of organisms, especially microorganisms.
- Why haven't advances in genetics led to the discovery of more genetic cues for kin discrimination?
- Does Crozier's paradox²¹⁶ explain why genetic kin discrimination seems to be rare in animals?
- To what extent do horizontal gene transfer and greenbeard interactions alter selection for social traits?

the dominant attempting the eviction, and individuals are more likely to accept eviction when they are closer relatives of the dominant. Consequently, there is less to gain by trying to evict non-relatives, who will resist this eviction, and so dominants are favoured to preferentially evict closer relatives⁵⁸. In addition, dispersal provides a kin selected benefit by reducing competition for those relatives left behind—this benefit will be greater for closer relatives⁵⁹.

1c. Quantifying Hamilton's rule. The above studies are qualitative, examining whether a higher relatedness is associated with greater cooperation. Other studies have used long-term field data, and detailed experiments, to quantify the parameters of Hamilton's rule⁶⁰ (Box 1). These studies have found that kin selection can completely explain cooperation in species ranging from long-tailed tits to vesicular stomatitis virus^{61,62}.

Costs and benefits

- Can we quantify, across species, how ecological variation leads to variation in the benefit or cost of cooperation?
- How broadly can variation in the direct benefit of cooperation explain variation in the level of cooperation, either within or across species?
- Can economic games help explain why cooperation evolved in humans, or do they just reveal proximate cognitive mechanisms (biases)?
- How can we explain variation in the extent to which cooperative species divide labour, and the mechanism used to divide labour?

Conflict and enforcement

- Why is cheating observed in some systems, but not others?
- Is it reasonable to think of cancer and similar 'deleterious mutations' as a form of cheating?
- How often do organisms respond to cheating by 'going private'? And how do we detect cooperation in the evolutionary history of a 'privatized' trait?
- Why are enforcement mechanisms, such as 'sanctions', important in some species, but not others?
- To what extent do holobiome and microbiome interactions represent between-species mutualisms that can be explained with existing theory^{217,218}?
- Can cooperation and conflict help explain the evolution of brain size¹²³? If so, do invertebrates and vertebrates differ in fundamental ways?
- Why is cooperation lost from species and what are the consequences^{92,219}?
- What are the factors that led major evolutionary transitions, by effectively eliminating conflict, and dividing labour to the point of mutual dependence (interdependence)^{1,220,221}?

New methods and new applications

- How can genetic and genomic methodologies be harnessed to help us understand the distribution of cooperation?
- Can the phenotypic gambit survive progress in genomics?
- What can be learnt from using genetic manipulations to follow the behaviour of individuals?
- Can population genetic studies help us explain the factors driving selection for cooperation in natural populations?
- How can we exploit novel opportunities for both experimental and comparative studies of cooperation offered by taxa such as bacteria and viruses?

2. Ecological determinants of cooperation can be hard to identify. While we have a good understanding of the cost (C) and benefit (B) of cooperation in particular species, we often lack broad ecological explanations for why the benefits of cooperation vary across species⁶³. What ecological factors cause B/C to vary across species, and hence determine when cooperation is favoured? This contrasts with the numerous clear examples of how variation in R can explain when cooperation is favoured (Insight 1).

In some cases, the role of ecological factors has even become less clear. In birds, cooperative breeding has long been known to be more common in harsh environments, where temperatures are hot and rainfall is unpredictable^{64–66}. This led to the hypothesis that harsh environments favour cooperation, because they increased the relative benefit of cooperating (higher B/C). However, this pattern appears to be a consequence, not a driver, of cooperation—the correlation arises because cooperative species are better able to

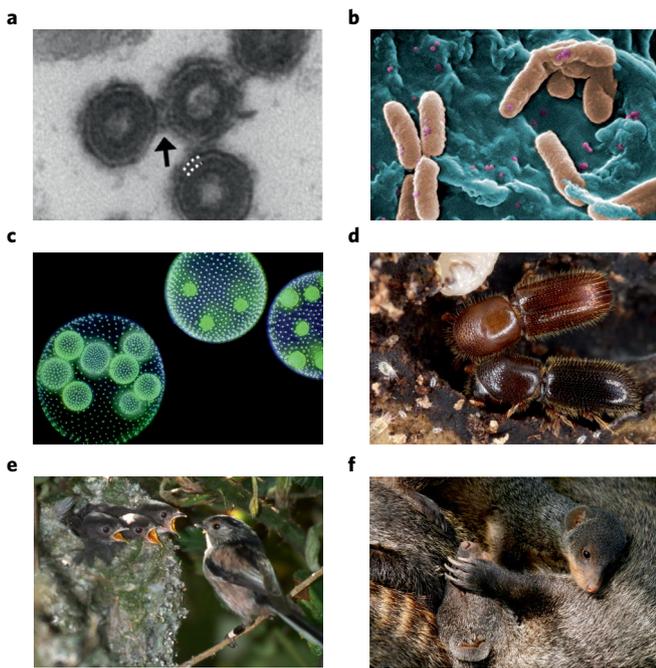


Fig. 1 | Cooperation across the tree of life. a–f. Examples of cooperation include: vesicular stomatitis virus aggregates into multiple virus co-infection units (arrows) and produce proteins that help other viruses overcome host defences^{52,204} (**a**); *P. aeruginosa* bacteria produce and secrete iron-scavenging siderophores that benefit neighbouring cells⁹¹ (**b**); *Volvox carteri* algae form multicellular groups where some sterile helper cells beat their flagella to keep the colony afloat²⁰⁵ (**c**); *Xyleborinus saxesenii* ambrosia beetles have sterile helpers²⁰⁶ (**d**); long-tailed tits are cooperative breeders, where individuals preferentially help closer relatives⁵⁵ (**e**); banded mongooses form cooperative groups, where the dominant will preferentially evict closer relatives⁵⁸ (negative kin discrimination) (**f**). Studies on cooperation in these species have used a mixture of methodologies: observational, experimental, comparative across-species, experimental evolution and genomic. Credit: panel **a** adapted with permission from ref. ²⁰⁷, Springer Nature Ltd; CDC/Janice Haney Carr (**b**); Frank Fox (**c**); Gernot Kunz and Peter Biedermann (**d**); Andrew MacColl (**e**); Nature Picture Library / Alamy Stock Photo (**f**).

colonize harsh environments, rather than cooperation being favoured in harsh environments¹³. Other recent comparative analyses that raise questions about the direction of causality include studies of rodents and sponge shrimp^{63,67}.

A possible complication is that the factors influencing the benefit and cost of cooperation vary across species, making it hard to quantify their influence in a comparable way. For example, in different species, the advantage of cooperation could depend on breeding site availability, climate, competition with other species, or food availability⁶⁸.

Another possibility is that the importance of variation across species in B and C is dwarfed by the consequences of variation in R . Relatedness shows considerable variation across species and so can have a large influence on whether cooperation is favoured (whether $RB - C > 0$). In contrast, maybe cooperation usually provides some efficiency benefit, such that B/C is usually > 1 and just doesn't vary much across species. If R varies a lot more than B/C , then it will be much easier to detect an influence of R than B/C . We are not saying that relatedness is the only variable that matters, just that if it varies more, we should expect its influence to be easier to detect. The influence of B and C could perhaps be more easily detected by examining interactions with R —for example, not all monogamous species are cooperative^{21,69,70}.

3. Direct and indirect benefits disentangled. A number of animal studies have shown that the direct benefits of cooperation can still be substantial, even in species where helping seems to be primarily explained by kin selection. For example, in *Polistes* wasps, although cooperation appears to usually be explained by kin selection, some individuals help at nests where they are not related to the dominant female⁷¹. This seems to be because subordinate helpers can gain significant direct benefits from helping, by inheriting a nest after the death of the dominant^{72,73}.

In birds, the sex that remains, and therefore has a chance of inheriting the nest, helps at higher levels than the sex that disperses, and so is less likely to gain a direct benefit from helping⁷⁴. A role of direct fitness benefits in birds is further supported by the observation that longer subordinate lifespans, which can increase the chance of inheriting a patch, have favoured the evolution of cooperative breeding, but especially in species where rates of polyandry are high, and so kin selection will be weaker⁷⁵. It is important to disentangle direct and indirect benefits of cooperation, to clarify the relevant theoretical predictions and because evidence for one does not negate the other.

4. Microbes have sophisticated conditional behaviours. Studies on a range of animal species have shown how individuals adjust their level of cooperation in response to changes in the cost and benefit of cooperation^{48,76–79}. Recent research has shown that microorganisms have similarly sophisticated conditional behaviours.

The costs and benefits of cooperating can depend on the environment. A common form of cooperation in microorganisms is the production of some factor that is excreted from cells, and which then provides some 'public good' benefit to the local group of cells—for example, iron-scavenging molecules, or an enzyme to digest protein^{15,27}. In the bacteria *Pseudomonas aeruginosa*, a higher cell density allows cells to more easily share the benefit of producing public goods⁸⁰. Cells use a form of signalling, termed quorum sensing, to upregulate the production of public goods at high density, and hence increase the level of cooperation when it provides greater benefits²⁷. The increased benefits of cooperating at high density can also select for the formation of multicellular cooperative groups, as appears to occur in yeast^{81,82}.

The cost of producing public goods can depend on resource availability^{83,84}. *P. aeruginosa* increases the production of one factor, rhamnolipid biosurfactant, which aids movement, when there is more carbon available, making that rhamnolipid less costly to produce⁸⁵.

Group formation can provide defence against predators, or aid in predation. By aggregating together into groups, algae make it harder for predators to eat them⁸⁶. Clumping is costly in the absence of predators because competition for resources is increased; facultative clumping is favoured, therefore, where the behaviour is triggered only when predators are detected⁸⁶. More generally, obligate multicellularity has evolved only when groups form clonally, with dividing cells sticking together²². Experimental studies on algae have shown that the mechanism of group formation is heritable and can evolve by selection⁸⁷.

5. The invisible dynamics of cheating have been revealed. Scratch the surface of a cooperative society and you will usually find conflict bubbling underneath. An extreme form of conflict is 'cheating', where individuals that avoid the costs of cooperating can still gain the benefits of others cooperating⁸⁸. Recent work has allowed the detection of the previously invisible dynamics of cheating across a diversity of organisms. In particular, genetic studies in microbes—slime moulds and bacteria—have allowed us to examine the occurrence of cheating, and the form that it takes, in natural populations^{10,40,41,89–92}.

5a. Persistence of cheats. Theory suggests that restrictive conditions can be required for cheats to coexist with cooperators. When

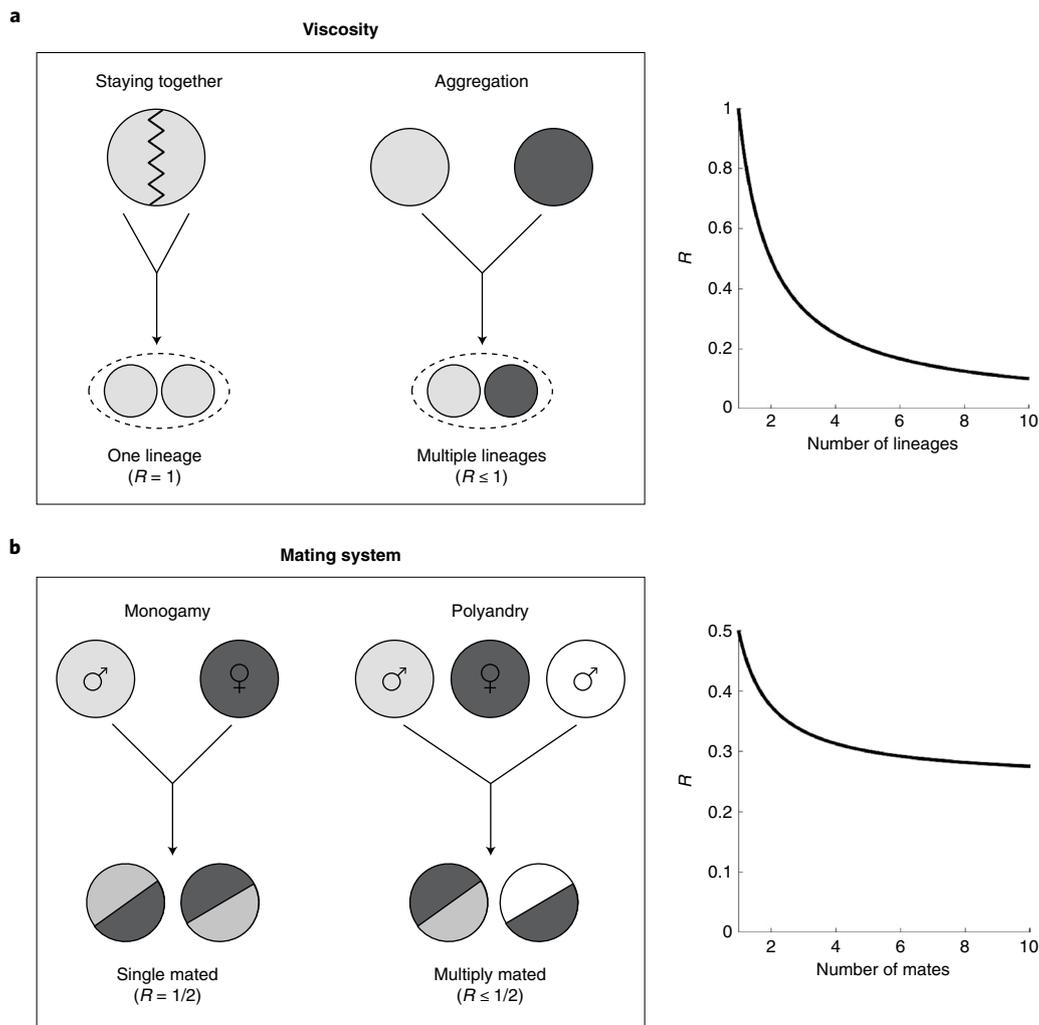


Fig. 2 | Group formation and relatedness. The method of group formation determines relatedness within groups, and so influences whether cooperation is favoured. **a**, Population viscosity: when offspring stay with their parent (staying together, in a family group), this leads to higher relatedness than when individuals aggregate together post-dispersal (with potential non-kin). Specifically, if a group is formed by n unrelated lineages, then the relatedness within that group will be $R = 1/n$. An asexual species is shown, but the same pattern occurs in sexual species. **b**, Mating system: when females mate with a single male (monogamy), this leads to a higher relatedness between her offspring (full siblings), compared with when females mate with multiple males (polyandry; half siblings). Specifically, if a diploid female mates with m males, then the average relatedness between her offspring will be $R = 0.25 + 0.25/m$. An analogous pattern applies in haplodiploids, where a female is related to her sisters by $R = 0.25 + 0.5/m^{208}$.

originally developing inclusive fitness theory, Hamilton² found that the relative fitness of cooperators does not depend on how common they are in a population. This lack of frequency dependence means that either cooperation is favoured and so cheats would be eliminated, or cooperation is not favoured and so you couldn't observe cheats exploiting cooperators. Given this result, which suggests that cheating will not be evolutionarily stable, how can we explain observations of cheating?

More recent theory has shown that a number of factors can lead to cheats having a higher fitness when rare (frequency dependence), allowing cheats and cooperators to coexist. For example, when cooperation provides some direct benefit, or when the benefits of cooperation are diminishing rather than increasing linearly^{93–95}. These factors have been shown to explain coexistence of cheats and cooperators in bacteria and yeast^{94–96}. Frequency dependence also requires non-additivity, where genes cause large variation in the level of cooperation (strong selection). In bacteria, viruses and other microorganisms, single 'knock out' mutations can eliminate cooperative behaviours, causing large variation in cooperation,

which could help provide an explanation for why cheats are more commonly observed in these taxa^{95,97}.

An alternative explanation for the observation of cheating is that cheats are maintained in a population at mutation–selection balance^{98,99}. Mutation causes the loss of cooperation, which then gives the appearance of cheating as those non-cooperators are selected out of the population. In this case, not cooperating would represent a deleterious mutation rather than a cheating adaptation. However, estimates from bacteria suggest that mutation–selection balance would lead to one non-cooperator in every 10,000–100,000 individuals, which is much lower than has been observed empirically⁹⁸. Consequently, the observation of non-cooperators is more likely to be explained by frequency dependent cheating.

5b. Resistance to cheats. When cheats are maintained in a population, cooperators will be selected to avoid exploitation, or reduce the extent to which they can be exploited. An example of such a strategy has been observed in laboratory selection experiments on bacteria, and could also explain why many extracellular public goods and

Table 1 | Maybe not explaining cooperation

Suggested explanation for cooperation	Potential problems
A pleiotropic link between cooperation and a trait with a large personal (private) benefit (metabolic constraint/coregulation) ^{184–190} . The idea here is that if cooperation is lost, then the directly beneficial trait would also be lost, and that the direct benefit could outweigh the cost of cooperation. Similar arguments have been made for ‘hormonal pleiotropy’ in social insects ¹⁹¹ .	Pleiotropic links can favour any trait and not preferentially cooperation. If the genetic architecture is not fixed, individuals could evolve to perform the directly beneficial trait and not cooperate ¹⁹² . In addition, the role of kin selection had already been established in these species, and so explaining cooperation was not a problem ¹⁹² . Causality can also go in both directions—in cases where some cooperation is favoured, pleiotropy can be selected to reduce cheat build-up.
The down-regulation of cooperation at certain times (metabolic prudence or facultative cooperation) ^{190,193} .	Individuals will be selected to reduce their level of cooperation when the benefit is lower or cost is greater (Insight 4). However, this is not an answer to ‘why cooperate?’—a mechanism such as kin selection is still required to explain when cooperation is carried out.
The regulation of cooperation by quorum sensing in bacteria ¹⁹⁰ .	Quorum sensing restricts cooperation to times when it appears to be more cost effective. An explanation is still required for why cooperate at those times.
Genes for cooperation could hitch hike with mutations that are advantageous in a new environment (adaptive race) ^{194,195} .	This hypothesis doesn’t favour cooperation per se, as cheats could also hitch hike ¹⁹⁵ . Furthermore, any effects are only transient, as competition between cheats and cooperators can still take place within populations of locally adapted genomes.
Cooperation is favoured at greenbeard genes, which can identify copies of themselves in other individuals and preferentially help those individuals ^{196,197} .	There are genes that have the properties of greenbeards. However, it is not clear if it is the greenbeard effect per se (linkage) that is favouring cooperation ^{198,199} . Cooperation may have been favoured anyway, due to kin selection, with the greenbeard affect just a mechanistic byproduct.
Horizontal gene transfer can increase relatedness for cooperative genes by ‘reinfesting cheats’ ^{200–202} .	If there are cheat plasmids that don’t cooperate, then horizontal gene transfer doesn’t necessarily favour cooperation ²⁰³ . Although there is some evidence from <i>Escherichia coli</i> that cooperative genes are more likely to be found on mobile elements ²⁰¹ , there are alternative explanations ²⁰⁴ .
Discoveries about the genetic architecture and mechanisms underlying cooperation in microorganisms have led to a number of new explanations for cooperation being suggested. However, there is a lack of evidence that these mechanisms provide explanations for cooperation. In some cases, the suggested explanations arise from over-interpretation of short-term evolutionary dynamics, and/or from implicitly assuming that the genetic architecture cannot evolve (mixing proximate and ultimate explanations of behaviour). Cooperation is usually more parsimoniously explained by standard explanations, such as kin selection, whose role had often already been demonstrated.	

signalling molecules released by bacteria come in different types (specificity)^{100–104}. Another example can be seen in flowering plants, which reduce exploitation by nectar-robbing cheats by restricting or altering the time of day at which they provide nectar rewards for pollinators¹⁰⁵.

An even more extreme response to cheating has been observed in the bacteria *P. aeruginosa*, where individuals stopped cooperating and ‘went private’. In infections of the lung in humans with cystic fibrosis, the invasion of cheats that did not produce iron-scavenging siderophore molecules (a public good) led to the complete loss of siderophore production⁹¹. This was then followed by strains upregulating an alternative ‘private’ mechanism of acquiring iron, which is not cooperative and so cannot be exploited¹⁰⁶.

6. Genetic architecture sometimes matters. Most research on cooperation ignores the underlying genetics and assumes that all phenotypes are theoretically possible (phenotypic gambit¹⁰⁷). Detailed characterization of the genetics underlying some cooperative traits has helped us to understand where and why genetics can matter.

6a. Supergenes. Research on the fire ant, *Solenopsis invicta*, has shown how genetic architecture is key to the maintenance of different strategies within populations¹⁰⁸. In this species, colonies form with either a single or multiple queens. The difference is driven by a supergene—a large inversion, covering 55% of an entire chromosome, with suppressed recombination. This supergene also controls traits where the optimum depends on the number of queens, such as queen size and fecundity. Consequently, the supergene allows life history traits to be adaptively adjusted (linked) depending on the social strategy (single or multiple queens). Supergenes appear to control social organization in a number of ant species^{109,110}.

6b. Genetic red herrings. A range of genetic discoveries in bacteria and slime moulds have led to suggestions of novel mechanisms to explain cooperation. These include the discovery of pleiotropic links between cooperation and private traits, the regulation of cooperation by quorum sensing, and hitch hiking with advantageous mutations (Table 1).

However, there are potential problems with all these suggestions (Table 1). In some cases, the hypothesis relies on the assumption that the genetic architecture itself cannot evolve. In other cases, the genetic mechanism provides a way to vary the level of cooperation, but is not an answer to ‘why cooperate?’. Furthermore, cooperation can usually be explained by some other mechanism, such as kin selection.

Overall, there is a lack of evidence that genetic architecture determines when cooperation is favoured (Table 1). We are not saying that it is not possible for genetic architecture to help explain cooperation, rather that the mechanisms suggested, so far, lack convincing support, and there are usually simpler explanations.

7. Humans aren’t special in that way. A number of experimental laboratory studies examining human behaviour in economic games have found that individuals cooperate more than might be expected from their own selfish interests¹¹¹. This has led to a widely held conclusion that humans are especially altruistic and cooperate in ways that are not easily explained by evolutionary theory¹¹².

This conclusion is based, however, on the assumption that laboratory economic games reflect evolutionary pressures, and that humans play ‘perfectly’. In addition, it has been pointed out that experiments using economic games often lack appropriate controls and null hypotheses^{113–115}. More recent experiments have suggested that humans do not play economic games perfectly, and instead learn over time how to increase the money that they earn from the

game^{116,117}. Consequently, what looked like altruism was actually confusion, followed by learning to be less confused. Furthermore, many instances of human cooperation are better explained as mutually beneficial cooperation, stabilized by enforcement mechanisms such as reciprocity, rather than altruistic cooperation^{118–121}. What matters for natural selection is the average lifetime consequences of a behaviour in the natural environment, not short-term consequences in an unnatural environment.

In short, humans are not especially altruistic. Cells forming the fruiting body of a slime mould, 20% of which sacrifice themselves as stalk cells to help disperse others as spores, are more altruistic than a group of humans¹⁴. What appears to be special about humans is the extent to which enforcement mechanisms such as reciprocity are used to stabilize cooperation, and how we attempt to evade those mechanisms^{111,122}. Indeed, it has even been suggested that brain size is a response to conflict in cooperative social groups¹²³. Humans also stand out in their ability to learn from others. It is currently a matter of debate whether this potential for ‘cultural evolution’ favours increased or decreased cooperation^{124–128}.

Insights 8 and 9

We are now in a position to start making big picture generalizations about why cooperation is favoured, both within (Insight 8) and between (Insight 9) species.

8. Indirect benefits play the main role in explaining cooperation within species. The relative importance of direct and indirect fitness benefits for explaining cooperation within species has long been debated¹²⁹. Has recent research allowed us to move forward on this debate?

There has been growing evidence for indirect fitness benefits (kin selection) playing the major role in explaining cooperation within species. Considering animals, such as birds, mammals and insects, the data suggest that relatedness is a key determinant of which species cooperate, and how much individuals cooperate (Insight 1). Furthermore, long-term field studies on species such as long-tailed tits have shown cases where cooperation can be completely explained by indirect benefits^{60,61}. Considering bacteria and other microbes, clonal growth means that cells will tend to interact with close relatives, and the forms of cooperation that are observed can be explained relatively easily by indirect benefits^{15,27,43,130}.

We also have a clearer idea of the factors that lead to indirect fitness benefits. Population structure and group formation play similar roles in ensuring high relatedness, at all levels of biology (Insight 1; Fig. 2). The early stages in the evolution of life required cooperation between simple replicators, which may also have been favoured due to population structure keeping relatives together^{131,132}. In contrast, while the possible role of haplodiploid genetics has attracted much attention, both theory and empirical data have led to many concluding that it was a red herring^{133–139}.

We are not saying that there are never direct benefits to cooperation, or that enforcement never occurs. Insight 3 provides some elegant examples of how direct fitness benefits can be important for cooperation within species, and enforcement is reviewed elsewhere¹⁴⁰. Instead, our point is that statistically speaking, direct fitness benefits seem much less important in explaining the distribution and diversity of within-species cooperation. This makes sense, because the potential for indirect benefits can arise easily, whenever population structure keeps relatives together². In contrast, mechanisms to provide or enforce direct fitness benefits to cooperation can be much harder to evolve initially, and/or require individuals to be already cooperating to some extent^{141–143}. One of the clearest examples of enforcement favouring higher levels of cooperation is policing in the social insects, which is favoured by indirect fitness benefits, and can be thought of as a form of kin discrimination¹⁴⁴.

Direct fitness benefits appear to be more important in explaining less costly forms of cooperation. Evidence supporting a role for mechanisms such as reciprocity tend to come from cooperative behaviours that are relatively low cost, such as grooming in primates¹⁴⁵. Similarly, there are bird species where unrelated individuals form cooperative groups, but in those species cooperation tends to be joint incubation or defence of territory, and does not involve giving up the chance to breed²³. The fitness consequences of behaviours such as reciprocal grooming or joint territory defence are likely to be marginal relative to the sacrifice of personal reproduction to become a subordinate helper.

9. There are two ways to make a stable mutualism. Both theoretical and empirical work have suggested that there are two ways in which cooperation between different species (mutualisms) tend to be maintained: shared interests and enforcement.

9a. Shared interests. Cooperative mutualisms are favoured when the reproductive interests of different species are so entwined that each species gains from cooperating with the other (shared interests; Fig. 3a)¹⁴⁶. The easiest way for this to occur is when a small number of symbionts are transmitted vertically to each offspring of their host. In this case, the symbionts within a host are highly related, possibly clonal and eliminating most within-host conflict; in addition, the symbionts benefit from helping the host, because the host could then produce more offspring, who could carry more symbionts^{146,147}. The hosts, in turn, are selected to help their symbionts, because those symbionts provide them a service. A classic example of this would be the *Buchnera* bacteria that synthesize amino acids for their aphid hosts¹⁴⁸.

The role of shared reproductive interests has been supported by a comparative study across species, and experimental studies. Across 38 bacterial symbioses, vertically transmitted symbionts provided an average of twice the fitness benefit to their host, relative to horizontally transmitted symbionts¹⁴⁹. Theory suggests that the influence of transmission route is mainly via its influence on relatedness, and hence the level of within-host conflict¹⁴⁷. Analogously, experimental evolution studies on interacting microbial species have shown that vertical transmission and spatial structuring both favours increased cooperation between species^{150,151}. This role of transmission route, via its influence on symbiont relatedness, is analogous to the role of group formation in Insight 1.

Symbiont transmission route also influences genome evolution. Vertically transmitted symbionts have smaller genomes than horizontally transmitted symbionts¹⁴⁹. This is thought to reflect the usefulness of many traits becoming reduced when living entirely within a host, with relaxed selection then allowing inactivation and deletion of these non-essential genes¹⁵². The benefit that symbionts provide to their hosts is greater in species with smaller genomes; given that genomes reduce over time, this suggests that longer periods of host–symbiont coevolution lead to greater reliance on symbionts and/or more beneficial symbionts¹⁴⁹. Some genes are also moved from symbionts to their hosts¹⁵³.

9b. Enforcement. The second common explanation for cooperative mutualisms is when cooperation is enforced (Fig. 3b)^{140,154}. When members of one species interact with multiple partners of the other species, this can lead to conflict¹⁴⁶. For example, if a host contains numerous symbiont strains, this will reduce the relatedness between symbionts and hence reduce the indirect fitness benefits gained from helping the host, and therefore helping the other symbionts within the host¹⁵⁵. In this case, cooperation can be enforced by rewarding cooperation and/or punishing non-cooperation (sanctions)¹⁵⁵. Leguminous plants cut off the oxygen supply to rhizobia bacteria that are relatively poor at fixing nitrogen¹⁵⁶. Fig trees abort and reduce resource supply to fruits where the pollinator wasps did not pollinate sufficient flowers^{157,158}.

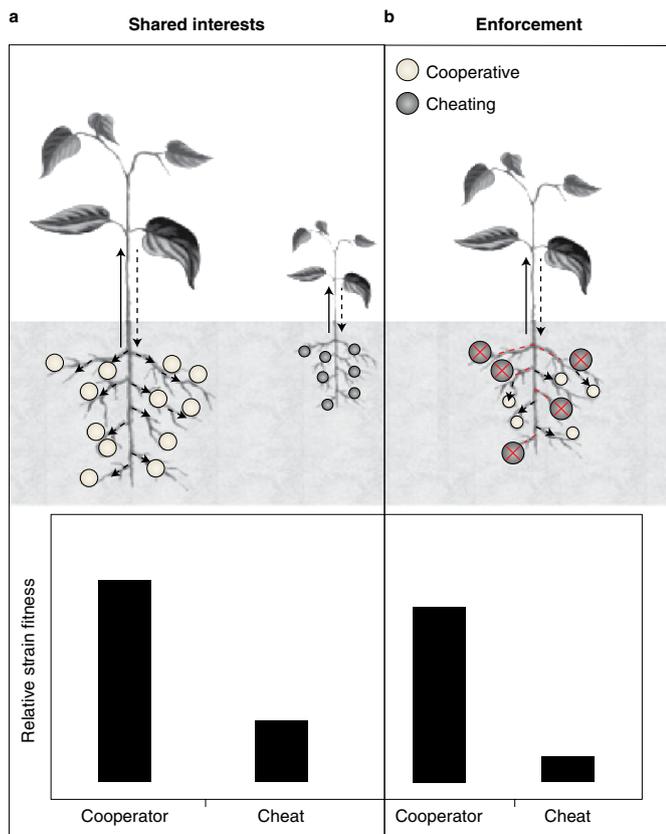


Fig. 3 | Two ways to stable mutualism. a, Mutualistic cooperation is favoured when the reproductive interests of different species are so entwined that each species gains from cooperating with the other (shared interests). For example, when vertical transmission leads to a host containing a clonal population of symbionts, any benefits of cooperating with a host would be clone mates. Another way of looking at this is that cooperators (open nodules) and non-cooperative cheats (filled nodules) would be in different hosts, and so cooperators gain the benefit of being in ‘helped’ hosts, whereas cheats do not. **b**, Mutualistic cooperation can also be enforced, by rewarding cooperators (open nodules) and/or stopping interactions with non-cooperative cheats (filled nodules). The solid arrows show resources being transferred from symbionts to the host, and the dashed arrows show resources being transferred from the host to the symbionts. Figure adapted with permission from ref. ²⁰⁹, John Wiley and Sons.

Enforcement can also be bidirectional, such as when mycorrhizal fungi trade phosphorous with plants for carbohydrates¹⁵⁹. Resource trading of this kind can lead to more elaborate strategies—fungi appear to move phosphorous across their mycelial network to locations where phosphorous is more limiting, and so a better trade can be made¹⁶⁰. The suppression of genes for selfish distorting behaviour by the ‘parliament of the genes’ is analogous to this between-species enforcement^{161,162}.

From a theoretical perspective, the finding that mutualisms tend to be stabilized by either shared interests or enforcement makes sense. The conditions that lead to conflict and reduce shared interest, such as interacting with a large number of partners, are exactly the conditions that are expected to favour enforcement¹⁶³.

9c. Maintenance versus origin. It is useful to distinguish maintenance of cooperation from its evolutionary origin⁵. Our discussion in this section has focused on the maintenance of cooperative mutualisms. While enforcement can lead to higher levels of cooperation, it requires some initial level of cooperation to evolve^{141–143}. It is, therefore,

likely that mutualisms initially evolved via shared interests, before enforcement evolved to increase the level of cooperation¹⁶⁴.

Insight 10

Cooperation is fundamental to the success and growth of many organisms. Consequently, whenever we want to reduce the growth of damaging organisms, such as parasites, or increase the growth of beneficial organisms, manipulating cooperation could be a useful tool.

10. Cooperation can be exploited for applied purposes. 10a.

Managing parasites and pathogens. Disrupting cooperation has at least three applications for managing parasites and pathogens. First, the level of cooperation has a large influence on parasite growth and virulence, the damage caused to the host. Indeed, traits termed ‘virulence factors’ by microbiologists appear to usually be cooperative public goods¹⁶⁵. Consequently, if cooperation can be disrupted, virulence can be reduced. Experiments on the bacteria *P. aeruginosa* have shown that the addition of non-cooperative cheats to an infection reduced the mortality rates of rats by 50%¹⁶⁶. The accumulation of defective interfering particles, which represent a form of cheating in viruses, leads to less severe outcomes of viral infections in humans, and is being developed as an antiviral therapy^{167,168}.

Second, as well as disrupting infections, cheats could be used as a ‘Trojan horse’ to introduce medically beneficial alleles into a population, such as antibiotic resistance or antibacterial toxins¹⁶⁹. For this or virulence disruption to work, cheats need only have short-term success, spreading within a host—such therapies can work even when cheats cannot transmit successfully between hosts.

Third, it can be harder for parasites to evolve resistance against intervention techniques that disrupt cooperative behaviours, than against treatments such as antibiotics that directly kill individuals¹⁷⁰. If cooperation is disrupted, this effectively makes all individuals cheats. Consequently, if there was a ‘resistance’ mutation that switched cooperation back on, the carrier of this mutation would be surrounded by cheats, making it harder to spread. This theory has been supported by an experimental evolution study on *Salmonella*, where resistance against standard antimicrobials rapidly evolves, but resistance to an inhibitor of cooperative biofilm formation did not evolve¹⁷¹. Nonetheless, we are a long way from convincing clinicians that it is useful to add more parasites (cheats), or that it is better to use interventions that don’t directly kill parasites, to avoid selecting for resistance in those parasites.

10b. Other applications. There are many other areas where we have not yet begun to realize the full potential for exploiting our understanding of cooperation. These include optimizing machine–machine cooperation in artificial intelligence collectives, such as fleets of autonomous cars or interacting financial trading algorithms, as well as designing artificial intelligence algorithms so as to minimize the potential for human–machine conflict^{172,173}. The maintenance of cooperation is required for efficient bio-industry applications, including using bacteria to biodegrade pollutants and detoxify, or algae to produce biofuels^{174,175}. Agricultural efficiency in crops or livestock can be increased by ‘social selection’ for increased cooperation or decreased competitiveness, rather than individual yield^{175,176}.

Conclusions

While the inclusive fitness approach has provided the framework for the main insights made in the study of cooperation, it has also attracted controversy, which might suggest a field in disarray to an outside observer^{176–178}. Welch argued that analogous controversy has arisen multiple times for research on adaptation, for reasons that do not reflect problems with the approach¹⁷⁹. There is a repeated pattern where approaches such as inclusive fitness theory lead to

major advances in our understanding of adaptation, and where the resulting attention generates charges of narrowness and oversimplification. These charges are, however, misplaced, because it is the simplifications made by theory that facilitate its application to data^{107,179,180}. In biology, theory is not an abstract enterprise, it is the interface between theory and data that matters. Scientific progress is not shaped by whether ideas are ‘liked’ or ‘disliked’, but by making parsimonious predictions that hold up time and time again, generating new counterintuitive predictions that achieve additional confirmation. That is the achievement of inclusive fitness theory¹⁸¹.

The existence of some controversy therefore reflects a productive and healthy field, where spectacular advances are being made. As well as explaining cooperation in particular species, these advances have illuminated broad generalizations, where the same factors seem to play analogous roles across the tree of life. This makes things pleasingly simpler for those of us studying cooperation—rather than a different explanation for every species, we can have a single explanatory framework—that is an amazing achievement! Furthermore, progress in the study of cooperation has demonstrated how the behavioural ecology approach, originally developed to study animals, can be successfully applied to any form of organism, from bacteria to viruses^{182,183}. The recent progress summarized here has opened up a great number of new problems to solve, and it is as exciting a time to be studying cooperation as it has ever been (Box 2).

Received: 21 April 2020; Accepted: 11 December 2020;

Published online: 28 January 2021

References

- Bourke, A. F. G. *Principles of Social Evolution* (OUP, 2011).
- Hamilton, W. D. The genetical evolution of social behaviour. I & II. *J. Theor. Biol.* **7**, 1–52 (1964).
- Sachs, J. L., Mueller, U. G., Wilcox, T. P. & Bull, J. J. The evolution of cooperation. *Q. Rev. Biol.* **79**, 135–160 (2004).
- Lehmann, L. & Keller, L. The evolution of cooperation and altruism – a general framework and a classification of models. *J. Evol. Biol.* **19**, 1365–1376 (2006).
- West, S. A., Griffin, A. S. & Gardner, A. Evolutionary explanations for cooperation. *Curr. Biol.* **17**, R661–R672 (2007).
- Trivers, R. The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 35–57 (1971).
- Velicer, G. J., Kroos, L. & Lenski, R. E. Developmental cheating in the social bacterium *Myxococcus xanthus*. *Nature* **404**, 598–601 (2000).
- McCutcheon, J. P. & Moran, N. A. Parallel genomic evolution and metabolic interdependence in an ancient symbiosis. *Proc. Natl Acad. Sci. USA* **104**, 19392–19397 (2007).
- Spribille, T. et al. Basidiomycete yeasts in the cortex of ascomycete macrolichens. *Science* **353**, 488–492 (2016).
- Ostrowski, E. A. et al. Genomic signatures of cooperation and conflict in the social amoeba. *Curr. Biol.* **25**, 1661–1665 (2015).
- Hadfield, J. D. & Nakagawa, S. General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *J. Evol. Biol.* **23**, 494–508 (2010).
- Garamszegi, L. Z. *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology* (Springer, 2014).
- Cornwallis, C. K. et al. Cooperation facilitates the colonization of harsh environments. *Nat. Ecol. Evol.* **1**, 0057 (2017).
- Strassmann, J. E., Zhu, Y. & Queller, D. C. Altruism and social cheating in the social amoeba *Dictyostelium discoideum*. *Nature* **408**, 965–967 (2000).
- Griffin, A. S., West, S. A. & Buckling, A. Cooperation and competition in pathogenic bacteria. *Nature* **430**, 1024–1027 (2004).
- Turner, P. E. & Chao, L. Prisoner’s dilemma in an RNA virus. *Nature* **398**, 441–443 (1999).
- West, S. A., Griffin, A. S. & Gardner, A. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* **20**, 415–432 (2007).
- Queller, D. C. & Strassmann, J. E. Kin selection and social insects. *BioScience* **48**, 165–175 (1998).
- Boomsma, J. J. Kin selection versus sexual selection: why the ends do not meet. *Curr. Biol.* **17**, R673–R683 (2007).
- Reeve, H. K. & Keller, L. Partitioning of reproduction in mother–daughter versus sibling associations – a test of optimal skew theory. *Am. Nat.* **145**, 119–132 (1995).
- Hughes, W. O. H., Oldroyd, B. P., Beekman, M. & Ratnieks, F. L. W. Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* **320**, 1213–1216 (2008).
- Fisher, R. M., Cornwallis, C. K. & West, S. A. Group formation, relatedness, and the evolution of multicellularity. *Curr. Biol.* **23**, 1120–1125 (2013).
- Downing, P. A., Griffin, A. S. & Cornwallis, C. K. Group formation and the evolutionary pathway to complex sociality in birds. *Nat. Ecol. Evol.* **215**, 479–486 (2020).
- Cornwallis, C. K., West, S. A., Davis, K. E. & Griffin, A. S. Promiscuity and the evolutionary transition to complex societies. *Nature* **466**, 969–972 (2011).
- Duffy, J. E. & Macdonald, K. S. Kin structure, ecology and the evolution of social organization in shrimp: a comparative analysis. *Proc. R. Soc. B* **277**, 575–584 (2009).
- Green, J. P. & Hatchwell, B. J. Inclusive fitness consequences of dispersal decisions in a cooperatively breeding bird, the long-tailed tit (*Aegithalos caudatus*). *Proc. Natl Acad. Sci. USA* **115**, 12011–12016 (2018).
- Diggle, S. P., West, S. A., Griffin, A. S. & Campbell, G. S. Cooperation and conflict in quorum-sensing bacterial populations. *Nature* **450**, 411–414 (2007).
- Rumbaugh, K. P. et al. Kin selection, quorum sensing and virulence in pathogenic bacteria. *Proc. R. Soc. B* **279**, 3584–3588 (2012).
- Pollitt, E. J. G., West, S. A., Crusz, S. A., Burton-Chellew, M. N. & Diggle, S. P. Cooperation, quorum sensing, and evolution of virulence in *Staphylococcus aureus*. *Infect. Immun.* **82**, 1045–1051 (2014).
- Kuzdzal-Fick, J. J., Queller, D. C., Fox, S. A. & Strassmann, J. E. High relatedness is necessary and sufficient to maintain multicellularity in *Dictyostelium*. *Science* **334**, 1548–1551 (2011).
- Bastiaans, E., Debets, A. J. M. & Aanen, D. K. Experimental evolution reveals that high relatedness protects multicellular cooperation from cheaters. *Nat. Commun.* **7**, 11435 (2016).
- Frost, I. et al. Cooperation, competition and antibiotic resistance in bacterial colonies. *ISME J.* **12**, 1582–1593 (2018).
- Linksvayer, T. A. & Wade, M. J. Genes with social effects are expected to harbor more sequence variation within and between species. *Evolution* **63**, 1685–1696 (2009).
- Van Dyken, J. D. & Wade, M. J. Detecting the molecular signature of social conflict: theory and a test with bacterial quorum sensing genes. *Am. Nat.* **179**, 436–450 (2012).
- Hall, D. W. & Goodisman, M. A. D. The effects of kin selection on rates of molecular evolution in social insects. *Evolution* **66**, 2080–2093 (2012).
- Hall, D. W., Yi, S. V. & Goodisman, M. A. D. Kin selection, genomics and caste-antagonistic pleiotropy. *Biol. Lett.* **9**, 20130309 (2013).
- Hunt, B. G. et al. Relaxed selection is a precursor to the evolution of phenotypic plasticity. *Proc. Natl Acad. Sci. USA* **108**, 15936–15941 (2011).
- Hunt, B. G. et al. Sociality is linked to rates of protein evolution in a highly social insect. *Mol. Biol. Evol.* **27**, 497–500 (2010).
- Warner, M. R., Mikheyev, A. S. & Linksvayer, T. A. Genomic signature of kin selection in an ant with obligately sterile workers. *Mol. Biol. Evol.* **34**, 1780–1787 (2017).
- Noh, S., Geist, K. S., Tian, X., Strassmann, J. E. & Queller, D. C. Genetic signatures of microbial altruism and cheating in social amoebas in the wild. *Proc. Natl Acad. Sci. USA* **115**, 3096–3101 (2018).
- de Oliveira, J. L. et al. Conditional expression explains molecular evolution of social genes in a microbe. *Nat. Commun.* **10**, 3284 (2019).
- Nadell, C. D., Drescher, K. & Foster, K. R. Spatial structure, cooperation and competition in biofilms. *Nat. Rev. Microbiol.* **14**, 589–600 (2016).
- Xavier, J. B. & Foster, K. R. Cooperation and conflict in microbial biofilms. *Proc. Natl Acad. Sci. USA* **104**, 876–881 (2007).
- Kümmerli, R., Griffin, A. S., West, S. A., Buckling, A. & Harrison, F. Viscous medium promotes cooperation in the pathogenic bacterium *Pseudomonas aeruginosa*. *Proc. R. Soc. B* **276**, 3531–3538 (2009).
- Drescher, K., Nadell, C. D., Stone, H. A., Wingreen, N. S. & Bassler, B. L. Solutions to the public goods dilemma in bacterial biofilms. *Curr. Biol.* **24**, 50–55 (2014).
- Bruce, J. B., West, S. A. & Griffin, A. S. Functional amyloids promote retention of public goods in bacteria. *Proc. R. Soc. B* **286**, 20190709 (2019).
- Mehdiabadi, N. J. et al. Kin preference in a social microbe. *Nature* **442**, 881–882 (2006).
- Barve, S., Koenig, W. D., Haydock, J. & Walters, E. L. Habitat saturation results in joint-nesting female coalitions in a social bird. *Am. Nat.* **193**, 830–840 (2019).
- Green, J. P. et al. The genetic basis of kin recognition in a cooperatively breeding mammal. *Curr. Biol.* **25**, 2631–2641 (2015).
- Lihoreau, M. & Rivault, C. Kin recognition via cuticular hydrocarbons shapes cockroach social life. *Behav. Ecol.* **20**, 46–53 (2008).
- Nam, K.-B., Simeoni, M., Sharp, S. P. & Hatchwell, B. J. Kinship affects investment by helpers in a cooperatively breeding bird. *Proc. R. Soc. B* **277**, 3299–3306 (2010).

52. Madgwick, P. G., Stewart, B., Belcher, L. J., Thompson, C. R. L. & Wolf, J. B. Strategic investment explains patterns of cooperation and cheating in a microbe. *Proc. Natl Acad. Sci. USA* **115**, E4823–E4832 (2018).
53. Guerrieri, F. J. et al. Ants recognize foes and not friends. *Proc. R. Soc. B* **276**, 2461–2468 (2009).
54. Duffy, E., Morrison, C. & Macdonald, K. Colony defense and behavioral differentiation in the eusocial shrimp *Synalpheus regalis*. *Behav. Ecol. Sociobiol.* **51**, 488–495 (2002).
55. Leedale, A. E., Lachlan, R. F., Robinson, E. J. H. & Hatchwell, B. J. Helping decisions and kin recognition in long-tailed tits: is call similarity used to direct help towards kin? *Phil. Trans. R. Soc. B* **375**, 20190565 (2020).
56. Cornwallis, C. K., West, S. A. & Griffin, A. S. Routes to indirect fitness in cooperatively breeding vertebrates: kin discrimination and limited dispersal. *J. Evol. Biol.* **22**, 2445–2457 (2009).
57. Duncan, C., Gaynor, D., Clutton-Brock, T. H. & Dyble, M. The evolution of indiscriminate altruism in a cooperatively breeding mammal. *Am. Nat.* **193**, 841–851 (2019).
58. Thompson, F. J. et al. Explaining negative kin discrimination in a cooperative mammal society. *Proc. Natl Acad. Sci. USA* **114**, 5207–5212 (2017).
59. Hamilton, W. D. & May, R. M. Dispersal in stable habitats. *Nature* **269**, 578–581 (1977).
60. Bourke, A. F. G. Hamilton's rule and the causes of social evolution. *Phil. Trans. R. Soc. B* **369**, 20130362 (2014).
61. Hatchwell, B. J., Gullett, P. R. & Adams, M. J. Helping in cooperatively breeding long-tailed tits: a test of Hamilton's rule. *Phil. Trans. R. Soc. B* **369**, 20130565 (2014).
62. Domingo-Calap, P., Segredo-Otero, E., Duran-Moreno, M. & Sanjuán, R. Social evolution of innate immunity evasion in a virus. *Nat. Microbiol.* **4**, 1006–1013 (2019).
63. Firman, R. C., Rubenstein, D. R., Moran, J. M., Rowe, K. C. & Buzatto, B. A. Extreme and variable climatic conditions drive the evolution of sociality in Australian rodents. *Curr. Biol.* **30**, 691–697 (2020).
64. Arnold, K. E. & Owens, I. Cooperative breeding in birds: the role of ecology. *Behav. Ecol.* **10**, 465–471 (1999).
65. Jetz, W. & Rubenstein, D. R. Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr. Biol.* **21**, 72–78 (2010).
66. Rubenstein, D. R. & Lovette, I. J. Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr. Biol.* **17**, 1414–1419 (2007).
67. Brooks, K. C., Maia, R., Duffy, J. E., Hultgren, K. M. & Rubenstein, D. R. Ecological generalism facilitates the evolution of sociality in snapping shrimps. *Ecol. Lett.* **20**, 1516–1525 (2017).
68. Lin, Y.-H., Chan, S.-F., Rubenstein, D. R., Liu, M. & Shen, S.-F. Resolving the paradox of environmental quality and sociality: the ecological causes and consequences of cooperative breeding in two lineages of birds. *Am. Nat.* **194**, 207–216 (2019).
69. Lukas, D. & Clutton-Brock, T. H. Cooperative breeding and monogamy in mammalian societies. *Proc. R. Soc. B* **279**, 2151–2156 (2012).
70. Cornwallis, C. K., West, S. A., Davis, K. E. & Griffin, A. S. Promiscuity and the evolutionary transition to complex societies. *Nature* **466**, 969–972 (2010).
71. Queller, D. C. et al. Unrelated helpers in a social insect. *Nature* **405**, 784–787 (2000).
72. Leadbeater, E., Carruthers, J. M., Green, J. P., Rosser, N. S. & Field, J. Nest inheritance is the missing source of direct fitness in a primitively eusocial insect. *Science* **333**, 874–876 (2011).
73. Korb, J. & Hartfelder, K. Life history and development - a framework for understanding developmental plasticity in lower termites. *Biol. Rev.* **83**, 295–313 (2008).
74. Downing, P. A., Griffin, A. S. & Cornwallis, C. K. Sex differences in helping effort reveal the effect of future reproduction on cooperative behaviour in birds. *Proc. R. Soc. B* **285**, 20181164 (2018).
75. Downing, P. A., Cornwallis, C. K. & Griffin, A. S. Sex, long life and the evolutionary transition to cooperative breeding in birds. *Proc. R. Soc. B* **282**, 20151663 (2015).
76. Komdeur, J. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* **358**, 493–495 (1992).
77. Clutton-Brock, T. H. et al. Contributions to cooperative rearing in meerkats. *Anim. Behav.* **61**, 705–710 (2001).
78. Field, J., Cronin, A. & Bridge, C. Future fitness and helping in social queues. *Nature* **441**, 214–217 (2006).
79. Cant, M. A., Llop, J. B. & Field, J. Individual variation in social aggression and the probability of inheritance: theory and a field test. *Am. Nat.* **167**, 837–852 (2006).
80. Darch, S. E., West, S. A., Winzer, K. & Diggle, S. P. Density-dependent fitness benefits in quorum-sensing bacterial populations. *Proc. Natl Acad. Sci. USA* **109**, 8259–8263 (2012).
81. Biernaskie, J. M. & West, S. A. Cooperation, clumping and the evolution of multicellularity. *Proc. R. Soc. B* **282**, 20151075 (2015).
82. Koschwanez, J. H., Foster, K. R. & Murray, A. W. Improved use of a public good selects for the evolution of undifferentiated multicellularity. *eLife* **2**, e00367 (2013).
83. Sexton, D. J. & Schuster, M. Nutrient limitation determines the fitness of cheaters in bacterial siderophore cooperation. *Nat. Commun.* **8**, 230 (2017).
84. Connelly, B. D., Bruger, E. L., McKinley, P. K. & Waters, C. M. Resource abundance and the critical transition to cooperation. *J. Evol. Biol.* **30**, 750–761 (2017).
85. Xavier, J. B., Kim, W. & Foster, K. R. A molecular mechanism that stabilizes cooperative secretions in *Pseudomonas aeruginosa*. *Mol. Microbiol.* **79**, 166–179 (2010).
86. Kapsetaki, S. E. & West, S. A. The costs and benefits of multicellular group formation in algae. *Evolution* **73**, 1296–1308 (2019).
87. Ratcliff, W. C. et al. Experimental evolution of an alternating uni- and multicellular life cycle in *Chlamydomonas reinhardtii*. *Nat. Commun.* **4**, 2742 (2013).
88. Ghoul, M., Griffin, A. S. & West, S. A. Toward an evolutionary definition of cheating. *Evolution* **68**, 318–331 (2014).
89. Cordero, O. X., Ventouras, L.-A., DeLong, E. F. & Polz, M. F. Public good dynamics drive evolution of iron acquisition strategies in natural bacterio-plankton populations. *Proc. Natl Acad. Sci. USA* **109**, 20059–20064 (2012).
90. Gano-Cohen, K. A. et al. Recurrent mutualism breakdown events in a legume rhizobia metapopulation. *Proc. R. Soc. B* **287**, 20192549 (2020).
91. Andersen, S. B., Marvig, R. L., Molin, S., Krogh Johansen, H. & Griffin, A. S. Long-term social dynamics drive loss of function in pathogenic bacteria. *Proc. Natl Acad. Sci. USA* **112**, 10756–10761 (2015).
92. Sachs, J. L., Ehinger, M. O. & Simms, E. L. Origins of cheating and loss of symbiosis in wild *Bradyrhizobium*. *J. Evol. Biol.* **23**, 1075–1089 (2010).
93. Patel, M., Raymond, B., Bonsall, M. B. & West, S. A. Crystal toxins and the volunteer's dilemma in bacteria. *J. Evol. Biol.* **32**, 310–319 (2019).
94. Gore, J., Youk, H. & van Oudenaarden, A. Snowdrift game dynamics and facultative cheating in yeast. *Nature* **459**, 253–256 (2009).
95. Ross-Gillespie, A., Gardner, A., West, S. A. & Griffin, A. S. Frequency dependence and cooperation: theory and a test with bacteria. *Am. Nat.* **170**, 331–342 (2007).
96. Lujan, A. M., Gomez, P. & Buckling, A. Siderophore cooperation of the bacterium *Pseudomonas fluorescens* in soil. *Biol. Lett.* **11**, 20140934 (2015).
97. Meir, M. et al. Competition between social cheater viruses is driven by mechanistically different cheating strategies. *Sci. Adv.* **6**, eabb7990 (2020).
98. Van Dyken, J. D., Linksvayer, T. A. & Wade, M. J. Kin selection–mutation balance: a model for the origin, maintenance, and consequences of social cheating. *Am. Nat.* **177**, 288–300 (2011).
99. Jandér, K. C. & Steidinger, B. S. Why mutualist partners vary in quality: mutation-selection balance and incentives to cheat in the fig tree-fig wasp mutualism. *Ecol. Lett.* **20**, 922–932 (2017).
100. Butaitė, E., Baumgartner, M., Wyder, S. & Kümmerli, R. Siderophore cheating and cheating resistance shape competition for iron in soil and freshwater *Pseudomonas* communities. *Nat. Commun.* **8**, 414 (2017).
101. Kümmerli, R. et al. Co-evolutionary dynamics between public good producers and cheaters in the bacterium *Pseudomonas aeruginosa*. *J. Evol. Biol.* **28**, 2264–2274 (2015).
102. Bruce, J. B., Cooper, G. A., Chabas, H., West, S. A. & Griffin, A. S. Cheating and resistance to cheating in natural populations of the bacterium *Pseudomonas fluorescens*. *Evolution* **71**, 2484–2495 (2017).
103. Pollak, S. et al. Facultative cheating supports the coexistence of diverse quorum-sensing alleles. *Proc. Natl Acad. Sci. USA* **113**, 2152–2157 (2016).
104. Even-Tov, E. et al. Social evolution selects for redundancy in bacterial quorum sensing. *PLoS Biol.* **14**, e1002386 (2016).
105. Barker, J. L. & Bronstein, J. L. Temporal structure in cooperative interactions: what does the timing of exploitation tell us about its cost? *PLoS Biol.* **14**, e1002371 (2016).
106. Andersen, S. B. et al. Privatisation rescues function following loss of cooperation. *eLife* **7**, e38594 (2018).
107. Grafen, A. in *Behavioural Ecology: An Evolutionary Approach* (eds Krebs, J. R. & Davies, N. B.) 62–84 (Wiley-Blackwell, 1984).
108. Wang, J. et al. A Y-like social chromosome causes alternative colony organization in fire ants. *Nature* **493**, 664–668 (2013).
109. Avril, A., Purcell, J., Béniguel, S. & Chapuisat, M. Maternal effect killing by a supergene controlling ant social organization. *Proc. Natl Acad. Sci. USA* **117**, 17130–17134 (2020).
110. Yan, Z. et al. Evolution of a supergene that regulates a trans-species social polymorphism. *Nat. Ecol. Evol.* **4**, 240–249 (2020).
111. Fehr, E. & Schurtenberger, I. Normative foundations of human cooperation. *Nat. Hum. Behav.* **2**, 458–468 (2018).
112. Fehr, E. & Fischbacher, U. The nature of human altruism. *Nature* **425**, 785–791 (2003).
113. Burton-Chellaw, M. N., Mouden, E. C. & West, S. A. Conditional cooperation and confusion in public-goods experiments. *Proc. Natl Acad. Sci. USA* **113**, 1291–1296 (2016).

114. Kümmerli, R., Burton-Chellew, M. N., Ross-Gillespie, A. & West, S. A. Resistance to extreme strategies, rather than prosocial preferences, can explain human cooperation in public goods games. *Proc. Natl Acad. Sci. USA* **107**, 10125–10130 (2010).
115. Burton-Chellew, M. N. & West, S. A. Prosocial preferences do not explain human cooperation in public-goods games. *Proc. Natl Acad. Sci. USA* **110**, 216–221 (2013).
116. Burton-Chellew, M. N., Nax, H. H. & West, S. A. Payoff-based learning explains the decline in cooperation in public goods games. *Proc. R. Soc. B* **282**, 20142678 (2015).
117. Bayer, R.-C., Renner, E. & Sausgruber, R. Confusion and learning in the voluntary contributions game. *Exp. Econ.* **16**, 478–496 (2013).
118. Barclay, P. Reciprocity creates a stake in one's partner, or why you should cooperate even when anonymous. *Proc. R. Soc. B* **287**, 20200819 (2020).
119. Jaeggi, A. V., Hooper, P. L., Beheim, B. A., Kaplan, H. & Gurven, M. Reciprocal exchange patterned by market forces helps explain cooperation in a small-scale society. *Curr. Biol.* **26**, 2180–2187 (2016).
120. Kasper, C. & Mulder, M. B. Who helps and why? *Curr. Anthropol.* **56**, 701–732 (2015).
121. Guala, F. Reciprocity: weak or strong? What punishment experiments do (and do not) demonstrate. *Behav. Brain Sci.* **35**, 1–15 (2012).
122. Kurzban, R., Burton-Chellew, M. N. & West, S. A. The evolution of altruism in humans. *Annu. Rev. Psychol.* **66**, 575–599 (2015).
123. Lukas, D. & Clutton-Brock, T. H. Social complexity and kinship in animal societies. *Ecol. Lett.* **21**, 1129–1134 (2018).
124. Molleman, L., Quiñones, A. E. & Weissing, F. J. Cultural evolution of cooperation: the interplay between forms of social learning and group selection. *Evol. Hum. Behav.* **34**, 342–349 (2013).
125. van den Berg, P., Molleman, L. & Weissing, F. J. Focus on the success of others leads to selfish behavior. *Proc. Natl Acad. Sci. USA* **112**, 2912–2917 (2015).
126. Burton-Chellew, M. N., El Mouden, C. & West, S. A. Social learning and the demise of costly cooperation in humans. *Proc. R. Soc. B* **284**, 20170067 (2017).
127. Lehmann, L., Feldman, M. W. & Foster, K. R. Cultural transmission can inhibit the evolution of altruistic helping. *Am. Nat.* **172**, 12–24 (2008).
128. Boyd, R. & Richerson, P. J. Culture and the evolution of human cooperation. *Phil. Trans. R. Soc. B* **364**, 3281–3288 (2009).
129. Clutton-Brock, T. H. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* **296**, 69–72 (2002).
130. Gilbert, O. M., Foster, K. R., Mehdiabadi, N. J., Strassmann, J. E. & Queller, D. C. High relatedness maintains multicellular cooperation in a social amoeba by controlling cheater mutants. *Proc. Natl Acad. Sci. USA* **104**, 8913–8917 (2007).
131. Higgs, P. G. & Lehman, N. The RNA world: molecular cooperation at the origins of life. *Nat. Rev. Genet.* **16**, 7–17 (2014).
132. Levin, S. R. & West, S. A. The evolution of cooperation in simple molecular replicators. *Proc. R. Soc. B* **284**, 20171967 (2017).
133. Gardner, A., Alpedrinha, J. A. C. & West, S. A. Haplodiploidy and the evolution of eusociality: split sex ratios. *Am. Nat.* **179**, 240–256 (2012).
134. Alpedrinha, J. A. C., Gardner, A. & West, S. A. Haplodiploidy and the evolution of eusociality: worker revolution. *Am. Nat.* **184**, 303–317 (2014).
135. Rautiala, P., Helanterä, H. & Puurtinen, M. Unmatedness promotes the evolution of helping more in diploids than in haploids. *Am. Nat.* **184**, 318–325 (2014).
136. Rautiala, P., Helanterä, H. & Puurtinen, M. The evolutionary dynamics of adaptive virginity, sex-allocation, and altruistic helping in haplodiploid animals. *Evolution* **72**, 30–38 (2017).
137. Quiñones, A. E. & Pen, I. A unified model of Hymenopteran preadaptations that trigger the evolutionary transition to eusociality. *Nat. Commun.* **8**, 15920 (2017).
138. Quiñones, A. E., Henriques, G. J. B. & Pen, I. Queen–worker conflict can drive the evolution of social polymorphism and split sex ratios in facultatively eusocial life cycles. *Evolution* **74**, 15–28 (2019).
139. Ross, L., Gardner, A., Hardy, N. & West, S. A. Ecology, not the genetics of sex determination, determines who helps in eusocial populations. *Curr. Biol.* **23**, 2383–2387 (2013).
140. Ågren, J. A., Davies, N. G. & Foster, K. R. Enforcement is central to the evolution of cooperation. *Nat. Ecol. Evol.* **3**, 1018–1029 (2019).
141. Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. B* **268**, 187–196 (2001).
142. Axelrod, R. & Hamilton, W. D. The evolution of cooperation. *Science* **211**, 1390–1396 (1981).
143. Gardner, A. & West, S. A. Cooperation and punishment, especially in humans. *Am. Nat.* **164**, 753–764 (2004).
144. Wenseleers, T. & Ratnieks, F. L. W. Enforced altruism in insect societies. *Nature* **444**, 50 (2006).
145. Schino, G. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behav. Ecol.* **18**, 115–120 (2006).
146. Frank, S. A. Kin selection and virulence in the evolution of protocells and parasites. *Proc. R. Soc. B* **258**, 153–161 (1994).
147. Leeks, A., Santos dos, M. & West, S. A. Transmission, relatedness, and the evolution of cooperative symbionts. *J. Evol. Biol.* **32**, 1036–1045 (2019).
148. Moran, N. A., McCutcheon, J. P. & Nakabachi, A. Genomics and evolution of heritable bacterial symbionts. *Annu. Rev. Genet.* **42**, 165–190 (2008).
149. Fisher, R. M., Henry, L. M., Cornwallis, C. K., Kiers, E. T. & West, S. A. The evolution of host–symbiont dependence. *Nat. Commun.* **8**, 15973 (2017).
150. Harcombe, W. Novel cooperation experimentally evolved between species. *Evolution* **64**, 2166–2172 (2010).
151. Harcombe, W. R., Chacón, J. M., Adamowicz, E. M., Chubiz, L. M. & Marx, C. J. Evolution of bidirectional costly mutualism from byproduct consumption. *Proc. Natl Acad. Sci. USA* **115**, 12000–12004 (2018).
152. McCutcheon, J. P. & Moran, N. A. Extreme genome reduction in symbiotic bacteria. *Nature* **10**, 13–26 (2011).
153. Husnik, F. & McCutcheon, J. P. Functional horizontal gene transfer from bacteria to eukaryotes. *Nat. Rev. Microbiol.* **16**, 67–79 (2017).
154. Frank, S. A. Repression of competition and the evolution of cooperation. *Evolution* **57**, 693–705 (2003).
155. West, S. A., Kiers, E. T., Simms, E. L. & Denison, R. F. Sanctions and mutualism stability: why do rhizobia fix nitrogen? *Proc. R. Soc. B* **269**, 685–694 (2002).
156. Kiers, E. T., Rousseau, R. A., West, S. A. & Denison, R. F. Host sanctions and the legume–rhizobium mutualism. *Nature* **425**, 78–81 (2003).
157. Jandér, K. C. & Herre, E. A. Host sanctions and pollinator cheating in the fig tree–fig wasp mutualism. *Proc. R. Soc. B* **277**, 1481–1488 (2010).
158. Jandér, K. C., Herre, E. A. & Simms, E. L. Precision of host sanctions in the fig tree–fig wasp mutualism: consequences for uncooperative symbionts. *Ecol. Lett.* **15**, 1362–1369 (2012).
159. Kiers, E. T. et al. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* **333**, 880–882 (2011).
160. Whiteside, M. D. et al. Mycorrhizal fungi respond to resource inequality by moving phosphorus from rich to poor patches across networks. *Curr. Biol.* **29**, 2043–2050 (2019).
161. Leigh, E. G. Jr *Adaptation and Diversity* (Freeman, Cooper & Company, 1971).
162. Scott, T. W. & West, S. A. Adaptation is maintained by the parliament of genes. *Nat. Commun.* **10**, 5163 (2019).
163. Wyatt, G. A. K., Kiers, E. T., Gardner, A. & West, S. A. A biological market analysis of the plant–mycorrhizal symbiosis. *Evolution* **68**, 2603–2618 (2014).
164. West, S. A., Kiers, E. T., Pen, I. & Denison, R. F. Sanctions and mutualism stability: when should less beneficial mutualists be tolerated? *J. Evol. Biol.* **15**, 830–837 (2002).
165. West, S. A., Diggle, S. P., Buckling, A., Gardner, A. & Griffin, A. S. The social lives of microbes. *Annu. Rev. Ecol. Evol. Syst.* **38**, 53–77 (2007).
166. Rumbaugh, K. P. et al. Quorum sensing and the social evolution of bacterial virulence. *Curr. Biol.* **19**, 341–345 (2009).
167. Vasilijević, J. et al. Reduced accumulation of defective viral genomes contributes to severe outcome in influenza virus infected patients. *PLoS Pathog.* **13**, e1006650 (2017).
168. Tanner, E. J., Kirkegaard, K. A. & Weinberger, L. S. Exploiting genetic interference for antiviral therapy. *PLoS Genet.* **12**, e1005986 (2016).
169. Brown, S. P., West, S. A., Diggle, S. P. & Griffin, A. S. Social evolution in micro-organisms and a Trojan horse approach to medical intervention strategies. *Phil. Trans. R. Soc. B* **364**, 3157–3168 (2009).
170. Andre, J.-B. & Letters, B. G. E. Multicellular organization in bacteria as a target for drug therapy. *Ecol. Lett.* **85**, 800–810 (2005).
171. Dieltjens, L. et al. Inhibiting bacterial cooperation is an evolutionarily robust anti-biofilm strategy. *Nat. Commun.* **11**, 107 (2019).
172. Rahwan, I. et al. Machine behaviour. *Nature* **568**, 477–486 (2019).
173. Crandall, J. W. et al. Cooperating with machines. *Nat. Commun.* **9**, 233 (2018).
174. Hesse, E. et al. Ecological selection of siderophore-producing microbial taxa in response to heavy metal contamination. *Ecol. Lett.* **21**, 117–127 (2017).
175. Nikel, P. I., Silva-Rocha, R., Benedetti, I. & de Lorenzo, V. The private life of environmental bacteria: pollutant biodegradation at the single cell level. *Environ. Microbiol.* **16**, 628–642 (2014).
176. Nowak, M. A., Tarnita, C. E. & Wilson, E. O. The evolution of eusociality. *Nature* **466**, 1057–1062 (2010).
177. Nowak, M. A., McAvoy, A., Allen, B. & Wilson, E. O. The general form of Hamilton's rule makes no predictions and cannot be tested empirically. *Proc. Natl Acad. Sci. USA* **114**, 5665–5670 (2017).
178. Nowak, M. A. & Allen, B. Inclusive fitness theorizing invokes phenomena that are not relevant for the evolution of eusociality. *PLoS Biol.* **13**, e1002134 (2015).
179. Welch, J. J. What's wrong with evolutionary biology? *Biol. Philos.* **32**, 263–279 (2017).

180. Grafen, A. A geometric view of relatedness. *Oxf. Surv. Evol. Biol.* **2**, 28–89 (1985).
181. Abbot, P. et al. Inclusive fitness theory and eusociality. *Nature* **471**, E1–E4 (2011).
182. Parker, G. A. & Maynard Smith, J. Optimality theory in evolutionary biology. *Nature* **348**, 27–33 (1990).
183. Davies, N. B., Krebs, J. R. & West, S. A. *An Introduction to Behavioural Ecology* 4th Edn (Wiley–Blackwell, 2012).
184. Parker, K. R., Shaulsky, G., Strassmann, J. E. & Queller, D. C. Pleiotropy as a mechanism to stabilize cooperation. *Nature* **431**, 693–696 (2004).
185. Mitri, S. & Foster, K. R. Pleiotropy and the low cost of individual traits promote cooperation. *Evolution* **70**, 488–494 (2016).
186. Wang, M., Schaefer, A. L., Dandekar, A. A. & Greenberg, E. P. Quorum sensing and policing of *Pseudomonas aeruginosa* social cheaters. *Proc. Natl Acad. Sci. USA* **112**, 2187–2191 (2015).
187. Dandekar, A. A. & Chugani, S. Bacterial quorum sensing and metabolic incentives to cooperate. *Science* **338**, 264–266 (2012).
188. Majerczyk, C. & Schneider, E. Quorum sensing control of Type VI secretion factors restricts the proliferation of quorum-sensing mutants. *eLife* **5**, e14712 (2016).
189. Frénoy, A., Taddei, F. & Misevic, D. Genetic architecture promotes the evolution and maintenance of cooperation. *PLoS Comput. Biol.* **9**, e1003339 (2013).
190. Özkaya, Ö., Xavier, K. B., Dionisio, F. & Balbontin, R. Maintenance of microbial cooperation mediated by public goods in single and multiple traits scenarios. *J. Bacteriol.* **199**, e00297 (2017).
191. Oliveira, R. C. et al. Hormonal pleiotropy helps maintain queen signal honesty in a highly eusocial wasp. *Sci. Rep.* **7**, 1654 (2017).
192. Santos dos, M., Ghoul, M. & West, S. A. Pleiotropy, cooperation, and the social evolution of genetic architecture. *PLoS Biol.* **16**, e2006671 (2018).
193. Bruger, E. & Waters, C. Sharing the sandbox: evolutionary mechanisms that maintain bacterial cooperation. *F1000Res* **4**, 1504 (2015).
194. Waite, A. J. & Shou, W. Adaptation to a new environment allows cooperators to purge cheaters stochastically. *Proc. Natl Acad. Sci. USA* **109**, 19079–19086 (2012).
195. Morgan, A. D., Quigley, B. J. Z., Brown, S. P. & Buckling, A. Selection on non-social traits limits the invasion of social cheats. *Ecol. Lett.* **15**, 841–846 (2012).
196. Queller, D. C., Ponte, E., Bozzaro, S. & Strassmann, J. E. Single-gene greenbeard effects in the social amoeba *Dictyostelium discoideum*. *Science* **299**, 105–106 (2003).
197. Smukalla, S. et al. *FLO1* is a variable green beard gene that drives biofilm-like cooperation in budding yeast. *Cell* **135**, 726–737 (2008).
198. Madgwick, P. G., Belcher, L. J. & Wolf, J. B. Greenbeard genes: theory and reality. *Trends Ecol. Evol.* **34**, 1092–1103 (2019).
199. West, S. A. & Gardner, A. Greenbeards. *Evolution* **64**, 25–38 (2010).
200. Smith, J. The social evolution of bacterial pathogenesis. *Proc. R. Soc. B* **268**, 61–69 (2001).
201. Nogueira, T. et al. Horizontal gene transfer of the secretome drives the evolution of bacterial cooperation and virulence. *Curr. Biol.* **19**, 1683–1691 (2009).
202. McGinty, S. E., Lehmann, L., Brown, S. P. & Rankin, D. J. The interplay between relatedness and horizontal gene transfer drives the evolution of plasmid-carried public goods. *Proc. R. Soc. B* **280**, 20130400 (2013).
203. McGinty, S. E., Rankin, D. J. & Brown, S. P. Horizontal gene transfer and the evolution of bacterial cooperation. *Evolution* **65**, 21–32 (2010).
204. Ghoul, M., Andersen, S. B. & West, S. A. Sociomics: using omic approaches to understand social evolution. *Trends Genet.* **33**, 408–419 (2017).
205. Hanschen, E. R., Ferris, P. J. & Michod, R. E. Early evolution of the genetic basis for soma in the Volvocaceae. *Evolution* **68**, 2014–2025 (2014).
206. Smith, S. M., Kent, D. S., Boomsma, J. J. & Stow, A. J. Monogamous sperm storage and permanent worker sterility in a long-lived ambrosia beetle. *Nat. Ecol. Evol.* **48**, 1009–1018 (2018).
207. Cuevas, J. M., Durán-Moreno, M. & Sanjuán, R. Multi-virion infectious units arise from free viral particles in an enveloped virus. *Nat. Microbiol.* **2**, 17078 (2017).
208. Hamilton, W. D. Altruism and related phenomena, mainly in social insects. *Annu. Rev. Ecol. Syst.* **3**, 193–232 (1972).
209. Kiers, E. T., Ratcliff, W. C. & Denison, R. F. Single-strain inoculation may create spurious correlations between legume fitness and rhizobial fitness. *New Phytol.* **198**, 4–9 (2013).
210. Hamilton, W. D. Evolution of altruistic behavior. *Am. Nat.* **97**, 354–356 (1963).
211. West, S. A. & Gardner, A. Adaptation and inclusive fitness review. *Curr. Biol.* **23**, R577–R584 (2013).
212. Taylor, P. D. & Frank, S. A. How to make a kin selection model. *J. Theor. Biol.* **180**, 27–37 (1996).
213. Grafen, A. Optimization of inclusive fitness. *J. Theor. Biol.* **238**, 541–563 (2006).
214. Trivers, R. & Hope, H. Haplodiploidy and the evolution of the social insects. *Science* **191**, 249–263 (1976).
215. Chai, Y., Chu, F., Kolter, R. & Losick, R. Bistability and biofilm formation in *Bacillus subtilis*. *Mol. Microbiol.* **67**, 254–263 (2008).
216. Crozier, R. H. Genetic clonal recognition abilities in marine invertebrates must be maintained by selection for something else. *Evolution* **40**, 1100–1101 (1986).
217. Moran, N. A. & Sloan, D. B. The hologenome concept: helpful or hollow? *PLoS Biol.* **13**, e1002311 (2015).
218. Foster, K. R., Schluter, J., Coyte, K. Z. & Rakoff-Nahoum, S. The evolution of the host microbiome as an ecosystem on a leash. *Nature* **548**, 43–51 (2017).
219. Werner, G. D. A. et al. Symbiont switching and alternative resource acquisition strategies drive mutualism breakdown. *Proc. Natl Acad. Sci. USA* **115**, 5229–5234 (2018).
220. Maynard Smith, J. & Szathmáry, E. *The Major Transitions in Evolution* (Oxford Univ. Press, 1995).
221. West, S. A., Fisher, R. M., Gardner, A. & Kiers, E. T. Major evolutionary transitions in individuality. *Proc. Natl Acad. Sci. USA* **112**, 10112–10119 (2015).

Acknowledgements

We thank the social evolution journal club for comments; K. Boomsma for a sentence that was very useful in our conclusion; the ERC (A.S.G., M.B.G. and S.A.W.) and St John's College (G.A.C.) for funding; and P. Biedermann, A. MacColl and R. Sanjuán for supplying photos.

Author contributions

All authors conceived and wrote the manuscript. G.A.C. and M.B.G. constructed the figures.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41559-020-01384-x>.

Correspondence should be addressed to S.A.W.

Peer review information *Nature Ecology & Evolution* thanks the anonymous reviewers for their contribution to the peer review of this work.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© Springer Nature Limited 2021