

The tragedy of the commons in evolutionary biology

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Garrett Hardin's tragedy of the commons is an analogy that shows how individuals driven by self-interest can end up destroying the resource upon which they all depend. The proposed solutions for humans rely on highly advanced skills such as negotiation, which raises the question of how non-human organisms manage to resolve similar tragedies. In recent years, this question has promoted evolutionary biologists to apply the tragedy of the commons to a wide range of biological systems. Here, we provide tools to categorize different types of tragedy and review different mechanisms, including kinship, policing and diminishing returns that can resolve conflicts that could otherwise end in tragedy. A central open question, however, is how often biological systems are able to resolve these scenarios rather than drive themselves extinct through individual-level selection favouring self-interested behaviours.

The tragedy of the commons

The tragedy of the commons (see Glossary) provides a useful analogy allowing us to understand why shared resources, such as fisheries or the global climate, tend to undergo human overexploitation [1]. The analogy, which dates back over a century before Hardin's original paper [2], describes the consequences of individuals selfishly overexploiting a common resource. The tragedy of the commons was originally applied to a group of herders grazing cattle on common land. Each herder only gains a benefit from his own flock, but when a herder adds more cattle to the land to graze, everyone shares the cost, which comes from reducing the amount of forage per cattle. If the herders are driven only by economic self-interest, they will each realize that it is to their advantage to always add another animal to the common: they sacrifice the good of the group (by forgoing sustainable use of the resource) for their own selfish gain. Thus, herders will continue to add animals, eventually leading to a 'tragedy' in which the pasture is destroyed by overgrazing [1].

The difficulties inherent in protecting shared common resources, such as marine stocks or clean air, are well known: whereas everyone benefits from an intact resource, there is an individual-level temptation to cheat (e.g. to

overexploit or pollute), because cheating brings economic advantages to the individual, whereas costs are distributed among all individuals (Box 1). The lesson drawn from these studies is that solving the dilemma often requires negotiation and sanctions on disobedient individuals. This changes the payoffs, so that group-beneficial behaviour also becomes optimal for the individual: an example would be imposing heavier taxes on polluting industries. Hardin's own main solution to the tragedy of the commons was state governance and privatization of the resource in question [1]; in general, social norms as well as individual morality have been considered good candidates for preventing over-exploitation of common resources.

Despite citing Lack's work on population regulation [3] to contrast population regulation in birds with human population growth, Hardin did not venture to extend his analogy to the problems of evolutionary ecology. However, if the tragedy can only be avoided when higher-level incentives are invoked, as in the case of legal incentives,

Glossary

Cheater: an individual that gains a benefit from the collective, without investing in the collective itself. These individuals can also be called 'free-riders'.

Collapsing tragedy: a situation in which selfish competition or free-riding escalates until the resource is fully depleted. This can cause the collapse of the entire population (i.e. extinction) if the resource was essential.

Component tragedy: a tragedy of the commons in which escalated competition stops before a collapse is reached.

Cooperation: the act of individuals paying an individual cost to contribute to a collective benefit.

Individual-level selection: selection acting at the level of the individual, to favour individuals or genes that maximise their own fitness.

Overexploitation: the depletion of a resource beyond the point at which sustainable use is possible.

Payoff: the overall benefits and costs gained from a particular strategy or behaviour.

Public good: a common resource that benefits all individuals in a group.

Resolution: the absence of a tragedy of the commons. That is, a situation in which inherent conflict causes no group-level costs.

Social good: a public good that is shared by all members of a population or group and is specifically created by cooperating individuals.

Species-level selection: selection that arises by differential extinction of species.

Tragedy of the commons: a situation in which individual competition reduces the resource over which individuals compete, resulting in lower overall fitness for all members of a group or population.

Zero-sum game: a situation in which one individual's gain is matched by other individuals' loss. Cutting a cake and chess are both examples of zero-sum games.

Box 1. The tragedy of the commons in human environmental problems

Hardin's original essay dealt with both pollution and human overpopulation [1], but the main point of his article was that a common resource would always be overexploited when utilized by self-interested individuals. Pollution, climate change and over-exploitation of fisheries all involve public goods suffering from the free-rider problem, and are thus examples of the tragedy of the commons. For example, the collapse of North Atlantic cod [52] shows how easily common resources can be overexploited. People tend to value their own short-term self-interests over the long-term good of the planet, so it is difficult to solve environmental problems by appealing to individual goodwill only. Public awareness of resource limitation can even hasten overexploitation: endangered species are traded at higher prices when their perceived rarity increases [53]. Convincing participants to behave in a group-beneficial way requires that individuals trust that the desired outcome is reachable and that free-riders will not benefit. Such trust is difficult to create whenever data and experience show otherwise.

A flipside of the tragedy of the commons is that avoiding it can often be beneficial to the players involved, and can be described as win-win situations if policies are improved. For example, right whales often become entangled in lobster fishing gear. Although fishermen are not keen to reduce their income, a comparison of Canadian and American lobster fisheries shows that reducing the risk of entanglement can be achieved with no economic cost [54]: reducing fishing effort leads to improved yield of lobsters per recruit. Similarly, despite considerable resistance and cynicism, marine reserves (areas where fishing is prohibited) can benefit all fishermen, even over the short-term [55]. Policy negotiations are difficult in these situations, because people distrust others, but also because long-term benefits are rarely given sufficient weight [56]. Without extensive education, such benefits are met with scepticism. For example, the population dynamic arguments that relate catch effort to expected yield in fisheries are not intuitively obvious. Easily perceived individual benefits would help to solve these problems. For example, using people's desire to improve their social reputation could prevent exploitation of the common good, as is seen in experimental 'climate games' in which participants improve their reputation by investing publicly to sustain the global climate [57].

The examples in Table 1 show a wide range of tragedies, dealing with different resources, from external resources to social goods created by either cooperation or competitive restraint. What is striking is that organisms with little cognitive ability are frequently able to resolve the tragedy with little or no cognitive or communicative abilities. With our advantage of communication and foresight, solutions to human tragedies of the commons should be within reach, but they are best solved, as Hardin advocated, using 'mutual coercion, mutually agreed upon'.

this raises the question of how non-human organisms can avoid overexploiting the resources on which they depend. After the group selection debate of the 1960s [4], it should be clear that this question is not trivial: natural selection acts primarily at the level of the gene, and therefore favours individuals that serve their own selfish interests [5]. Nevertheless, it is only in the last decade that the tragedy of the commons analogy has become increasingly used by evolutionary biologists (Table 1) to explain why selfish individuals in animal and plant populations do not evolve to destroy the collective resource (for examples, see Refs [6–13]).

A tragedy of the commons in evolutionary biology refers to a situation in which individual competition over a resource reduces the resource itself, which can in turn reduce the fitness of the whole group [14]. The tragedies

discussed here can apply to a range of levels: groups, populations or species. The concept has been used in a diversity of fields in biology, ranging from plant competition for resources (for example, see [7]) to the evolution of cooperation and conflict in insect societies (for example, see [9]). What the tragedies have in common is that individuals are selfishly maximizing their own fitness at the expense of the productivity of the group or population. Here, we seek to review how the tragedy of the commons is used in the literature, with the hope of highlighting that the underlying principles are the same, regardless of the system or the level at which the tragedy of the commons occurs.

Types of tragedy

Despite the relatively recent acquisition of the tragedy of the commons analogy into evolutionary biology (but see [14]), not all studies use the same definition for a tragedy of the commons, and there are many related terms (see Glossary). As confusing terminology can hinder the development of a field [15], here we seek to define different forms of the tragedy of the commons (Tables 1 and 2). What these tragedies all have in common is that individual selfishness reduces the resource over which individuals are competing and lowers group fitness. The tragedy of the commons in evolutionary biology, therefore, encompasses what social scientists call a public good game, or an N-person prisoner's dilemma (for example, see [16]).

Resources prone to a tragedy of the commons

One can distinguish three types of group-level costs of competition that might result in a tragedy of the commons (Table 2). The first, which fits exactly with Hardin's original analogy, involves individuals selfishly exploiting a common resource until the resource is reduced to the point that the individuals no longer can persist on it. Examples include simple competition for food, but reproductive traits, such as high virulence in parasites [17] and laying larger clutches in an attempt to out-reproduce others, can also be involved. Although it has been suggested that only competition over an extrinsic resource should be viewed as a tragedy of the commons (for example, see [18]), evolutionary biologists have applied the term to a much wider range of contexts (for example, see [6,8,9,12,19]). Figure 1a shows the case of bacteriophages surrounding a bacterium [12], a system that is prone to a tragedy of the commons when the virulence of the phages becomes so high that they destroy the bacteria on which they exist.

Although Hardin's analogy was originally applied to the overexploitation of an external resource, evolutionary biologists have realized that the analogy reflects a wide range of social dilemmas and can potentially unify several fields. The tragedy of the commons has mostly been applied to social goods formed by cooperation (see Tables 1 and 2). Social goods come in two, analogous forms. Most commonly the definition of a tragedy of the commons has been extended to cover what we term 'social goods' (also known as public goods, illustrated by the example of stalk production in Figure 1b). These are cases in which the resource does not exist extrinsically and instead it arises in a social context either through individuals investing in

Table 1. Scenarios where the tragedy of the commons (TOC) has been applied to evolutionary biology

Context	Which type of potential TOC?	Does TOC occur?	Study organisms	Refs ^a
Virulence	External resource: competition within the host leads to higher/lower than optimal virulence	Yes, but component only: multiple strains produce higher virulence	Parasites, malaria, bacteria	[12,17,2,5,58]
		No: competition restrained by severe resource limitation (small host size)	Cestodes	[59]
		No: multiple infections facilitate each other	Virus phages	[60]
Interspecific mutualism	Social goods, type a: lack of cooperation leads to lower than optimal virulence Social goods, type a: mutualisms break down because of cheating by either party See above	Yes, but component only: multiple strains prevent forming of collaborative, virulent structures	Parasites in general	[61]
		Yes, but component only: cheating persists when cheaters can avoid host sanctions	Plant–microorganism interactions	[62]
		No: prevented by kin benefits, vertical transmission or local horizontal transmission, partner choice and host sanctions; also by diminishing returns	Plant–microorganism interactions, ant/termite–fungus mutualisms	[8,40]
Social cooperation and conflict	Social goods, type a: cooperation breaks down due to individual interests See above See above	Yes, collapse: cheaters potentially drive population extinct	Microbes	[11,63]
		Yes, but component only: when policing is impossible	Social insects	[9]
		No: prevented by policing or punishment	Social insects	[6,39]
Intra-organismal conflict	Social goods, type a: competition between genetic lineages within an individual leads to lower individual fitness	No: prevented by competition for reputation	Humans	[64,65]
		No: prevented by rock–paper–scissor dynamics	Humans	[66]
		Yes, but component only: chimaeras are less productive than single-clone individuals	Slime moulds	[67]
Intra-genomic conflict	Social goods, type a: conflict between sex chromosomes over sex ratio Social goods, type a: selfish genetic elements promote unfair meiosis	No: suppressed by autosomes	Genomes	[14]
		No: suppressed by ‘parliament of the genes’, in which genes not linked to the genes for meiotic drive are selected to suppress the selfish behaviour	Genomes	[14]
Parent–offspring conflict	Social goods, type b: competition between offspring is costly	Yes, but component only: offspring begging is so costly that it reduces offspring size	Plants	[68]
		External resource: male harassment harms population See above	Lizards	[13]
Sexual conflict	See above	No: prevented by reduced benefit of harassment at lower population sizes, or female counter-adaptations	Theory	[11]
		Social goods, type b: competition for mates leads to lower productivity	Theory	[69]
Competition over sex ratio	Social goods, type b: large males are selected for although they have lower fecundity Social goods, type b: both mating partners in simultaneous hermaphrodites prefer to play female	Yes, but component only: males invest in sperm rather than nuptial gifts	Fish	[11]
		Yes, collapse (theoretical prediction)	Fish	[11]
		No: partners who refuse the male role are punished	Sea slugs	[70]
Resource competition	Social goods, type b: reproductive competition forces queens to overproduce eggs, enabling workers to skew the sex ratio against the optimum of queens	Yes, but component only: sex ratio in multiple-queen colonies is more female biased than the queen optimum	Ants	[71]
		Social goods, type b: competition for light/resources forces plants to invest in growth (roots/height) rather than productivity (shoots/seeds) See above	Plants	[7,10,72]
Resource competition	See above	Yes, but component only: production is suboptimal	Plants	[7,10,72]
		No: prevented by human intervention (crop selection)	Plants	[10]
		Yes, but component only: competition for water favours aggressive water users, although they have lower productivity	Plants	[73]
		No: prevented by kin selection and/or spatial segregation	Plants	[73]
Resource competition	Social Goods, type b: competition leads to high fixation rate of energy but low yield See above	Yes, but component only: species that face competition use high rate/low yield mechanisms	Microbes	[74]
		No: prevented by spatial structuring or costs to cheating	Microbes	[74]

^aThe references included here explicitly describe their study systems as a tragedy of the commons. Clearly, many other studies address the same issues.

Table 2. A 2 by 3 classification of the types of resource prone to a tragedy of the commons

Resource		Conceptual description of resource	Example of resource	Example of a tragedy of the commons involving the resource
Type 1 A pre-existing resource		An extrinsic resource over which individuals in a group or population compete	Females (in the context of male–male competition)	Male competition for females leads to decline in female numbers [13,75]
Type 2 Social goods	(a) Social goods – formed by cooperation	A cooperative environment – social goods, which are formed by individuals within a group cooperating	Cooperative formation of stalks	Microbe cheaters that would usually cooperate drive the population extinct [19]
	(b) Social goods – formed by restraining from conflict	A non-competitive environment – individuals restrain from conflict	Short plants that can invest all resources towards reproduction	Competition for light forces plants to invest in growth rather than productivity [10]

cooperation or restraining from engaging in conflict with conspecifics. In the case of cooperation being the social good (type 2a in Table 2), the tragedy of the commons arises if noncontributing cheaters can gain their share of the common goods provided by cooperating individuals (for example, see [20]). Behaviours vulnerable to such a tragedy include sentinel behaviour in cooperatively breeding meerkats (for example, see Ref. [21]), invertase production in yeast, which helps groups of yeast cells to break down sucrose [22], and workers choosing to work rather than reproduce in social insect colonies [9].

For example, individuals of the bacteria *Myxococcus xanthus* cooperate to form complex fruiting structures which release spores. 'Cheating' individuals, which do not invest in building non-spore parts of the fruiting structures, produce more spores than wild-type individuals, and can therefore invade and destroy the social good, causing the population to become extinct [19]. In all of these cases, a well-functioning unit produces the best group fitness (i.e. mean fitness per individual), but it might be advantageous for the individual in question to free-ride and not contribute to the social good.

The second type of social good (type 2b in Table 2) involves individuals restraining from potentially competitive acts. For example, in territorial conflicts, the resource (the area over which fighting occurs) might remain intact, but the costs are paid by individuals who spend energy and time fighting. Engaging in conflict brings costs to all group members, either through increased injury or having to invest more in conflict. This is best illustrated by the case of plant competition for light (Figure 1c), where the extrinsic resource (light) remains intact [10]. Taller plants gain more access to light to compete with their neighbours, and so are relatively more successful than shorter plants. But height cannot be achieved without investment in sturdy vertical biomass. Selection therefore favours plants that grow taller and shade their shorter neighbours. But any attempt to outgrow one's neighbour is a zero-sum game (see Glossary). Therefore, assuming that vertical structures contribute nothing to fecundity, we can predict taller trees but less overall productivity. Such investment is wasteful at the group level in a similar vein to when people sitting in audiences are forced to stand up if the first rows do so, until everyone pays the cost of having to stand up without any remaining improvement in the view to the stage. Tall plant populations, which likewise invest in an essentially zero-sum game, are indeed less productive [10].

This example highlights how not all competition is 'tragic'. If plant A outcompetes plant B so that A, through gaining all the light, is equally productive as the whole group of A and B would have been in a non-competitive situation, there is no tragedy. But the investment necessary to outcompete others might give rise to a tragedy, as such, if investment reduces overall productivity. It can then be argued that individuals have destroyed the common good created by restraining from competition. In other words, the group would do collectively better if all plants were shorter, but individuals that invest in taller structures will gain more light themselves while shading their conspecifics, and those selfish individuals will therefore have a higher fitness in any situation. A tragedy can also occur in plant competition when the relevant structure is the root, and there is a reduction in fecundity through investment in below-ground competition [7,23].

Microbial biofilm production is an analogous situation, in which production of extracellular polymers helps individual cells to push their descendents upwards to gain much needed oxygen [24]. As a side effect, polymer production by these tall piles of cells suffocates non-polymer-producing neighbours [24]. This situation is analogous to plant competition for light, in that vertical growth provides a competitive advantage over conspecifics, but comes at an overall cost to the group: individuals that produce polymers create a competitive environment that will lower overall group productivity.

Bacteriocin production in bacteria could likewise be seen as a tragedy of the commons. The production of bacteriocins kills other conspecifics, as well as the focal individual [25,26], but can benefit immune clonemates at the expense of susceptible, unrelated bacteria that are the target of the bacteriocins. Bacteriocin production creates a situation in which group productivity is reduced: although the individuals that produce the antibiotics stand to benefit, the group would do better if everyone restrained from producing bacteriocins. In this case, the social good is living in a bacteriocin-free environment, and this good is destroyed when all individuals produce bacteriocins. It is worthwhile noting that bacteriocin production is also susceptible to a type 2a social goods tragedy, in that it might be advantageous for immune bacteria to cheat by refraining from producing bacteriocins themselves (for example, see [27]). Indeed, the same behaviour might often include conflict over multiple types of resource and hence different types of tragedy.

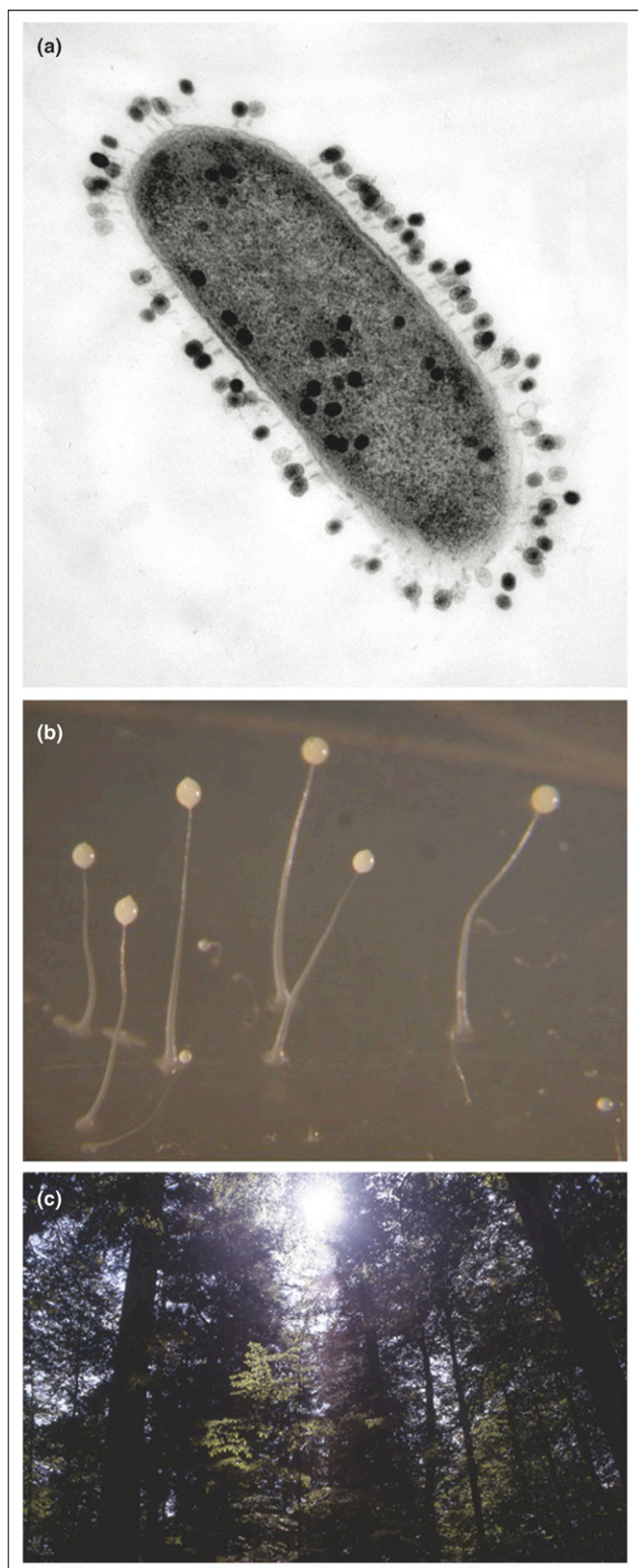


Figure 1. Examples of the three types of resource over which a tragedy of the commons (ToC) might occur. **(a)** Overexploitation of a pre-existing resource (type 1 in Table 2), shown here by virus phages overexploiting a host bacteria [12], **(b)** *Dictyostelium discoideum*, in which a tragedy of the commons might occur if too many individuals invest in producing more spores, while abstaining from investing in the stalk structure necessary for reproduction [67], **(c)** plant competition for light, where a tragedy of the commons might occur when individuals forgo the noncompetitive environment created by abstaining from growing taller [76]. Photos by (a) J. Wertz, (b) K.R. Foster and (c) D.J. Rankin.

Collapsing and component tragedies

The tragedy of the commons is commonly defined as a situation in which the selfish actions of individuals result in the complete collapse of the resource over which they are competing [1]. It is therefore important to add another layer of classification: how the tragedy affects the productivity of a group (note that the term ‘group’ should be interpreted widely, extending to populations or species, depending on the scale and consequences of interactions among individuals).

As such, we define a ‘collapsing’ tragedy as a situation in which selfish individual behaviour results in the entire resource vanishing (Figure 2). For example, if the resource is a social good formed by cooperation, collapse would mean that the group loses the cooperative behaviour in question, and the social good ceases to exist. This type of tragedy can lead to the extinction of the whole group, if the resource or the social good was essential for its survival. An example of a ‘collapsing’ tragedy is worker reproduction in the Cape honey bee, when workers cease to help the colony and instead invest in their own selfish reproduction, leading to very few individuals becoming workers, and in turn, colony collapse [28].

Losing the resource completely is the most obvious form of a tragedy of the commons, but empirically it is difficult to observe resources that have already collapsed. A slightly weaker form of the tragedy of the commons occurs when the resource has been depleted, but not to the extent that it disappears completely. We define such a tragedy as a ‘component’ tragedy, the word ‘component’ being borrowed from the Allee effect literature [29]. A component Allee effect is a density-dependent process that reduces some component of fitness at low densities, and it differs from demographic Allee effects in that the component Allee effect does not necessarily diminish population growth, because other fitness components might compensate. Component tragedies similarly result in a lower average fitness for the group, as a result of selfish competition, but the group is still able to persist on the resource in question (type 1 in Table 2) or benefit to some degree from the social

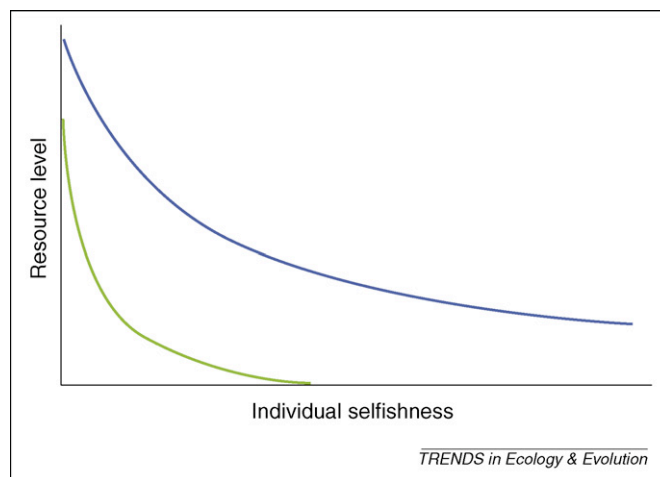


Figure 2. Component and collapsing tragedies of the commons. We define a collapsing tragedy (green line) as a tragedy in which complete selfishness causes the loss of all of the resource in question. A component tragedy is a tragedy in which selfishness reduces the resource, but not to the extent that it is lost completely (blue line).

good (type 2a and 2b in Table 2): the resource has not disappeared completely. Figure 2 shows the conceptual difference between a component and a collapsing tragedy of the commons.

Component tragedies are likely to be very common (Table 1), as they simply reflect the argument from the levels of selection debate that individual-level selection is usually stronger than higher-level selection. One could argue that a too broad definition renders a term less useful – indeed, whenever there is conflict between individual and common good, the latter is expected to be sacrificed, to some extent at least. However, not all competitive scenarios lead to component tragedies. Therefore, there is no tautology. Instead, identifying whether and under which conditions such tragedies occur should be useful. Likewise, it is important to differentiate between component and collapsing tragedies.

Interestingly, the same trait might be observed at many points of the continuum between component tragedy and collapse. An example of this is caste fate in social insects [9]: if all individuals become queens, the colony breaks down and a collapsing tragedy is reached [28]. However, a partial resolution of the conflict turns the situation into a component tragedy, as in *Melipona* bees, when more workers than the colony optimum, but not all, become queens. This example demonstrates that a component tragedy is a relative concept: a decrease in group fitness compared with a hypothetical situation in which individuals would behave ‘unselfishly’. Indeed, what counts as zero selfishness is a question with many possible answers. A sensible suggestion [8] is that the extent of a given tragedy could be measured as the deviation in group success from that of a group in which individuals share the same interests and behave in a way that is optimal for the group. In some cases, it can also be useful to quantify the opposite deviation, that is how far away is the group resource from complete collapse [30].

Resolving the tragedy

One of the main advantages of using the tragedy of the commons as an analogy in evolutionary biology is that it forces us to ask the question why a tragedy of the commons is *not* observed in a particular scenario [14,30] (Table 1). The fact that we can observe significant amounts of cooperation despite the selfish interests of free-riders and cheaters raises the question of why component tragedies do not always become collapsing tragedies, or why individuals in some cases cooperate so diligently that even component tragedies are absent. The latter can be defined as a ‘resolved conflict’ and is illustrated by cases of no significant colony-level costs of conflicts in insect colonies [30].

Restraining might be individually optimal

By definition, a tragedy of the commons will not arise if there are direct benefits to restraint. Therefore, apparently ‘resolved’ tragedies might, upon examination, turn out not to be tragedies in the first place. Direct benefits of restraint behaviour are especially likely to occur with social goods. For example, in sentinel behaviour in meerkats, cheating might not confer benefits if vigilant individuals have a direct personal advantage from being watchful [21].

Population structure and kin selection

One of the most commonly invoked mechanisms whereby conflicts might be resolved – both fully or partially (i.e. leading to a component rather than a collapsing tragedy) – is kin selection [31]. In the absence of policing mechanisms, if individuals interact locally with other highly related individuals, but compete for resources with all individuals in a population, competitive restraint will be favoured [32]. Kin selection (also mathematically interpretable as group selection, for example see [15]) is likely to be important in any situation in which populations are structured in some way [33], such as into groups [34] or in space [35]. Population structure helps to align the interests of the individual with the interests of the group. This means that any reduction in group productivity that results from individual-level selfishness will come at an inclusive fitness cost to the focal individual, and hence overexploiting a common resource will be less beneficial. As a result, groups of related individuals that show restraint in competition over a common resource will be favoured over groups in which individual-level competition results in a tragedy of the commons.

Coercion and punishment

Coercion and punishment are among the most widely studied mechanisms for avoiding a tragedy of the commons, both in the evolutionary literature [6,36–38] and in human sociobiology studies (for example, see [38]). These factors play a part in private ownership of the resource (e.g. attempts to steal are punished) as well as in governmental control of resources [1] through the manipulation of payoffs (e.g. via taxes). Coercion (in which individuals manipulate and put pressure on others) has been shown to be a potential force in altering the payoffs in animal societies [6]. Perhaps the most sophisticated examples can be found in social insect colonies, where ‘policing’ individuals ensure that colony workers act to the benefit of the whole colony and do not reproduce for their own selfish interest: worker-laid eggs are regularly eaten by other workers [39].

Although punishment can undoubtedly stabilize cooperation, for example between legumes and their rhizome bacteria [40], it is interesting to note that such behaviour can also be subject to a social goods tragedy of the commons in itself. We face a second-order free-rider problem: when punishment is costly to the punisher, there is an individual-level temptation not to punish cheaters (for example, see [41]). As such, higher-order punishment (punishing individuals who do not punish) might be needed in such a scenario [41]. But because this raises the same free-rider question at a higher level (i.e. why not save energy by not punishing those who do not punish), punishment is undoubtedly easier to explain in cases in which the punishing act itself is not costly, such as egg-eating by policing workers, or when punishers receive more cooperation from others [42].

Diminishing returns and ecological feedbacks

The benefits from overexploiting a resource are not always linear: they often diminish as individuals try to compete more intensely for them. Diminishing returns can therefore prevent a tragedy by reducing the overall benefit

gained from increasingly investing in a selfish behaviour (for example, see [8]). Diminishing returns are likely to be common in a range of organisms, particularly when the individuals cannot make full use of the extra resources that they acquire [8]. For example, the reproductive benefit of possessing an ever-increasing territory is very likely diminishing: extremely large territories prevent the individual from utilizing all its resources, because other factors become limiting (ultimately, speed of travel while foraging could prevent collecting all resources). Thus, diminishing returns might put a break on overexploitation. Diminishing returns might also resolve potential public good tragedies, as in the case of blood sharing by vampire bats. Hungry bats need blood much more than bats that have fed recently, and this diminishing benefit of the state of an individual can alter the balance of reciprocal aid by diminishing the benefit gained by a cheater who will not share with other individuals even when it has fed properly [8].

Feedback between the size of the population (or group) and the intensity of conflict [43,44] is a related phenomenon that is also likely to be important in reducing the intensity of conflicts. If conflict and competition have a negative impact on the number of individuals in a population, then this will automatically change the number of individuals there are to interact with, ultimately affecting the structure of the 'game' [43]. Thus, selective pressures differ between low densities and high densities, creating a feedback between adaptive individual behaviour and population density. The strength of this feedback could therefore have an influence on the strength of the conflict itself, thereby preventing a collapsing tragedy [43]. A potential example is quorum sensing in bacteriocin production [45], in which individual bacteria reduce their production of bacteriocins when the population density is low.

What if the tragedy is not resolved?

Collapsing tragedies can be difficult to observe because they often destroy the study object (the group or population, or the behavioural function that creates public goods). However, this does not necessarily transfer the subject to evolutionary oblivion, when we consider that extinctions might have consequences for higher levels of selection, such as group selection or species-level selection [14,34,46]. Recent work demonstrates the potential for so-called evolutionary suicide (for example, see [11]): precisely because individual-level selection typically prevails over higher-level selection, evolution is predicted to favour selfish individuals to the extent that it can lead to extinction of higher-level biological structures. Cancer, a selfish form of cell growth [47], can kill individual organisms. Similarly if individual-level conflict can cause population extinction, collapsing tragedies might have a large effect on species persistence: those overexploiting common goods are denied prolonged existence. This might result in selection at the species level [11,46,48]. Species-level selection can thus act as a 'conflict-limiting' mechanism, if species that have evolved high levels of conflict are driven extinct sooner than species in which conflicts are milder [49]. Recent results suggest that even if actual evolutionary suicide is not occurring, species with strong conflicts can render themselves vulnerable to competitive exclusion, and thus

competition with other species can dramatically affect species persistence (for examples, see [48,50]).

If the tragedy of the commons can act as a selective force at the level of the species, we would expect to observe traits that limit or resolve the tragedy. Extant organisms are expected to have robust mechanisms against at least the most commonly occurring cheater mutants, because any collapsing tragedies that have occurred have weeded out populations that lack such mechanisms. For example, in social amoebae, certain cheating genotypes cannot proliferate because of pleiotropic effects preventing spore formation [51]. It is possible that such genetic architecture, which constrains cheating, could be selected for at the species level [48].

Conclusion

Hardin's analogy remains a powerful one for describing how the selfish interests of individuals can bring about costs to all members of a group or population. Whether or not such conflicts are fully resolved, remain at the state of a component tragedy or lead to a total collapse in group productivity is a major question that has implications for social evolution, levels of selection, ecology of resource use and several other important phenomena. The rising tide of research in the context of the tragedy of the commons will prove most useful if the types of tragedy involved are clearly defined, and if the studies provide a clear scale for calculating how far the group-level costs are from their possible minima or maxima.

Perhaps the most challenging question lies in addressing the relative frequency at which tragedies arise with or without mechanisms to prevent them from reaching total collapses. Groups subject to a total collapse have a far shorter lifespan, which makes them difficult to study. In the light of ever-growing environmental concerns, thinking about the tragedy of the commons in evolutionary biology is of interest not only because of these evolutionary implications, but also because of the applied analogy to human societies dealing with environmental and other public goods problems (Box 1).

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