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The Tragedy of the Commons in Evolutionary Biology

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Abstract

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 tragedies, and review different mechanisms that can resolve conflicts that could otherwise end in tragedy, including kinship, policing and diminishing returns. 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 prior to Hardin’s original paper [2], describes the consequences of individuals selfishly over-exploiting a common resource. The tragedy of the commons was originally applied to a group of herders grazing cattle on a 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” where 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: while 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 while costs are distributed among all individuals (see 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 overexploitation 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, this raises the question of how non-human organisms can avoid overexploiting the resources they depend on. 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 which 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 [e.g. 6, 7-13].

A tragedy of the commons in evolutionary biology refers to a situation where 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, population or species. The concept has been used in a diversity of fields in biology, ranging from plant-competition for resources [e.g. 7] to the evolution of cooperation and conflict in insect societies [e.g. 9]. What the tragedies have in common is that individuals are selfishly maximizing their own fitness at the expensive 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 tragedies

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 [e.g. 16].

Resources prone to a tragedy of the commons

One can distinguish between three types of group-level costs of competition, which may 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 can also be involved, such as high virulence in parasites [17] and laying larger clutches in an attempt to out-reproduce others. While it has been suggested that only competition over an extrinsic resource should be viewed as a tragedy of the commons [e.g. 18], evolutionary biologists have applied the term to a much wider range of contexts [e.g. 6, 8, 9, 12, 19]. Figure 2a shows the case of bacteriphages surrounding a bacteria [12], a system which is prone to a tragedy of the commons when the virulence of the phages becomes so high that they destroy the bacterio on which they exist.

While Hardin's analogy was originally applied to the over-exploitation of an external resource, evolutionary biologists have realised that the analogy reflects a wide range of social dilemmas, and can potentially unify a number of 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

2b). These are cases where the resource does not exist extrinsically, instead it arises in a social context either through individuals investing in 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 commons arises if non-contributing cheaters can gain their share of the common goods provided by cooperating individuals [e.g. 20]. Behaviours vulnerable to such a tragedy include sentinel behaviour in cooperatively breeding meerkats [e.g. 21], invertase production in yeast, which helps groups of yeast cells to break down sucrose, [22] or workers choosing to work rather than reproduce in social insect colonies [9].

For example, individuals of the bacteria *Myxoccocus xanthus* cooperate to form complex fruiting structures which release spores. “Cheating” individuals, which don’t 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 go extinct [19]. In all of these cases, a well functioning unit produces the best group fitness (i.e. mean fitness per individual), but it may 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) may 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 2c), where the extrinsic resource (light) remains intact [10]. Taller plants gain more access to light in order 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 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 may give rise to a tragedy, as such investment reduces overall productivity. Individuals can then be argued to have destroyed the common good created by restraining from competition. In other words, collectively the group would do better if all plants were shorter, but individuals which invest in taller structures gain more light themselves and shade their conspecifics, will 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, where production of extracellular polymers help individual cells push their descendents upwards to gain much needed oxygen [24]. As a side effect, polymer production by these tall piles of cells suffocate non-polymer producing neighbours [24]. This 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 which produce polymers create a competitive environment which will lower overall group productivity.

Bacteriocin production in bacteria may likewise be seen as a tragedy of the commons. The production of bacteriocins kill other conspecifics, as well as the focal individual [25, 26], but can benefit immune clonemates at the expense of susceptible, unrelated bacteria, which are the target of the bacteriocins. Bacteriocin production creates a situation where group productivity is reduced: while the individuals which 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 may be advantageous for immune bacteria to cheat by refraining from producing bacteriocins themselves [e.g. 27]. Indeed, the same behaviour may often include conflict over multiple types of resources and hence different types of tragedy.

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 between individuals).

As such, we define a “collapsing” tragedy as a situation where selfish individual behaviour results in the entire resource vanishing (figure 1). For example, if the currency 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, where 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 the “component” tragedy, the word “component” being borrowed from the Allee effect literature [29]. A component Allee effect is a density-dependent process which 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 good (type 2 and 2b in table 2): the resource has not disappeared completely. Figure 1 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 (see Box 2). 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 may 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, where more workers than the colony optimum, but not all, become queens. This demonstrates that a component tragedy is a relative concept: a decrease in group fitness compared to 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 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, i.e. 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 [Table 1, 14, 30]. 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 may be individually optimal

By definition, a tragedy of the commons will not arise if there are direct benefits to restraint. Therefore, apparently 'resolved' tragedies may, 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 may 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 may be resolved — both fully or partially (i.e. leading to component rather than 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 [e.g. 15]) is likely to be important in any situation where 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 which results from individual-level selfishness will come at an inclusive fitness cost to the focal individual, and hence over-exploiting a common resource will be less beneficial. As a result, groups of related individuals which 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] as well as in human sociobiology studies [e.g. 38]. These factors play a part in private ownership of the resource (e.g. attempts to steal are punished) as well as governmental control of resources [1] through the manipulation of payoffs (e. g. via taxes). Coercion (where 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].

While punishment can undoubtedly stabilize cooperation, for example between legumes and their rhizome bacteria [40], it is interesting to note that such behaviour also can 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 [e.g. 41]. As such, higher-order punishment (punishing individuals who do not punish) may 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 behaviours [e.g. 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 may put a break on overexploitation. Diminishing returns may also resolve potential public good tragedies, as in the case of blood sharing by vampire bats. Hungry bats need blood much more than ones that have recently fed, 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], where 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 may 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 [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 may have a large effect on species persistence: those overexploiting common goods are denied prolonged existence. This may 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 [e.g. 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 which limit or resolve the tragedy. Extant organisms are expected to have robust mechanisms against at least the most commonly occurring cheater mutants, as any collapsing tragedies that have occurred have weeded out populations that lack such mechanisms. For example, in social amoebas, 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 tragedies 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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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 where 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 which maximise their own fitness.

Over-exploitation: The depletion of a resource beyond the point where sustainable use is possible.

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

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

Resolution: Absence of tragedy, i.e. a situation where an 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 where 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 over-population [1], but the main point of his article was that a common resource would always be over-exploited when utilized by self-interested individuals. Pollution, climate change and overexploitation 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 over-exploited. 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. While fishermen are unkeen 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 fisherman, 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 skepticism. For example, the population dynamic arguments that relate catch effort to expected yield in fisheries are not intuitively obvious. Easily perceived short-term 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".

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

Context	Which type of potential TOC?	Does TOC occur?	Study organisms	References[1]
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, 25, 58]
		No: competition restrained by severe resource limitation (small host size)	Cestodes	[59]
		No, ER: multiple infections facilitate each other	Virus phages	[60]
	Social goods, type a): Lack of cooperation leads to lower than optimal virulence	**Yes, but component only** : multiple strains prevent forming of collaborative, virulent structures	Parasites in general	[61]
Interspecific mutualism	**Social goods, type a):** Mutualisms break down due to cheating by either party	**Yes, but component only**: cheating persists when cheaters can avoid host sanctions	Plant-microorganism interactions	[62]
	See above	**No**: prevented by kin benefits, vertical transmission or local horizontal transmission, partner choice and host sanctions; also by	Plant-microorganism interactions, ant/termite – fungus mutualisms	[8, 40]

		diminishing returns		
Social cooperation and conflict	**Social Goods, type a):** Cooperation breaks down due to individual interests	**Yes, collapse**: cheaters potentially drive population extinct	Microbes	[11, 63]
	See above	**Yes, but component only**: when policing is impossible	Social insects	[9]
	See above	**No**: prevented by policing or punishment	Social insects	[6, 39]
		No: prevented by competition for reputation	Humans	[64, 65]
		No: prevented by rock-paper-scissor dynamics	Humans	[66]
Intra-organismal conflict	**Social goods, type a):** Competition between genetic lineages within an individual leads to lower individual fitness	**Yes, but component only**: chimeras are less productive than single-clone individuals	Slime molds	[67]
Intra-genomic conflict	**Social goods, type a):** Conflict between sex cromosomes over sex ratio	**No**: suppressed by autosomes	Genomes	[14]
	Social goods, type a): Selfish genetic	**No**: suppressed by “parliament of the genes”,	Genomes	[14]

	elements promote unfair meiosis	where genes not linked to the genes for meiotic drive are selected to suppress the selfish behaviour		
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]
Sexual conflict	**External Resource:** Male harassment harms population	**Yes, but component only**: male harassment leads to population decline	Lizards	[13]
	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	**Yes, but component only**: males invest in sperm rather than nuptial gifts	Theory	[69]
	Social goods, type b): Large males are selected for although they have lower fecundity	**Yes, collapse** (theoretical prediction)	Fish	[11]

	Social Goods, type b): Both mating partners in simultaneous hermaphrodites prefer to play female	**No**: partners who refuse the male role are punished	Sea slugs	[70]
Competition over sex-ratio	**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]
Resource competition	**Social Goods, type b):** Competition for light / resources forces plants to invest in growth (roots / height) rather than productivity (shoots / seeds)	**Yes, but component only**: production is suboptimal	Plants	[7, 10, 72]
	See above	**No**: prevented by human intervention (crop selection)	Plants	[10]
	Social Goods, type b): Competition for water leads to high water uptake but low yield	**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	Plants	[73]

	segregation		
Social Goods, type b): Competition leads to high fixation rate of energy but low yield	**Yes, but component only**: species which face competition use high rate / low yield mechanisms	Microbes	[74]
See above	**No**: prevented by spatial structuring or costs to cheating	Microbes	[74]

[1]The 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 resources 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, which 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, which can invest all resources towards reproduction	Competition for light forces plants to invest in growth rather than productivity [10]

Figure 1. Component and collapsing tragedies. We define a collapsing tragedy (green line) as one where complete selfishness causes the loss of all of the resource in question. A component tragedy is one where selfishness reduces the resource, but not to the extent where it is lost completely (blue line).

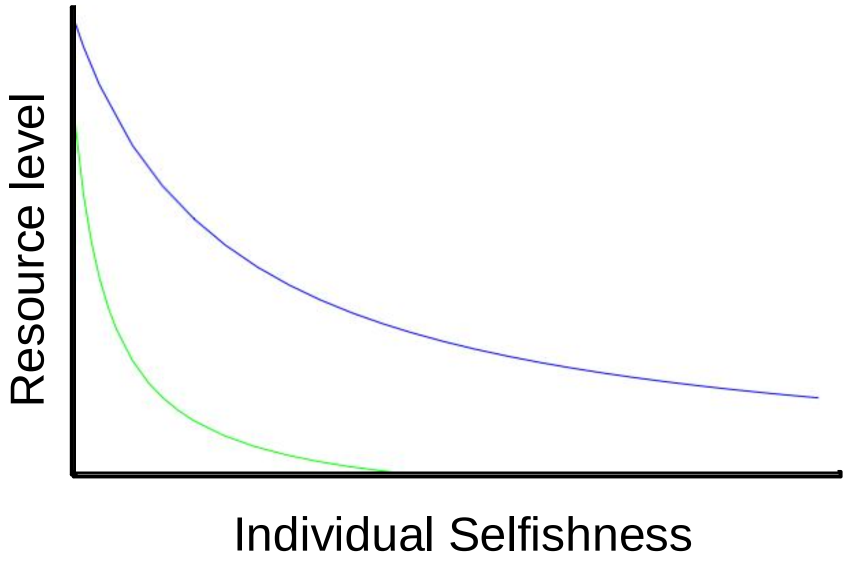

Figure 2. Examples of the three types of resources over which a tragedy of the commons may occur. (a) Over-exploitation of a pre-existing resource (type 1 in table 2), shown here by virus phages overexploiting a host bacteria [12], (b) *Dictyostelium discoideum*, where a tragedy of the commons may occur if too many individuals invest in producing more spores, whilst abstaining from investing in the stalk structure necessary for reproduction [67], (c) plant competition for light, where a tragedy of the commons may occur when individuals forego the non-competitive environment created by abstaining from growing taller [76]. Photos by B. Kerr (a), K.R. Foster (b) & D.J. Rankin (c).