The evolutionary and ecological consequences of cooperation

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Article Type: Awards Paper - Distinguished Achievement in the Conceptual Unification of the Biological Sciences Winner Address

Keywords: altruism, environmental change, inclusive fitness, niche breadth, speciation, symbiosis

Abstract

The last 30 years have seen major advances in our understanding of the evolution of cooperation – traits that have evolved because of the benefit they provide other individuals. In contrast, we have been much less successful in determining the consequences of cooperation for long-term ecological and evolutionary change. Studies of birds, insects and bacteria, suggest that cooperation has major consequences for fundamental features of life such as ecological niche-range, genetic variation within species and rates of species diversification. However, the role of cooperation in driving these changes is largely limited to hypotheses, as we lack both data and a general theoretical framework. We synthesise the progress that has been made and highlight the major gaps in our understanding for future study.

Introduction

Cooperation occurs at all levels of life. Genes cooperate to produce organisms, cells cooperate to produce multicellular organisms, and multicellular organisms cooperate to produce multicellular groups (Bourke 2011). Our understanding of how natural selection has favoured this cooperation has advanced considerably over the last 30 years (Box 1) (Sachs et al. 2004; West et al. 2007*b*; Bourke 2011; Taborsky et al. 2021; West et al. 2021; Boomsma 2023). This progress has resulted from successful integration of theory and empirical data: evolutionary theory predicts the conditions that favour cooperation, and empirical research has applied this theory to explain cooperation in a diversity of organisms, from viruses and bacteria to insects and birds.

In contrast, we have been much less successful in determining the longer-term ecological and genetic consequences of cooperation at the species level. Our distinction here is between the relatively shorter-term fitness consequences of cooperation at the individual level, which determine whether it is favoured by natural selection, and the longer-term consequences for species. These longer-term consequences include the habitats that species can exploit, the rates of speciation and extinction, and patterns of genetic variation. We lack answers to basic but fundamental questions about the longer-term consequences of cooperation. To give some concrete examples of the types of question we mean:

- Does cooperation influence the ability of species to exploit different environments (Cornwallis et al. 2017; Firman et al. 2020; Guindre-Parker and Rubenstein 2020)?
- Does cooperation influence the diversification of species, via extinction or speciation rates (Cornwallis et al. 2023)?
- Is cooperation especially important to the success of certain taxa or lifestyles, such as pathogenic bacteria?
- What are the consequences of cooperation at the genomic level, for factors such as genetic variation and genetic architecture (Linksvayer and Wade 2009, 2016; Dyken and Wade 2010, 2012; Dyken et al. 2011; Hall and Goodisman 2012; Hall et al. 2013; Ostrowski et al. 2015; Ghoul et al. 2017; Noh et al. 2018)?
- Does cooperation have the same or similar consequences across different taxa?
- Does cooperation within and between species have different consequences?

Progress in answering these kinds of questions requires the generation and testing of hypotheses. To provide a conceptual framework, we broadly classify the consequences of cooperation into two categories: (i) ecological, such as the type or diversity of environments in which organisms live (niche use); and (ii) genetic, such as patterns of diversity within species or the genetic architecture and underlying mechanisms (fig. 1). In the main parts of this paper, we provide examples where empirical research has already provided some evidence for the consequence of cooperation in these two areas. In each case we synthesise the existing research and highlight the outstanding problems.

We then ask whether cooperation has especially large consequences for certain taxa or lifestyles, and whether there are any applied implications of this research.

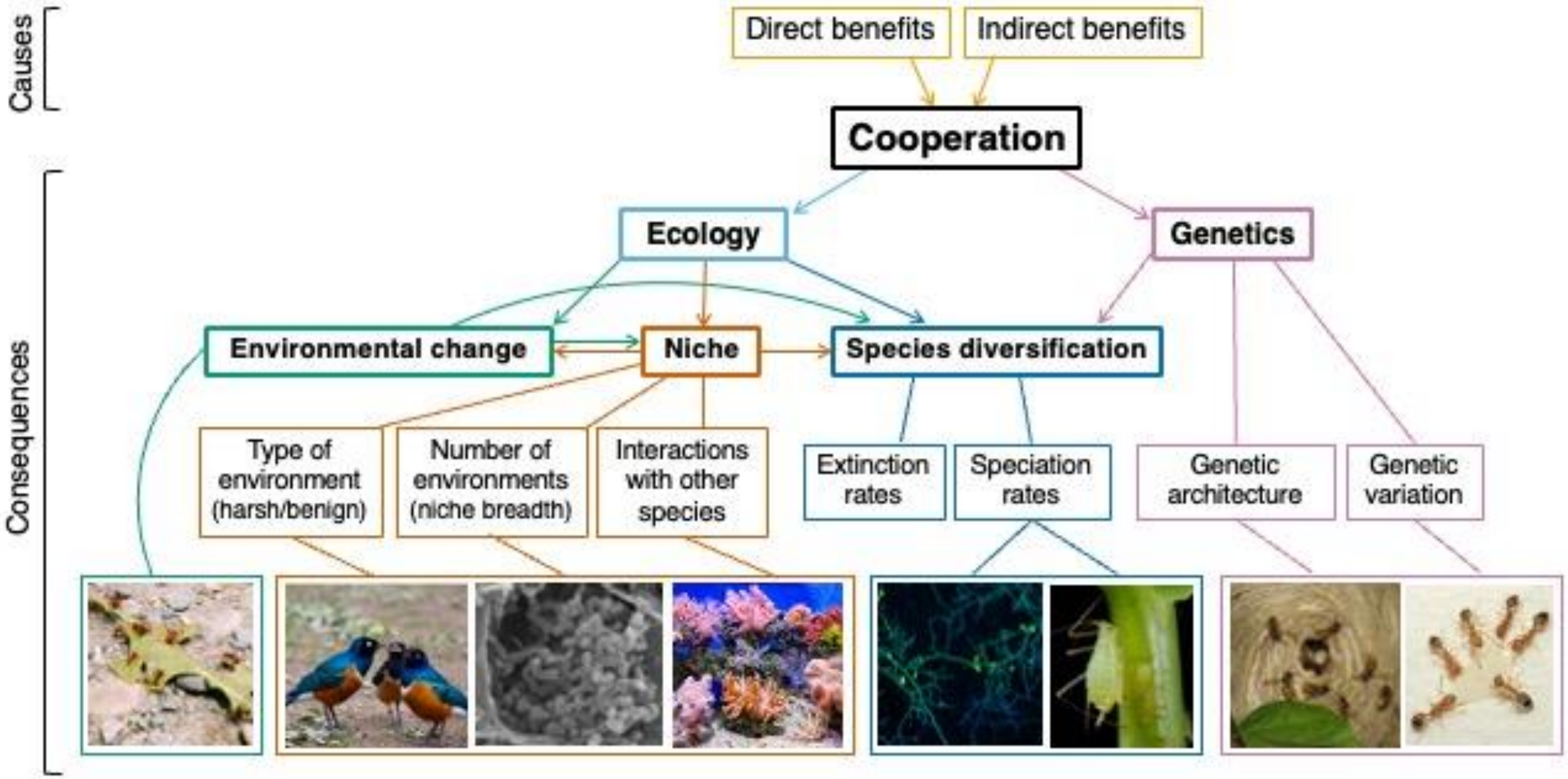

Figure 1: Cooperation can have major consequences for long-term ecological and evolutionary change. A classification dividing between ecological and genetic consequences. Examples from left to right: Leaf cutter ants are major herbivores in neotropical forests (*Attini* tribe). Cooperative breeding

allows birds such as superb starlings, *Lamprotomis superbus,* to live in harsh environments. Cooperation allows bacteria to live in a more diverse range of environments (niches) – image is Nitrogen-fixing bacteria (*Rhizobium sp.*) in a plant root nodule. Coral is a three-way symbiosis between the animals, *Symbiodinium* alga and apicomplexans, providing a habitat for many other species. The symbiosis with arbuscular mycorrhizal fungi helped their host plants colonize land. *Buchnera* bacterial symbionts provide their aphid hosts with essential amino acids, allowing them to live on plant sap (pea aphid, *Acyrthosiphon pisum*). Evidence of shared genetic toolkits controlling caste differentiation in Vespid wasps (Common Wasp, *Vespula vulgaris*). Signatures of kin selection for cooperation have been identified in the genomes of Pharoah ants, *Monomorium pharaonic*. Photos by: Ulrike Langer, Dennis Irrgang, Legume lover, Qui Nguyen, Oyarte Galvez, Shipher Wu, Donald Hobern, & Землеройкин .

Ecological consequences of cooperation

Species show considerable variation in the range of environments (niches) that they can colonise. Superb starlings can breed in African savannas, where both the temperature and variation in rainfall are high, whereas great tits breed in European woodlands, where temperatures are lower and variation in rainfall lower (Cornwallis et al. 2017). The bacterium *Pseudomonas aeruginosa* is found in variety of habitats, including water, soil, plants and animals. In contrast, *Mycobacterium tuberculosis,* which causes tuberculosis (TB), is highly adapted to human hosts and rarely found elsewhere. Can differences in cooperation help explain such variation? In this section we will review the relevant empirical studies and outline the major outstanding problems, especially the lack of a guiding theoretical framework.

Cooperation and consequences for the colonisation of harsh environments

Cooperative breeding birds are more likely to be found in harsh environments, where the temperature is higher and rainfall more variable (Arnold and Owens 1999; Rubenstein and Lovette 2007; Jetz and Rubenstein 2010; Griesser et al. 2017). This correlation has usually been taken as evidence for harsh environmental conditions favouring cooperative breeding. Causality could however be in the opposite direction, with cooperation facilitating the colonisation of harsh environments, or the correlation could be an artifact of correlations with another variable.

Ancestral state reconstruction provides a methodology for testing between the likelihood of these different causal hypotheses, by examining the order of evolutionary change (fig. 2A) (Cornwallis and Griffin 2024). Within birds, there was consistent support for the hypothesis that cooperative breeding facilitated the colonisation of harsh environments. The transition rate from living in a benign environment to living in a harsh environment was twice as high in cooperative as opposed to non-cooperative breeders (Cornwallis et al. 2017) (fig. 2B). In contrast, the transition rate from non-cooperative to cooperative breeding was not more likely in harsher environments (fig. 2B).

There are several other studies where the most likely direction of causality still needs to be tested (fig. 2C & 2D). For example, cooperative breeding mammals are more likely to be found in environments where annual rainfall is low (Lukas and Clutton-Brock 2017) (fig. 2D); Polistes wasp species which live in environments with greater short-term temperature fluctuations are more likely to form cooperative groups (Sheehan et al. 2015); ants with multiple worker castes (greater cooperative division of labour) are more likely to be found in hotter and drier climates (Richelière et al. 2022) (fig. 2C). These studies have used phylogenetic regressions to uncover correlations, but ancestral state construction has not yet been used test the relative likelihood of different causal hypotheses. An example of causality in the other direction is provided by work on Australian rodents, which found that transitions to some form of social group were more likely with low rainfall and high temperature variability (Firman et al. 2020). Causality could also be in both directions, leading to coevolution between cooperation and habitat use.

The consequences of cooperation across species can also be studied experimentally. Larger cooperative groups of the burying beetle *Nicrophorus nepalensis* were able to breed across a broader range of temperatures and elevations than smaller, non-cooperative groups (Sun et al. 2014). This was shown to be because larger groups are more effective against competitors, such as flies, which are more common at warmer temperatures. In ants, the development of large ‘supercolonies’ appears to help species to spread colonise and dominate as ‘invasive species’ (Fournier et al. 2019; Helantera 2022) .

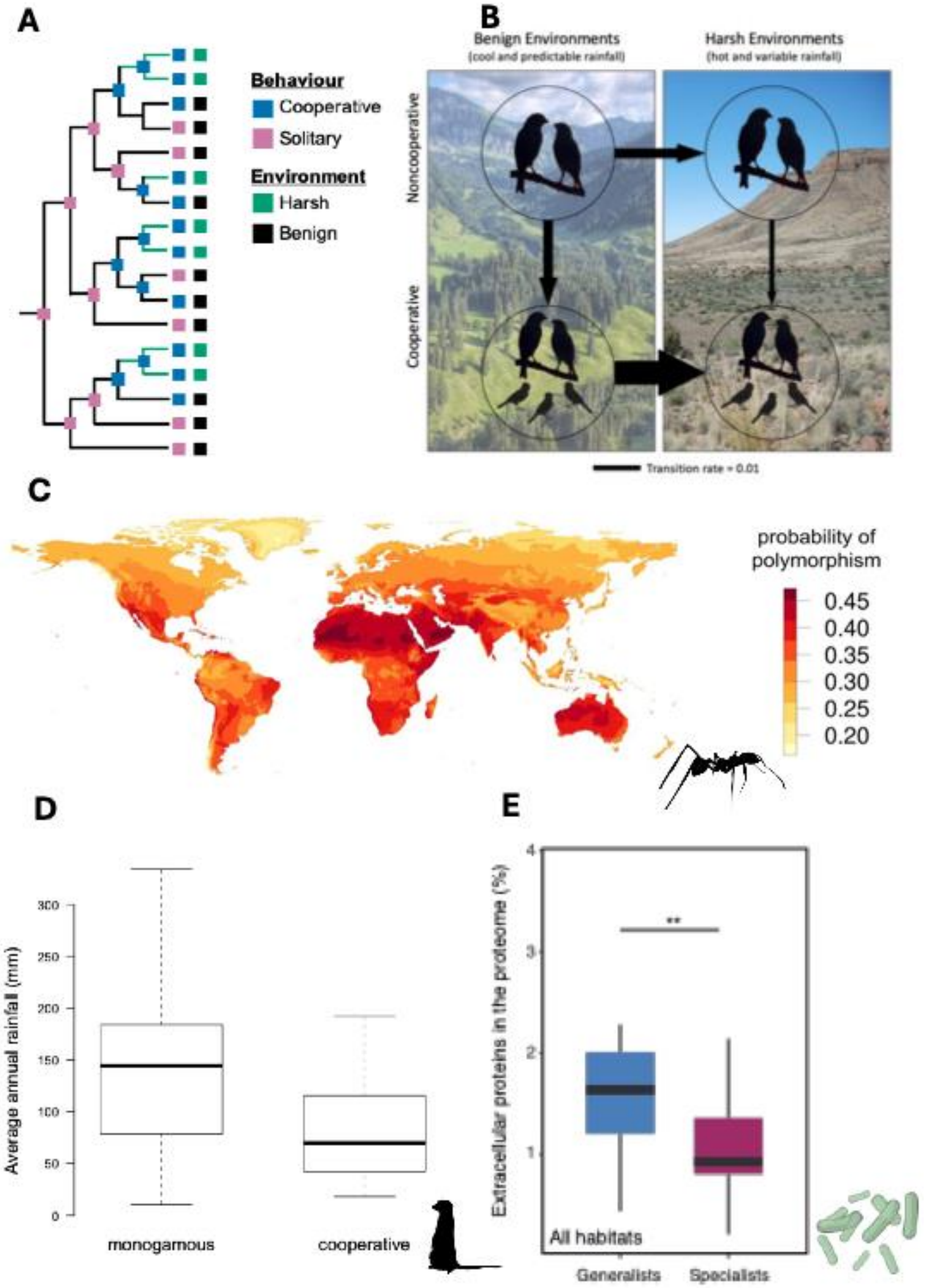

Figure 2: Consequences of cooperation for niche use. (A) Ancestral state construction allows the likelihood of different causal hypotheses to be compared. We use a hypothetical phylogeny to ask whether cooperation facilitated the colonisation of harsh environments or harsh environments facilitated the evolution of cooperation. Living species are cooperative breeders (pink squares) or

solitary (blue squares; non-cooperative) and live in harsh (green lines) or benign (black lines) environments. Cooperative breeding species are more likely to live in a harsh environment than solitary species. An analysis across estimated ancestral states shows that transitions to cooperative breeding (blue → pink squares) are not more likely to occur in harsh environments (along green lines), but that transitions to living in harsh environments (black → green lines) are more likely to occur in cooperative (pink species). This supports the causal hypothesis that cooperation facilitates the colonisation of harsh environments and does not support the hypothesis that harsh environments favoured the evolution of cooperation. (B) The transition rate from living in benign to harsh environments is significantly higher in cooperative breeding birds, compared with non-cooperative species. In contrast, the transition rate from non-cooperative to cooperative breeding is not higher in harsh environments (Cornwallis et al. 2017). (C) Ants that live in hotter and drier climates are more likely to have multiple worker castes (polymorphic workers) (Richelière et al. 2022). (D) Mammals that live in areas with lower rainfall are more likely to be cooperative breeders (Lukas and Clutton-Brock 2017). (E) Bacteria species found in a broad range of niches (generalists) have a higher proportion of genes which code for extracellular proteins than species found in few niches (specialists). Extracellular proteins are likely to represent cooperative public goods (Garcia-Garcera and Rocha 2020). Meerkat (*Suricata suricatta*) & ant (*Atta*) silhouettes by Michael Keesey & Courtney Rockenbach (PhyloPic; creative commons license). Bacteria from NIH bioart.

Cooperation and consequences for niche breadth

As well as being associated with harsh environments, cooperation may also have broader consequences for the range of environments (niches) that species can occupy or even the environments available to other species. Cooperation between species has resulted in the creation of entire eco-systems such as the mutualisms responsible for the formation of coral reefs and flowering plants. Cooperation within species may allow species to occupy a broader range of environments.

Consequences of between-species cooperation for niche breadth. Cooperation between species can have major consequences for determining the environments that species can exploit (Bronstein 1994). Symbioses with bacteria have allowed insects to expand to a range of diets that are low in B vitamins, including plant-based resources (phyloem, xylem or wood), plant parts (herbivory), fungi and blood (Cornwallis et al. 2023). This expansion to new habitats has also led to some spectacular changes in the species diversification rate – for example, herbivorous insect families with obligate symbionts have 15x as many species compared with herbivorous families without symbionts (Cornwallis et al. 2023).

There are even more extreme examples, which are crucial to the development and maintenance of numerous ecosystems. The symbiotic partnership between arbuscular mycorrhizal fungi and their host plants helped facilitate the colonization of land by plants over 400 million years ago (Remy et al. 1994) . Coral reefs are built upon a three-way symbiosis between the *Anthozoa* animals, *Symbiodinium* alga and apicomplexans that form coral (Kwong et al. 2019). Over 85% of flowering plants depend upon mutualistic cooperation with insects and other animals for pollination (Ollerton et al. 2011). Finally, cooperation can also impact ecosystems negatively. Leaf cutter ants account for approximately 25% of herbivory in Neotropical Forest ecosystems, harvesting 10-15% of leaves within their foraging range (Swanson et al. 2019). Cooperation between humans and honeyguides to exploit bee nests impacts upon both bees and the trees that contain their nests (Spottiswoode et al. 2016; Wal et al. 2022).

Consequences of within-species cooperation for niche-breadth. Bacterial species show considerable variation in the range of environments (niches) they can colonise - some have only ever been isolated from a single environment, whereas others are found in many (Kümmerli et al. 2014; McNally et al. 2014; Garcia-Garcera and Rocha 2020; Chen et al. 2021; Meijenfeldt et al. 2023).

Can cooperation help explain this variation in ‘niche breadth’? The evolutionary consequences of cooperation may be especially significant for bacteria and other microbes because they rely heavily on cooperation to exploit different environments (Griffin et al. 2004; Diggle et al. 2007; Sandoz et al. 2007; Chuang et al. 2009; Kümmerli and Brown 2010; Xavier et al. 2010; Cordero et al. 2012; Koschwanez et al. 2013; Dimitriu et al. 2014; Drescher et al. 2014; McNally et al. 2014; Ackermann 2015; Lyons and Kolter 2015; Bruce et al. 2017; Butaitė et al. 2017; Dragoš et al. 2018; O’Brien et al. 2018; Smith and Schuster 2019; Tai et al. 2022). Experimental studies have demonstrated that bacteria cooperate by secreting factors that provide a benefit to the local population of cells. These ‘public goods’ appear to play key roles in how bacteria acquire resources from their environment, and hence their ability to grow in different environments. For example, enzymes to break down proteins, and molecules to scavenge iron or aid movement.

Bacterial species which can colonise more environments possess more genes for extracellular proteins (fig. 2E) (McNally et al. 2014; Garcia-Garcera and Rocha 2020). These proteins are likely to act as public goods because they can diffuse away from the producing cell, potentially benefitting neighbouring cells. However, as with the correlations between cooperation and habitat use in animals, these results could be explained by multiple causal hypotheses. Cooperation could have facilitated the colonisation of more environments or living in a greater range of environments could favour increased cooperation.

Ancestral state reconstruction has since shown that species with a lower proportion of genes for cooperative traits are more likely to transition to exploiting a smaller number of environments (niche contraction) (Hao et al. 2024). A possible explanation for this result is that the cost of maintaining cooperative traits leads to more frequent gain and loss of cooperative genes depending upon environmental conditions. When they are lost, this can trigger niche contraction. In support of this explanation, a pangenome analysis found that genes for cooperative behaviours were more likely to be gained and lost at higher rates than genes for private behaviours (Hao et al. 2024). This means that cooperative genes are less likely to be found in the core genome (all the genomes sequenced in a species), and more likely to be found in the accessory genome (genes found in just a fraction of strains). Cooperation can simultaneously influence habitat use and gene gain/loss (genetic architecture), and how these are inter-linked.

The gain and loss of cooperation can also consequences for other species (Morris et al. 2012; Morris 2015) . Especially in microbes, the benefits of cooperative behaviours can be ‘leaky’ and shared with members of other species. Consequently, when a cooperative behaviour helps a species to live in a certain habitat, it could also help other species, that do not perform that behaviour, to also live in that habitat. For example, the extracellular enzyme invertase is secreted by yeast to decompose sucrose (Gore et al. 2009) . The presence of an invertase producing yeast in a fruit could therefore help other yeast species, that do not produce invertase, to colonise that fruit (Morris 2015) .

Consequences of cooperation for species diversification

There are several reasons why these ecological consequences of cooperation could also influence the rate at which species diversify. Cooperation could allow new habitats to be colonised, open gaps for speciation, decrease the extinction rate or aid in competition with other species. However, apart from the insect symbiosis example above, there is an almost complete lack of empirical work testing this hypothesis (Cornwallis et al. 2023). Advances in both molecular phylogenies and analytical methods offer a wealth of opportunities for examining species diversification (Nee 2006; Beaulieu et al. 2013; Maddison and FitzJohn 2015; Louca et al. 2018).

Outstanding problems

Research examining the consequences of cooperation for niche use is in its infancy and there is a wealth of unanswered questions. Across species studies investigating the consequences of cooperation for niche use are usually restricted to testing for correlations, and there is a need for studies that test for the most likely causal relationship. Detailed studies of single species are required to explain the across-species patterns. For example, how does cooperative breeding in birds, or multiple worker castes in ants, help individuals to survive and breed in harsh environments? Targeted comparisons can be made within species in which cooperative breeding may be present or absent to varying degrees, as it is in some birds (Cornwallis et al. 2017). Bioinformatic tools can be used to identify genes for cooperative traits in bacteria, allowing broad across species studies (Belcher et al. 2023*b*).

One of the reasons that we understand the evolution of cooperation so well is that inclusive fitness theory provides a relatively unified theoretical framework to explain it (Box 1). In contrast, a factor impeding research on the consequences of cooperation is that we lack a theoretical framework to predict and explain them. To what extent can we expect a similarly unified body of theory to explain the consequences of cooperation? The idea that cooperation could help colonise new environments is highly intuitive, and was proposed as far back as 1902, by the Russian prince, turned anarchist, Pyotr Kropotkin (Kropotkin 1902). However, as we discussed above, causality could also be in the opposite direction, and we need theory that allows for both possibilities.

One possible approach is to generate ‘eco-evolutionary feedback’ models that examine the interplay between ecology and cooperation to examine how each influence each other (Box 2) (*62*). For example, by examining how the level of cooperation can influence the type of environments which can be lived in, or the state of the environment, but also how environmental conditions influence selection for cooperation (Mullon et al. 2021; Prigent and Mullon 2023) . This approach could be used to develop a framework that predicts when we should see consistent patterns or variation across taxa. Any attempt to identify the critical biological details (parameters) would raise several questions. For example, do we just need to examine how environmental conditions influence the mean costs and benefits of cooperation (and vice versa), or do we also need to examine whether cooperation influences the variance in reproductive success (Kennedy et al. 2018; Santos et al. 2024)? As with previous theoretical developments it may be useful to develop theory for different scenarios and questions, and then later determine the extent to which they can be unified into a single framework (Charnov 1982; Frank 1998).

The form of cooperation may also be a crucial factor. For example, in vertebrates, we can differentiate between: (i) cooperative breeding species, which normally live in family groups and where helping is favoured because of indirect fitness benefits and (ii) communal breeding, which involves unrelated individuals coming together for mutual benefit (Downing et al. 2020). Communal breeding could represent a conditional response to harsh conditions that could be favoured in numerous species, whereas cooperative breeding will be restricted to relatively monogamous species which live in family groups (Cornwallis et al. 2010, 2017; Downing et al. 2020). Does that mean that cooperative breeding is more likely to facilitate colonisation of harsh environments, while communal breeding is more likely to be a response to harsh environments?

Genetic consequences of cooperation

We now turn to a second area - the genetic consequence of cooperation. There are theoretical reasons to expect cooperation to influence patterns of genetic variation within-species, which have gained some empirical support. In addition, there is increasing empirical evidence that cooperation can influence the evolution of the underlying genetic basis of traits (genetic architecture).

Consequences for patterns of genetic variation within species

An exciting aspect of this area is that we already have a theoretical framework for generating hypotheses for the effect of cooperation on patterns of genetic variation within-species, such as nucleotide diversity within populations. In this section we will summarise the theory, review the support for this theory, and outline the major outstanding problems.

Predicting genetic variation. Population genetic theory predicts that kin selection for cooperation will leave a signature, or 'footprint', at the genomic level (Linksvayer and Wade 2009, 2016; Dyken and Wade 2010, 2012; Dyken et al. 2011; Hall and Goodisman 2012; Hall et al. 2013). Consider a bacterial species that reproduces clonally. Genes that code for private traits provide a direct benefit to the individual expressing them. Genes that code for cooperative traits provide an indirect benefit to other cells in the population. In a clonal population, the cells that benefit from cooperation will also carry the cooperative gene, as relatedness $r = 1$. However, in a nonclonal population, the cells that benefit from cooperation might not carry the gene for cooperation, as relatedness $r < 1$.

If the benefits of cooperation go to cells that do not carry the gene for cooperation, then this reduces or 'relaxes' selection for cooperation relative to private traits, where the benefit of a gene always go to the individual carrying the gene. This relaxed selection when $r < 1$ results in an increased probability that deleterious mutations are maintained in the population, and a decreased probability of fixation for beneficial mutations (fig. 3A) (Linksvayer and Wade 2009, 2016; Dyken and Wade 2010, 2012; Dyken et al. 2011; Hall and Goodisman 2012; Hall et al. 2013). The consequence of this change in fixation probabilities, when $r < 1$, is that there is an accumulation of genetic variation, which can be tested for with population genetic analyses. Specifically, we predict an increased polymorphism and divergence in genes for cooperative behaviours relative to genes for private behaviours (fig. 3B). In contrast, the benefits of cooperation in clonal populations would always go to individuals carrying the gene for cooperation, and so selection would not be relaxed.

This leads to two predictions: (1) In non-clonal populations, genes controlling cooperative traits will have higher polymorphism and divergence, and more deleterious mutation, relative to genes for private behaviours (fig. 3B). (2) As relatedness decreases, genes for cooperative traits are predicted to have increasingly larger polymorphism and divergence, and more deleterious mutations (fig. 3C). An analogous prediction can be made for sexually reproducing species, but the critical value of relatedness is when helpers are equally related to their own offspring and those they are helping (full siblings, r=0.5), rather than clonal populations (Hall et al. 2013). In such studies it is important to control or test for alternative explanations such as variation in gene expression (Belcher et al. 2022, 2023*a*) .

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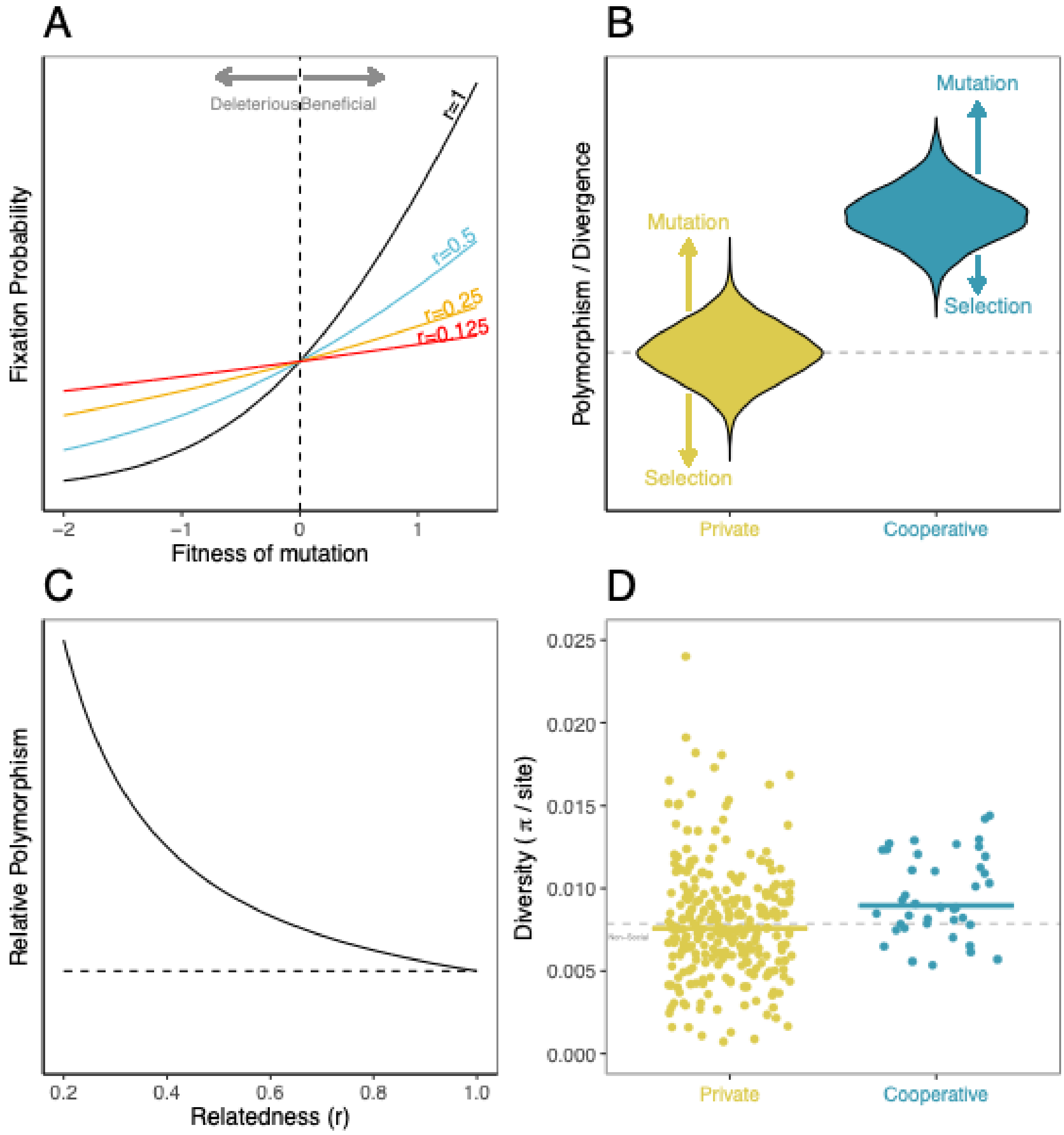

Figure 3: Consequences of cooperation for patterns of genetic diversity within-species. (A) Population genetic theory for cooperative traits (Linksvayer and Wade 2009, 2016; Dyken and Wade 2010, 2012; Dyken et al. 2011; Hall and Goodisman 2012; Hall et al. 2013). Mutations influencing private traits (black line) are: more likely to fix when they are beneficial relative to mutations influencing cooperative traits (coloured lines); and less likely to fix when deleterious. This effect is more pronounced with lower genetic relatedness (*r*) between interacting cells. (B) Consequently, genes for cooperation are predicted to have elevated polymorphism (and divergence; when *r*<1). (C) As relatedness decreases (lower *r*), genes for cooperation are predicted to have increasingly larger polymorphism (and divergence) relative to genes for private traits. The dashed

line shows the expectation for genes which control private traits. (D) Data from *P. aeruginosa* supports the prediction shown in panel B, with genes for cooperative traits (blue) showing significantly higher polymorphism than genes for private traits (yellow) (Belcher et al. 2022). The comparison is between cooperative and private traits controlled by quorum sensing, and each dot represents a gene. The same qualitative pattern has observed for other forms of cooperation (e.g. iron scavenging, antimicrobial resistance, toxins & movement) and in another species (*B. subtilis*) (Belcher et al. 2022, 2023*a*, 2023*b*).

Testing predictions I: Bacteria and other microbes. These theoretical predictions have been supported by data from two species of bacteria, *Pseudomonas aeruginosa* and *Bacillus subtilus*. Studies on both species found that genes for putatively cooperative traits (behaviours) showed increased polymorphism and divergence, and more deleterious mutation, relative to genes for private traits (fig. 3D) (Belcher et al. 2022, 2023*a*). The putatively cooperative traits studied included a number of factors which are produced by cells, released extracellularly and provide a benefit to the local population of cells, not just the cell that produced them (West et al. 2006, 2007*a*) . For example, extracellular enzymes to digest proteins, iron scavenging siderophore molecules, and bacteriocin toxins. These analyses supported the suggested role of kin selection for cooperation in these species and showed how cooperation can lead to increased genetic variation. Just as social evolution can help explain phenotypic variation across species, it appears that social evolution can help explain genetic variation.

In contrast, genes associated with non-cooperative cheating in the slime mould *Dictyostelium discoideum* did not show the elevated divergence consistent with relaxed selection. This pattern is however also predicted, because relatedness is almost clonal in this species (r=0.98) (Gilbert et al. 2007; Noh et al. 2018). Further analyses on *D. discoideum* also showed increased polymorphism that was consistent with cheats having an advantage when rare (frequency dependence or balancing selection) (Ostrowski et al. 2015). Different kinds of social interaction are predicted to generate different footprints at the genomic level (Ostrowski et al. 2015; Ghoul et al. 2017) .

Testing predictions II: Social insects. Relaxed selection on cooperative traits has also been detected in social insects. Transcriptome data has been used to identify genes for cooperative traits, depending on whether they are significantly upregulated in workers (cooperative genes) or queens (private genes) (Hall and Goodisman 2012; Warner et al. 2017; Chandra et al. 2018; Imrit et al. 2020; Taylor et al. 2021; Wyatt et al. 2023). If a gene is significantly upregulated in workers, that do not reproduce, then it can only be favoured because of its indirect fitness consequences *via* queen reproduction.

An analysis on the pharaoh ant, *Monomorium pharaonsis,* found relatively weak selection in worker-upregulated (cooperative) genes, relative to reproductive-upregulated (private) genes (Warner et al. 2017). This is predicted in this species, where there are multiple queens and so relatedness is relatively low. In addition, as also predicted by theory, a comparison of two species found greater variation in worker-upregulated genes in species where the queen mates multiply and so relatedness is lower (honeybee, *Apis mellifera*), relative to a species where the queen mates with only one male (fire ant, *Solenopsis Invicta*) (Hunt et al. 2010, 2011; Hall and Goodisman 2012).

The consequences of cooperation for patterns of genetic variability: future directions. The influence of cooperation on genetic variation has been examined in a very small number of bacteria and social insect species. Further empirical work is required to: (i) test the generality of the prediction that kin selection for cooperation leads to increased polymorphism, divergence and deleterious mutations; (ii) test whether this theory can be used to explain differences in the level of genetic variation across species. Previous studies have been limited by our ability to identify genes for cooperation with labour intensive methodologies, based on experimental results, but improved methods are being developed for this, using gene annotation in bacteria and gene expression data in social insects (Belcher et al. 2023*b*; Wyatt et al. 2023) . A potential problem with work in this area is that a negative result can be explained by either a high relatedness or the putatively cooperative traits being private (e.g. r=1 for an asexual species in fig. 3A).

While we already have a theoretical basis for how cooperation can influence genomic variation, there are several ways in which it needs to be extended to clarify predictions for different scenarios. Population genetic theory suggests that several factors other than kin selection for cooperation, including conditional expression, can also lead to increased polymorphism and divergence (Linksvayer and Wade 2009, 2016; Dyken and Wade 2010, 2012; Dyken et al. 2011; Hall and Goodisman 2012; Hall et al. 2013; Ostrowski et al. 2015; Ghoul et al. 2017; Noh et al. 2018). How do these factors interact? Another way of looking at this, is that previous theory has assumed that: 'all else is equal' across genes for private and cooperative traits (e.g. similar costs and benefits); and that alternative factors such as frequency dependent selection were not also operating. What if that is not the case? How can we control for the influence of other factors when testing for an influence of cooperation? In addition, what are the consequences of different levels of sociality, cooperation between species, or other types of social interaction, such as parent-offspring interactions in vertebrates. Can novel predictions be made for comparative studies across species?

Consequences of cooperation for genetic architecture

Cooperation can not only influence patterns of genetic variation - it can also facilitate or arise from changes in the genetic architecture (Ghoul et al. 2017). Possible changes to the genetic architecture include the evolution or acquisition of new genes, the rewiring of existing gene networks, change in genome size, and the evolution of supergenes (McCutcheon and Moran 2011; Simola et al. 2013; Wang et al. 2013; Kapheim et al. 2015; Hanschen et al. 2016; Mullon et al. 2018; Rubenstein et al.

2019; Lengronne et al. 2021; Taylor et al. 2021, 2024; Sumner et al. 2023; Wyatt et al. 2023). We might expect the consequences of cooperation for genetic architecture to depend upon the form of cooperation. Bacterial symbionts show extreme genome reduction, and symbiont species with smaller genomes provide greater benefits to their hosts (McCutcheon and Moran 2011; Fisher et al. 2017). Genome reduction is also seen in pathogens (Murray et al. 2020).

There are numerous ways in which cooperation could influence selection on the genetic architecture. Selection for a diversity of non-cooperative ‘cheats’, who fail to perform different cooperative behaviours, has been suggested to lead to genome fragmentation in multipartite viruses, where the genome is split into multiple segments, each of which is transmitted via a separate capsid (Leeks et al. 2023). In bacteria and other microbes, when the benefits of cooperation are ‘leaky’ and shared with other species, this can select for those other species to lose the genes for those cooperative behaviours (the ‘black queen hypothesis’) (Morris et al. 2012; Morris 2015). Cooperation and conflict between genes can influence selection on many selfish genes, their suppressors, and epigenetic functions such as imprinting (Haig 2002; Burt and Trivers 2006; Scott and West 2019). Cooperation could influence selection for and / or the atability of ‘supergenes’ (Mullon et al. 2018).

There is not yet been sufficient data collected to support a useful synthesis in this area, and we lack a theoretical framework. Consequently, several fundamental questions remain. How repeatable or predictable are these changes? Do we see some convergence at the genomic level, or do the mechanistic details vary? How is the influence of cooperation in bacteria influenced by horizontal gene transfer (Dewar et al. 2021, 2024; Scott et al. 2023; Hao et al. 2024)? Does cooperation favour the construction of pleiotropic links between cooperative and private traits, or does pleiotropy favour cooperation (Santos et al. 2018; Bentley et al. 2022). Can the different examples of consequences for genetic architecture be brought together into a single conceptual framework?

More generally, the study of cooperation has been essential to understanding variation and adaptation at the phenotypic level, and so we suspect that it is also highly likely to be important at the genomic level, for explaining both patterns of genetic variation and genetic architecture (Linksvayer and Wade 2009, 2016; Dyken and Wade 2010, 2012; Dyken et al. 2011; Hall and Goodisman 2012; Hall et al. 2013; Hanschen et al. 2016; Ghoul et al. 2017; Rubenstein et al. 2019; Sumner et al. 2023).

Is cooperation especially important for certain taxa or lifestyles?

We have attempted to synthesise across different taxa. But it is also worth stepping back and asking if we expect the consequences of cooperation to be especially large in certain taxa, or with certain lifestyles. We have already suggested that cooperation has major consequences for bacteria because it plays a key role in how they obtain resources from the environment. We also hypothesise that cooperation has especially important consequences for pathogenic bacteria. Cooperation can be critical to pathogen growth, and the damage that a pathogen causes to its host (virulence), by acquiring resources or tackling immune responses. For example, the survival rate after three days when mice were infected with *P. aeruginosa* can be increased from 0% to ≈50% by coinfecting with a non-cooperative 'cheat' (Rumbaugh et al. 2009). Does cooperation influence the evolution of antibiotic resistance, the ability to move to new host species, or the ability to become opportunistic pathogens (Yurtsev et al. 2013; McNally et al. 2014; Frost et al. 2018; Sheppard 2022; Ma et al. 2024)? It remains an open question whether cooperation is especially important for other taxa or lifestyles.

Applied implications

Before we conclude, are there also applied implications of the topics that we have discussed in this paper? Yes, the longer-term consequences of cooperation have implications for managing pathogens, conservation and biotechnology. Because cooperation is so important for the success of many pathogens, interventions that reduce cooperation can potentially also reduce virulence (Rumbaugh et al. 2009). Interventions that disrupt cooperation can be harder to evolve resistance to than antibiotics (André and Godelle 2005; Dieltjens et al. 2019). The introduction of non-cooperative cheats (‘cheat therapy’). has been used to reduce virulence in for viruses and could potentially also be applied to bacterial pathogens (Brown et al. 2009; Leeks et al. 2021). Can cheats be used as ‘trojan horses’ to drive useful genes into infections, such as antibiotic susceptibility (Brown et al. 2009; Mutlu et al. 2024)?

Considering conservation, if we know how cooperation influences the ability of species to survive in different environments, then we could predict how they will respond to climate change or other changes imposed by humans (Kiers et al. 2010). For example, will different types of cooperation make species more or less vulnerable to climate change, or require different conservation strategies? Considering biotechnology, many processes such as biodegradation of waste products or pollutants, rely on cooperation or cooperative division of labour to either break things down or to produce things (Nikel et al. 2014; Cavaliere et al. 2017; Rafieenia et al. 2022). Consequently, the causes and consequences of cooperation can be exploited to increase the efficiency of these processes. For example, could manipulations of the genetic architecture be used to reduce the short-term invasion of non-cooperative cheats that would reduce the efficiency of such bioprocesses (Santos et al. 2018) . Finally, human societies are built upon cooperation and so we can also apply any of the questions raised in this paper to humans. For example, can it be shown, analogous to the patterns in birds or bacteria, that cooperation has played a key role in determining where and how different human societies live.

Conclusions

We conclude by emphasising the enormous potential for future work, both theoretical and empirical. Except for some pivotal analyses of how cooperation can influence genetic variation, we largely lack a theoretical framework for understanding the longer-term consequences of cooperation. We suspect that it would first be useful to generate models for specific scenarios and then try to build up towards a theoretical overview. Empirically, with just a couple of notable exceptions, there is an almost complete lack of empirical work examining the consequences of cooperation. In what species does cooperation influence factors such as habitat use, patterns of diversification, genetic variability or genetic architecture? How widespread is the influence of cooperation? Is cooperation especially important for certain taxa or lifestyles? To what extent can we explain different cases with a single theoretical framework or identify broad patterns? Can exploit the consequences of cooperation to manage pathogens, aid conservation strategies or improve the efficiency of biotechnologies? The lack of research on these questions matters because there are reasons to expect the consequences of cooperation to be substantial, across a diversity of taxa.

Box 1. The evolution of cooperation.

A behaviour or trait is cooperative if it provides a benefit for another individual and has evolved at least partially because of this benefit (West et al. 2007*c*). Examples include subordinate helpers at the nest in cooperative breeding birds, the sterile workers of ants, and when bacteria produce ‘public goods’ that benefit the local group of cells. Inclusive fitness theory provides two broad categories of theoretical explanation for cooperation: direct fitness benefits and indirect fitness benefits (kin selection) (Sachs et al. 2004; West et al. 2007*b*; Boomsma 2023) .

Direct fitness benefits arise when cooperation increases the reproductive success of the actor that performs the cooperation (Trivers 1971; Axelrod and Hamilton 1981). In this case, cooperation is ‘mutually beneficial’, benefiting both the actor and the recipient. Direct benefits could arise as a simple consequence of cooperation. For example, the fitness of a symbiont could depend upon 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 cooperation (Hamilton 1964). 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 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 $rB\text{-}C>0$, 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 (Hamilton 1963, 1964). Indirect fitness benefits can explain altruistic 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).

There is a vast amount of evidence for how indirect benefits can explain altruistic cooperation within species, including: across species (e.g. higher levels of cooperation when relatedness is higher); observational (e.g. kin discrimination or finding that $rB\text{-}C>0$); experimental (e.g. manipulations of relatedness); and population genetic (signatures of kin selection for cooperation) studies (West et al. 2021). Furthermore, this work is across the entire tree of life from bacteria and slime moulds to insects and birds. Direct benefits are less important for explaining cooperation within species, where they are usually associated with less costly forms of cooperation, such as grooming.

Similarly, there is also much evidence for cooperation between species being favoured when there is a direct or indirect benefit to helping an individual of another species. This can occur because the reproductive interests of different species are intertwined (e.g. via horizontal transmission of symbionts) or when one partner enforces cooperation from the other partner (e.g. sanctions or trading) (Kiers et al. 2003, 2011).

The inclusive fitness benefits of cooperation also provide a framework for explaining when major evolutionary transition in individuality have taken place (Bourke 2011; West et al. 2015; Boomsma 2023). We have not considered major evolutionary transitions in this paper because they are relatively rare evolutionary events (albeit hugely important!), already covered elsewhere, and we are concerned with the more continuously varying macroevolutionary and macroecological processes such as habitat use, genetic variation and diversification.

Box 2. A theoretical framework to explain the consequences of cooperation.

Most theoretical models have used inclusive fitness or game theory to explore the factors that can favour cooperation (Box 1). In contrast, these models rarely explore the consequences of cooperation for ecological or evolutionary processes such as habitat use, or how those processes then feedback on the evolution of cooperation (i.e., *eco-evolutionary* feedback) (Lion 2018; Govaert et al. 2019; Yamamichi et al. 2020; Lion et al. 2023) .

Recent studies have developed theoretical models incorporating the feedback processes between cooperation and eco-environments, based on a common framework feedbacks (Weitz et al. 2016; Mullon and Lehmann 2018; Estrela et al. 2019; Tilman et al. 2020; Yamamichi et al. 2020; Mullon et al. 2021, 2024).To demonstrate this, we follow Tilman et al. (2020) by describing a model of joint dynamics of cooperation and environmental state, in which the population consists of cooperator (low-harvester; frequency p) and non-cooperator (high-harvester; frequency $1-p$), and the resource availability e (which determines the environmental state).

In general, the replicator-equation yields the frequency dynamics of the form $\mathrm{d}p/\mathrm{d}t = p\ (f\ (p, e) - m)$, where f is payoff to cooperator, and m is population-wide mean of payoff (i.e., average of f). This equation tells us that the evolutionary dynamics is determined not only by the frequency of the cooperators f but also on environmental state e. On the other hand, the environmental state may change with the fraction of cooperators, so we can write: $(\mathrm{d}e/\mathrm{d}t)\ \varepsilon = r\ (1 - k\ e\ )\ e - g(e, p)$, where r represents intrinsic growth of resource, k represents density-dependent degradation, g represents the effect of cooperation on the change in resource availability, and ε represents the relative timescale of the environmental dynamics (time in $\mathrm{d}e/\mathrm{d}t$) to evolutionary dynamics (time in $\mathrm{d}x/\mathrm{d}t$). Specifically, when $\varepsilon=0$, the environment is extremely fast whereas large ε leads to slow environmental changes. This framework allows for predicting the condition for either (i) the occurrence of stable, constant coexistence of cooperator and non-cooperator, or (ii) joint oscillation of evolutionary and environmental dynamics (Tilman et al. 2020). Depending on model assumptions, other consequences are possible, including chaotic dynamics. Parameters can be varied to determine their influence on the relationship between cooperation and environments (e.g., the timescale in Tilman et al 2020). As such, the modelling framework can help identify mechanisms of cooperation for other variables.

More generally, we could use a diversity of modelling frameworks to examine evolutionary and ecological dynamics. For instance, assuming polygenic effects on cooperative traits, we can combine quantitative genetics models with ecological or environmental dynamics, which is a well-established framework to model joint dynamics of ecology and evolution (Pelletier et al. 2009). Alternatively, we could make use of replicator dynamics for “qualitative” traits; for example, phenotypes like rock, paper, and scissors with explicit dependence on temporally varying environmental conditions (Sinervo and Lively 1996). Finally, whereas these modelling approaches are simple and analytically tractable, stochastic simulations (such as individual-based simulations) can incorporate various complex, and realistic, mechanisms of cooperation and environmental dynamics, which could allow for examining the effect of cooperation on population persistence for applied purposes such as conservation.

Acknowledgements

We thank: the *American Naturalist* for inviting this review; Zohar Katz, Gen Kurosawa & Sébastien Lion for useful comments; Charlie Cornwallis, Dieter Lucas, Gabriel Munoz & Eduardo Rocha for kindly providing figures; the European Research Council (834164) and St John's College, Oxford for funding.

Author Contribution statement

SAW conceptualised the paper. All authors contributed to the writing and figures.

Figure 2: B is figure 5 from (Cornwallis et al. 2017). C is figure 2 from (Richelière et al. 2022). D is figure 2a from (Lukas and Clutton-Brock 2017). E is Figure 6a in (Garcia-Garcera and Rocha 2020).

Supplementary Information

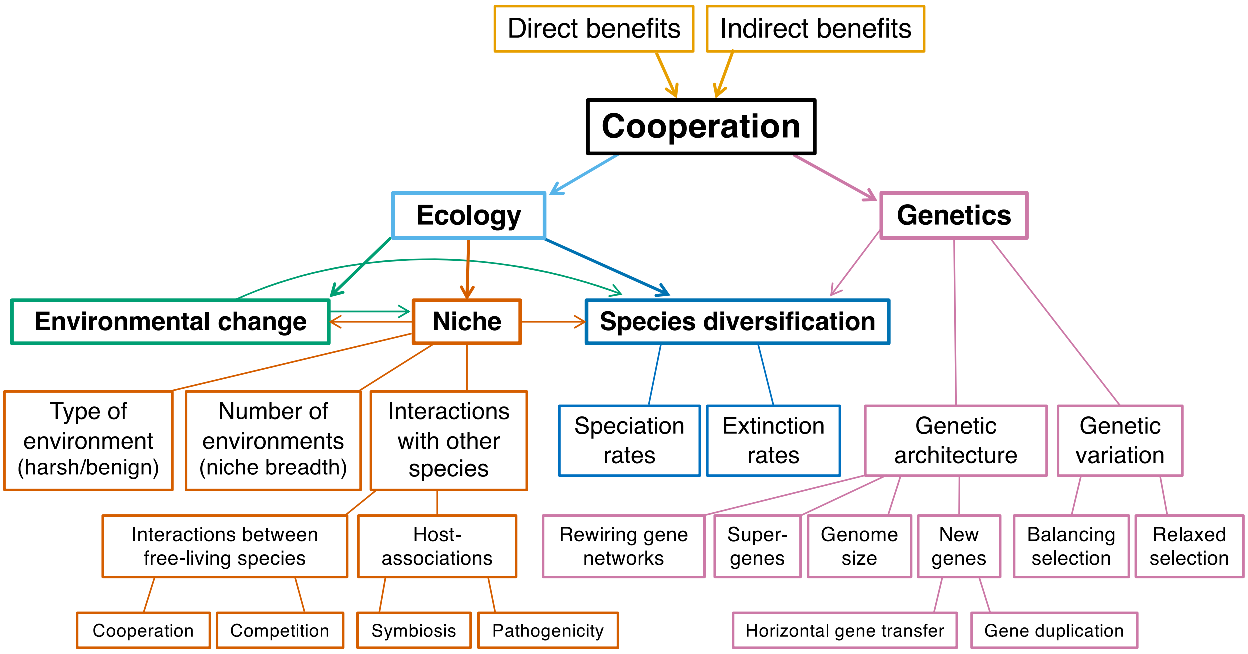

Figure S1: Cooperation can major consequences for long-term ecological and evolutionary change. A classification dividing between ecological and genetic consequences – providing a more detailed classification than the summary figure in the main text.

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