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1 **Trends in Ecology & Evolution, 2007**

2 **The Tragedy of the Commons in Evolutionary Biology**

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1 **Abstract**

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

15

16 **The Tragedy of the Commons**

17 The tragedy of the commons (see glossary) provides a useful analogy allowing us to
18 understand why shared resources, such as fisheries or the global climate, tend to
19 undergo human overexploitation [1]. The analogy, which dates back over a century
20 prior to Hardin's original paper [2], describes the consequences of individuals
21 selfishly over-exploiting a common resource. The tragedy of the commons was
22 originally applied to a group of herders grazing cattle on a common land. Each herder
23 only gains a benefit from his own flock, but when a herder adds more cattle to the

1 land to graze everyone shares the cost, which comes from reducing the amount of
2 forage per cattle. If the herders are driven only by economic self-interest, they will
3 each realize that it is to their advantage to always add another animal to the common:
4 they sacrifice the good of the group (by forgoing sustainable use of the resource) for
5 their own selfish gain. Thus, herders will continue to add animals, eventually leading
6 to a “tragedy” where the pasture is destroyed by overgrazing [1].

7 The difficulties inherent in protecting shared common resources, such as marine
8 stocks or clean air, are well known: while everyone benefits from an intact resource,
9 there is an individual-level temptation to cheat (e.g. to overexploit or pollute) because
10 cheating brings economic advantages to the individual while costs are distributed
11 among all individuals (see box 1). The lesson drawn from these studies is that solving
12 the dilemma often requires negotiation and sanctions on disobedient individuals. This
13 changes the payoffs, so that group-beneficial behaviour also becomes optimal for the
14 individual: an example would be imposing heavier taxes on polluting industries.
15 Hardin’s own main solution to the tragedy of the commons was state governance and
16 privatization of the resource in question [1]; in general, social norms as well as
17 individual morality have been considered good candidates for preventing
18 overexploitation of common resources.

19 Despite citing Lack’s work on population regulation [3] to contrast population
20 regulation in birds with human population growth, Hardin did not venture to extend
21 his analogy to the problems of evolutionary ecology. However, if the tragedy can only
22 be avoided when higher-level incentives are invoked, as in the case of legal
23 incentives, this raises the question of how non-human organisms can avoid
24 overexploiting the resources they depend on. After the group selection debate of the

1 1960s [4], it should be clear that this question is not trivial: natural selection acts
2 primarily at the level of the gene, and therefore favours individuals which serve their
3 own selfish interests [5]. Nevertheless, it is only in the last decade that the tragedy of
4 the commons analogy has become increasingly used by evolutionary biologists (Table
5 1) to explain why selfish individuals in animal and plant populations do not evolve to
6 destroy the collective resource [e.g. 6, 7-13].

7 A tragedy of the commons in evolutionary biology refers to a situation where
8 individual competition over a resource reduces the resource itself, which can in turn
9 reduce the fitness of the whole group [14]. The tragedies discussed here can apply to a
10 range of levels: groups, population or species. The concept has been used in a
11 diversity of fields in biology, ranging from plant-competition for resources [e.g. 7] to
12 the evolution of cooperation and conflict in insect societies [e.g. 9]. What the
13 tragedies have in common is that individuals are selfishly maximizing their own
14 fitness at the expense of the productivity of the group or population. Here we seek
15 to review how the tragedy of the commons is used in the literature, with the hope of
16 highlighting that the underlying principles are the same, regardless of the system or
17 the level at which the tragedy of the commons occurs.

18 **Types of tragedies**

19 Despite the relatively recent acquisition of the tragedy of the commons analogy into
20 evolutionary biology [but see 14], not all studies use the same definition for a tragedy
21 of the commons, and there are many related terms (see glossary). As confusing
22 terminology can hinder the development of a field [15], here we seek to define
23 different forms of the tragedy of the commons (tables 1 and 2). What these tragedies
24 all have in common is that individual selfishness reduces the resource over which

1 individuals are competing, and lowers group fitness. The tragedy of the commons in
2 evolutionary biology therefore encompasses what social scientists call a public good
3 game, or an N-person prisoner's dilemma [e.g. 16].

4 *Resources prone to a tragedy of the commons*

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

18 While Hardin's analogy was originally applied to the over-exploitation of an external
19 resource, evolutionary biologists have realised that the analogy reflects a wide range
20 of social dilemmas, and can potentially unify a number of fields. The tragedy of the
21 commons has mostly been applied to social goods formed by cooperation (see tables 1
22 and 2). Social goods come in two, analogous forms. Most commonly the definition of
23 a tragedy of the commons has been extended to cover what we term "social goods"
24 (also known as public goods, illustrated by the example of stalk production in figure

1 2b). These are cases where the resource does not exist extrinsically, instead it arises in
2 a social context either through individuals investing in cooperation, or restraining
3 from engaging in conflict with conspecifics. In the case of cooperation being the
4 social good (type 2a in table 2), the tragedy of commons arises if non-contributing
5 cheaters can gain their share of the common goods provided by cooperating
6 individuals [e.g. 20]. Behaviours vulnerable to such a tragedy include sentinel
7 behaviour in cooperatively breeding meerkats [e.g. 21], invertase production in yeast,
8 which helps groups of yeast cells to break down sucrose, [22] or workers choosing to
9 work rather than reproduce in social insect colonies [9].

10 For example, individuals of the bacteria *Myxococcus xanthus* cooperate to form
11 complex fruiting structures which release spores. “Cheating” individuals, which don’t
12 invest in building non-spore parts of the fruiting structures, produce more spores than
13 wild type individuals, and can therefore invade and destroy the social good, causing
14 the population to go extinct [19]. In all of these cases, a well functioning unit
15 produces the best group fitness (i.e. mean fitness per individual), but it may be
16 advantageous for the individual in question to free-ride and not contribute to the
17 social good.

18 The second type of social good (type 2b in table 2) involves individuals restraining
19 from potentially competitive acts. For example, in territorial conflicts, the resource
20 (the area over which fighting occurs) may remain intact, but the costs are paid by
21 individuals who spend energy and time fighting. Engaging in conflict brings costs to
22 all group members, either through increased injury or having to invest more in
23 conflict. This is best illustrated by the case of plant competition for light (figure 2c),
24 where the extrinsic resource (light) remains intact [10]. Taller plants gain more access

1 to light in order to compete with their neighbours, and so are relatively more
2 successful than shorter plants. But height cannot be achieved without investment in
3 sturdy vertical biomass. Selection therefore favours plants that grow taller and shade
4 their shorter neighbours. But any attempt to outgrow one's neighbour is a zero-sum
5 game (see Glossary). Therefore, assuming that vertical structures contribute nothing
6 to fecundity, we can predict taller trees, but less overall productivity. Such investment
7 is wasteful at the group level in a similar vein when people sitting in audiences are
8 forced to stand up if the first rows do so, until everyone pays the cost of having to
9 stand up without any remaining improvement in the view to the stage. Tall plant
10 populations, which likewise invest in an essentially zero-sum game, are indeed less
11 productive [10].

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

23 Microbial biofilm production is an analogous situation, where production of
24 extracellular polymers help individual cells push their descendents upwards to gain

1 much needed oxygen [24]. As a side effect, polymer production by these tall piles of
2 cells suffocate non-polymer producing neighbours [24]. This is analogous to plant
3 competition for light, in that vertical growth provides a competitive advantage over
4 conspecifics, but comes at an overall cost to the group: individuals which produce
5 polymers create a competitive environment which will lower overall group
6 productivity.

7 Bacteriocin production in bacteria may likewise be seen as a tragedy of the commons.
8 The production of bacteriocins kill other conspecifics, as well as the focal individual
9 [25, 26], but can benefit immune clonemates at the expense of susceptible, unrelated
10 bacteria, which are the target of the bacteriocins. Bacteriocin production creates a
11 situation where group productivity is reduced: while the individuals which produce
12 the antibiotics stand to benefit, the group would do better if everyone restrained from
13 producing bacteriocins. In this case, the social good is living in a bacteriocin-free
14 environment, and this good is destroyed when all individuals produce bacteriocins. It
15 is worthwhile noting that bacteriocin production is also susceptible to a type 2a social
16 goods tragedy, in that it may be advantageous for immune bacteria to cheat by
17 refraining from producing bacteriocins themselves [e.g. 27]. Indeed, the same
18 behaviour may often include conflict over multiple types of resources and hence
19 different types of tragedy.

20 *Collapsing and component tragedies*

21 The tragedy of the commons is commonly defined as a situation in which the selfish
22 actions of individuals result in the complete collapse of the resource over which they
23 are competing [1]. It is therefore important to add another layer of classification: how
24 the tragedy affects the productivity of a group (note that the term ‘group’ should be

1 interpreted widely, extending to populations or species, depending on the scale and
2 consequences of interactions between individuals).

3 As such, we define a “collapsing” tragedy as a situation where selfish individual
4 behaviour results in the entire resource vanishing (figure 1). For example, if the
5 currency is a social good formed by cooperation, collapse would mean that the group
6 loses the cooperative behaviour in question, and the social good ceases to exist. This
7 type of tragedy can lead to the extinction of the whole group, if the resource or the
8 social good was essential for its survival. An example of a “collapsing” tragedy is
9 worker reproduction in the Cape honey bee, where workers cease to help the colony
10 and instead invest in their own selfish reproduction, leading to very few individuals
11 becoming workers, and in turn, colony collapse [28].

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

1 shows the conceptual difference between a component and a collapsing tragedy of the
2 commons.

3 Component tragedies are likely to be very common (Table 1), as they simply reflect
4 the argument from the levels of selection debate that individual-level selection is
5 usually stronger than higher-level selection. One could argue that a too broad
6 definition renders a term less useful — indeed, whenever there is conflict between
7 individual and common good, the latter is expected to be sacrificed to some extent at
8 least. However, not all competitive scenarios lead to component tragedies (see Box 2).
9 Therefore, there is no tautology. Instead, identifying whether and under which
10 conditions such tragedies occur should be useful. Likewise, it is important to
11 differentiate between component and collapsing tragedies.

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

1 opposite deviation, i.e. how far away is the group resource from complete collapse
2 [30].

3 **Resolving the tragedy**

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

13 *Restraining may be individually optimal*

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

20 *Population structure and kin selection*

21 One of the most commonly invoked mechanisms whereby conflicts may be resolved
22 — both fully or partially (i.e. leading to component rather than collapsing tragedy) —

1 is kin selection [31]. In the absence of policing mechanisms, if individuals interact
2 locally with other highly related individuals, but compete for resources with all
3 individuals in a population, competitive restraint will be favoured [32]. Kin selection
4 (also mathematically interpretable as group selection [e.g. 15]) is likely to be
5 important in any situation where populations are structured in some way [33], such as
6 into groups [34] or in space [35]. Population structure helps to align the interests of
7 the individual with the interests of the group. This means that any reduction in group
8 productivity which results from individual-level selfishness will come at an inclusive
9 fitness cost to the focal individual, and hence over-exploiting a common resource will
10 be less beneficial. As a result, groups of related individuals which show restraint in
11 competition over a common resource will be favoured over groups in which
12 individual-level competition results in a tragedy of the commons.

13 *Coercion and punishment*

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

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

12 *Diminishing returns and ecological feedbacks*

13 The benefits from overexploiting a resource are not always linear: they often diminish
14 as individuals try to compete more intensely for them. Diminishing returns can
15 therefore prevent a tragedy by reducing the overall benefit gained from increasingly
16 investing in a selfish behaviours [e.g. 8]. Diminishing returns are likely to be common
17 in a range of organisms, particularly when the individuals cannot make full use of the
18 extra resources that they acquire [8]. For example, the reproductive benefit of
19 possessing an ever-increasing territory is very likely diminishing: extremely large
20 territories prevent the individual from utilizing all its resources because other factors
21 become limiting (ultimately, speed of travel while foraging could prevent collecting
22 all resources). Thus, diminishing returns may put a break on overexploitation.
23 Diminishing returns may also resolve potential public good tragedies, as in the case of
24 blood sharing by vampire bats. Hungry bats need blood much more than ones that

1 have recently fed, and this diminishing benefit of the state of an individual can alter
2 the balance of reciprocal aid by diminishing the benefit gained by a cheater who will
3 not share with other individuals even when it has fed properly [8].

4 Feedback between the size of the population (or group) and the intensity of conflict
5 [43, 44] is a related phenomenon that is also likely to be important in reducing the
6 intensity of conflicts. If conflict and competition have a negative impact on the
7 number of individuals in a population, then this will automatically change the number
8 of individuals there are to interact with, ultimately affecting the structure of the
9 “game” [43]. Thus, selective pressures differ between low densities and high
10 densities, creating a feedback between adaptive individual behaviour and population
11 density. The strength of this feedback could therefore have an influence on the
12 strength of the conflict itself, thereby preventing a collapsing tragedy [43]. A potential
13 example is quorum sensing in bacteriocin production [45], where individual bacteria
14 reduce their production of bacteriocins when the population density is low.

15 **What if the tragedy is not resolved?**

16 Collapsing tragedies can be difficult to observe because they often destroy the study
17 object (the group or population, or the behavioural function that creates public goods).
18 However, this does not necessarily transfer the subject to evolutionary oblivion when
19 we consider that extinctions may have consequences for higher levels of selection,
20 such as group selection or species-level selection [14, 34, 46]. Recent work
21 demonstrates the potential for so-called evolutionary suicide [see 11]: precisely
22 because individual-level selection typically prevails over higher-level selection,
23 evolution is predicted to favour selfish individuals to the extent that it can lead to
24 extinction of higher-level biological structures. Cancer, a selfish form of cell growth

1 [47], can kill individual organisms. Similarly if individual-level conflict can cause
2 population extinction, collapsing tragedies may have a large effect on species
3 persistence: those overexploiting common goods are denied prolonged existence. This
4 may result in selection at the species level [11, 46, 48].

5 Species-level selection can thus act as a “conflict limiting” mechanism if species that
6 have evolved high levels of conflict are driven extinct sooner than species in which
7 conflicts are milder [49]. Recent results suggest that even if actual evolutionary
8 suicide is not occurring, species with strong conflicts can render themselves
9 vulnerable to competitive exclusion, and thus competition with other species can
10 dramatically affect species persistence [e.g. 48, 50].

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

19 **Conclusion**

20 Hardin’s analogy remains a powerful one for describing how the selfish interests of
21 individuals can bring about costs to all members of a group or population. Whether or
22 not such conflicts are fully resolved, remain at the state of a component tragedy, or
23 lead to a total collapse in group productivity, is a major question that has implications

1 for social evolution, levels of selection, ecology of resource use, and several other
2 important phenomena. The rising tide of research, in the context of the tragedy of the
3 commons, will prove most useful if the types of tragedies involved are clearly
4 defined, and if the studies provide a clear scale for calculating how far the group-level
5 costs are from their possible minima or maxima.

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

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1 **Glossary**

2 **Cheater:** An individual that gains a benefit from the collective, without investing in
3 the collective itself. These individuals can also be called “free-riders”.

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

7 **Component tragedy:** A tragedy of the commons where escalated competition stops
8 before a collapse is reached.

9 **Cooperation:** The act of individuals paying an individual cost to contribute to a
10 collective benefit.

11 **Individual-level selection:** Selection acting at the level of the individual, to favour
12 individuals or genes which maximise their own fitness.

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

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

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

17 **Resolution:** Absence of tragedy, i.e. a situation where an inherent conflict causes no
18 group-level costs.

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

- 1 **Species-level selection:** Selection that arises by differential extinction of species.
- 2 **Tragedy of the commons:** A situation where individual competition reduces the
- 3 resource over which individuals compete, resulting in lower overall fitness for all
- 4 members of a group or population.
- 5 **Zero-sum game:** A situation in which one individual's gain is matched by other
- 6 individuals' loss. Cutting a cake and chess are both examples of zero-sum games.

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

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

16 A flipside of the tragedy of the commons is that avoiding it can often be beneficial to
17 the players involved, and can be described as win-win situations if policies are
18 improved. For example, right whales often become entangled in lobster fishing gear.
19 While fishermen are unkeen to reduce their income, a comparison of Canadian and
20 American lobster fisheries shows that reducing the risk of entanglement can be
21 achieved with no economic cost [54]: reducing fishing effort leads to improved yield
22 of lobsters per recruit. Similarly, despite considerable resistance and cynicism, marine
23 reserves (areas where fishing is prohibited) can benefit all fisherman, even over the
24 short-term [55]. Policy negotiations are difficult in these situations because people

1 distrust others, but also because long-term benefits are rarely given sufficient weight
2 [56]. Without extensive education, such benefits are met with skepticism. For
3 example, the population dynamic arguments that relate catch effort to expected yield
4 in fisheries are not intuitively obvious. Easily perceived short-term individual benefits
5 would help to solve these problems. For example, using people’s desire to improve
6 their social reputation could prevent exploitation of the common good, as is seen in
7 experimental “climate games” in which participants improve their reputation by
8 investing publicly to sustain the global climate [57].

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

16

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

1

2 ¹The references included here explicitly describe their study systems as a tragedy of the commons. Clearly, many other studies address the same issues.

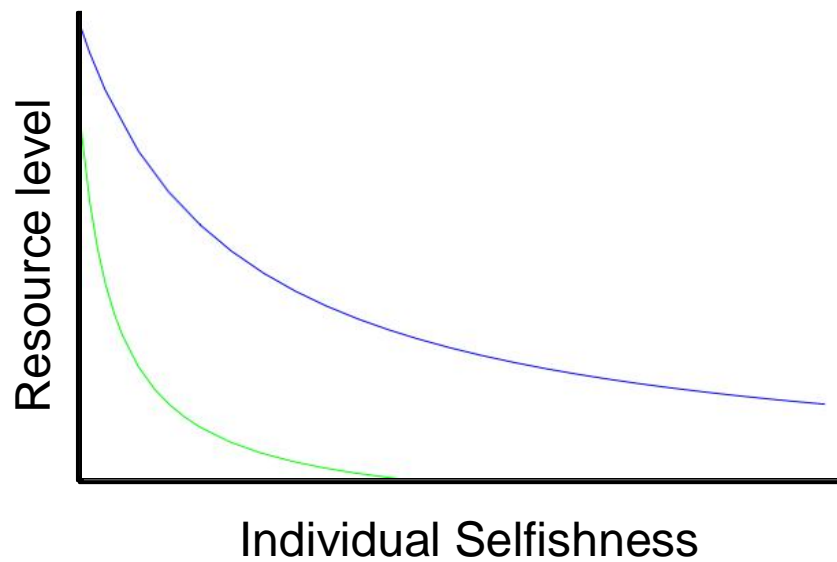
- 1 **Table 2.** A 2 by 3 classification of the types resources prone to a tragedy of the
- 2 commons

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]
	(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]
Type 2 Social Goods	(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]

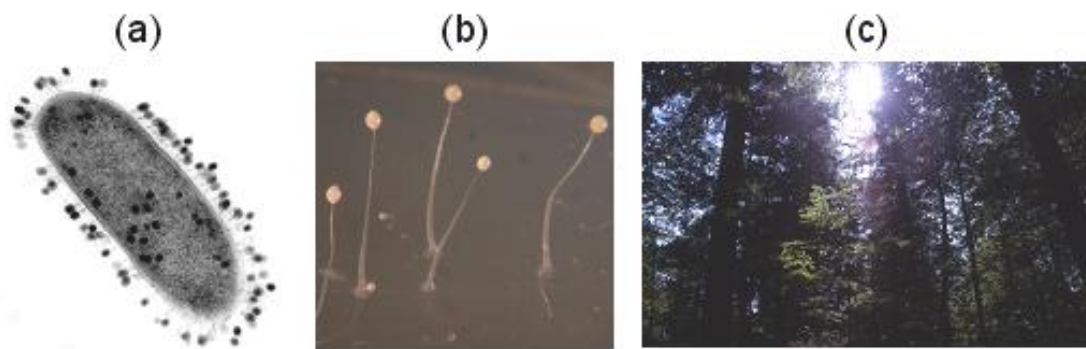
1 Figure 1. Component and collapsing tragedies. We define a collapsing tragedy (green
2 line) as one where complete selfishness causes the loss of all of the resource in
3 question. A component tragedy is one where selfishness reduces the resource, but not
4 to the extent where it is lost completely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

5

6



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



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