The Non-Tragedy of the Non-Linear Commons

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Abstract

Public goods are produced at all levels of the biological hierarchy, from the secretion of diffusible molecules by cells to social interactions in humans. However, the cooperation needed to produce public goods is vulnerable to exploitation by free-riders — the *Tragedy of the Commons*. The dominant solutions to this problem of collective action are that some form of positive assortment (due to kinship or spatial structure) or enforcement (reward and punishment) is necessary for public-goods cooperation to evolve and be maintained. However, these solutions are only needed when individual contributions to the public good accrue linearly, and the assumption of linearity is never true in biology. We explain how cooperation for *nonlinear* public goods is maintained endogenously and does not require positive-assortment or enforcement mechanisms, and we review the considerable empirical evidence for the existence and maintenance of nonlinear public goods in microbiology, cancer biology, and behavioral ecology. We argue that it is time to move beyond discussions about assortment and enforcement in the study of cooperation in biology.

Significance Statement

Fifty years ago, Garrett Hardin's *Tragedy of the Commons* galvanized research by arguing that exogenous mechanisms are needed to ensure the supply of public goods. Biologists have documented numerous exogenous mechanisms, such as kin-directed altruism, reciprocity, and spatial structure. Hardin's version of the public goods problem assumed linearity, which does indeed require

exogenous stabilizing mechanisms. However, public goods in nature are always nonlinear functions of individual contributions, and the production of nonlinear public goods can be stable without exogenous mechanisms. Numerous examples in microbiology, cancer, and behavioral ecology demonstrate this, but with rare exceptions, investigators have not recognized this. In this review, we explain how nonlinear public goods work, we describe empirical examples, and we suggest future areas of research.

The problem of public goods

"A central finding is that the world contains multiple types of individuals, some more willing than others to initiate reciprocity to achieve the benefits of collective action."

Elinor Ostrom (2000, J Econ Persp, 14:137*)*

The Tragedy of the Commons

Half a century ago, Garrett Hardin published *The Tragedy of the Commons (1)*, one of the most widely cited publications in both the natural and social sciences (2, 3). Although far from the first to write on public goods, Hardin's use of the commons metaphor crystallised and popularised the problem of public goods to the extent that it is now the paradigm of the problem of collective action.

In a commons (an open-access grazing pasture), each herdsman increases his own private income for every cow he adds, but each cow reduces the productive capacity of the pasture (the public good). Because the benefit of each additional cow is private, while the cost of reduced productivity is paid by all of the herdsmen, each individual herdsman is rationally, but perversely, incentivised to keep adding cows until the commons is destroyed. Refraining from exploiting a shared resource is not a rational strategy, and free-riding on the contributions of others enables non-cooperators to thrive at the expense of cooperators. Hence, the production and maintenance of public goods seems intrinsically unstable. The problem arises across biology and society (4), from the secretion of diffusible molecules by cells to humans protecting natural resources and reducing greenhouse-gas emissions.

Common explanations invoke positive assortment or enforcement

Hardin concluded that the maintenance of public goods requires "mutual coercion, mutually agreed upon," which, in human societies, can be achieved through resource privatisation or through enforcement (reward and punishment) imposed by higher authorities. Elinor Ostrom (5, 6) later shifted the focus to enforcement imposed by peers (social norms). In biology, cooperation traditionally (7) is ascribed to kin-directed altruism (8–10) or to preferential interactions with cooperators, caused for instance by persistent spatial structure (11–13) or assortment into similar trait-groups (14). These explanations are all forms of positive assortment (15). Biological explanations that invoke enforcement (punishment targeted at defectors and rewards given to cooperators) (13, 16) are analogous to Hardin's and Ostrom's ideas. We argue here that these explanations are not necessary for the evolution and maintenance of biological public goods.

Positive assortment and enforcement are not necessary because public goods are nonlinear

This view that positive assortment or enforcement is necessary for cooperation derives from the crucial and incorrect assumption that individual contributions to public goods accrue linearly (additively). But in biology, it is the rule that individual contributions accrue *nonlinearly*, and, as we will show, cooperation for *nonlinear* public goods is maintained endogenously. We are not claiming that assortment and enforcement are irrelevant; that is a separate debate about whether Hamilton's rule for kin selection holds only when the effect of kin-directed altruism is additive — an argument that dates back to the theory's origin (17–19) and has been recently revived (20–23). In fact, we believe that the debate over kin selection has diverted the field from a more fundamental insight: neither positive assortment nor enforcement is necessary to maintain cooperation for public goods.

Public goods in biology are nonlinear

Public goods in biology are almost always nonlinear functions of individual contributions (Fig. 1). In the case of diffusible molecules, nonlinearities arise because the effect of biological molecules (such as growth factors) on cell fitness is generally a sigmoidal function of their concentration, due to threshold dosage effects or cooperative binding of ligands (24–27). This is a well-established observation in microbiology (28–33). In social interactions, nonlinearities arise when just a portion of a group is large enough to successfully detect a predator (34–36), take down a difficult prey item (37–42), or reproduce successfully (43). In human society, herd immunity from vaccinations (44) and voting in winner-take-all elections (45) are examples of threshold public goods (an extreme case of nonlinearity), and in problems related to climate change, nonlinearities arise because there are critical greenhouse-gas concentrations below which ice sheets will not melt, corals will not dissolve, and the climate will avoid runaway feedback (46–49). To our knowledge, no linear public good in nature has ever been described. But the mismatch between linear theory and nonlinear reality remains roundly neglected.

The theory of nonlinear public goods

Linear public goods are unstable without positive assortment or enforcement

The problem of linear public goods as described by Hardin is known in game theory as the *N-person Prisoner's Dilemma* (NPD) (50, 51), an extension to multiple players of the famous two-player *Prisoner's Dilemma* (52). In the NPD, individuals in a group can be cooperators (who pay a contribution, at a cost *c*) or defectors (who do not contribute, and pay no cost). The contributions are summed, and the sum is multiplied by a reward factor *r* that yields the total benefit (the good), which is redistributed evenly (made public) to all the individuals, both cooperators and defectors (**Box 1**). On average, if there is no assortment, a cooperator and a defector find the same number of cooperators in the rest of their group (excluding itself), and consequently, every cooperator enjoys the additional benefit of having one more cooperator in its group (itself) but also pays the cost *c*. In this situation, unless the reward factor is huge (technically, when the *per capita* return on cooperation is larger than the group size, which is implausible unless group size is very small), the average fitness of a cooperator is lower than the average fitness of a defector, and cooperators are eliminated. Hence, no

one has an incentive to cooperate, and the consequence is a lower payoff for everybody — Hardin's Tragedy of the Commons. In the NPD, cooperation can only be rescued exogenously, either by causing individuals to be more likely to interact with others playing the same strategy (positive assortment) or, more trivially, by punishing defectors and rewarding cooperators (enforcement).

Nonlinear public goods can be stable without positive assortment or enforcement

The crucial (apparently innocuous) assumption of Hardin and the NPD is that the public good is a linear function of the number of cooperators (**Box 1**). This has been the (almost always implicit) assumption in most models of the evolution of cooperation. However, when the effect of cooperation is a nonlinear function of the number of cooperators, the results of the NPD do not hold. As the examples in **Fig. 1** illustrate, biological public goods take a variety of nonlinear shapes, most of which can be modelled using a logistic function defined by its steepness and the position of its inflection point (**Fig. 2**).

The key difference with the NPD is the possibility of a polymorphic equilibrium in which cooperators and defectors coexist stably when the cost/benefit ratio of cooperation is below a critical value (**Fig. 2**). Although this polymorphic equilibrium is inefficient (a higher amount of public good could be achieved by increasing the number of cooperators), its existence and its persistence do not require positive assortment or enforcement: *cooperation can be stable in well-mixed populations of unrelated individuals, including free-riders* — there is no need for genetic relatedness, spatial structure, repeated interactions, rewards, or punishment. Under some conditions, assortment can help cooperation, but, as we explain later, not always.

A verbal explanation using a threshold-effect public good

Consider the simplest type of nonlinearity: a threshold-effect public good. A threshold is simply a very steep sigmoid function in which the public good is produced if and only if at least k group members cooperate by each paying a cost c. A population of cooperators and defectors is randomly divided into groups of size n, the public good is produced in each group according to the number of cooperators and shared evenly, and the groups are remixed back into a single population before the next round, precluding positive assortment. (N.B. This assumption of multiple groups is not required (**Box 1**), but it makes the verbal explanation easier.)

1. Within each group, the cooperators have lower fitness than do the defectors. In groups with $<k$ cooperators, this is because no public good is produced, but cooperators still pay the cost c. In groups with $\geq k$ cooperators, cooperators and defectors receive the same individual fitness benefit b from their share of the public good, but cooperators also still pay the cost c.

2. However, averaged over the whole population, it is possible for cooperator fitness to be greater than defector fitness. This seeming contradiction, known as Simpson's Paradox (28), is simply due to the fact that, by definition, a larger proportion of cooperators are in the groups that successfully make the public good and enjoy a boost to fitness, while a larger proportion of defectors are in the groups that fail to make the public good.

3. Thus, even though the highest fitnesses of all accrue to the defectors in groups with ≥k cooperators, these fortunate few can be outweighed by the low fitnesses of the many defectors in defector-dominated groups that fail to enjoy any public good. (The least fortunate individuals are of course the few cooperators in defector-dominated groups.)

4. In short, cooperator and defector fitnesses are weighted by group membership, and the effect of nonlinearity is to increase the weighted average of cooperator fitness over defector fitness. In this threshold-effect example, since only the groups with ≥k cooperators produce the public good, the defector-dominated groups (with <k cooperators) receive zero fitness boost from public-goods production.

The logic for sigmoidal benefit curves is similar, except that public good is produced with numbers of cooperators in a group higher or lower than k, albeit to a declining extent, where k is now the inflection point of the sigmoid benefit curve (**Fig. 2**).

The dynamics of public goods production

We now examine the dynamics of public-goods production (**Fig. 2**). *When cooperators are at intermediate population frequency*, there are many groups for which adding one last cooperator (by mutation) results in much more public good being produced, because the group is in the steep region of the benefit curve. Correspondingly, adding one last defector (by mutation) results in much less public good being produced. Since the first type of group has marginally more cooperators and much more public good to go around, while the second type has marginally more defectors and much less public good, cooperators have a higher tendency to be in the groups with much more public good and thus to increase in frequency.

In contrast, when cooperators are at low or high population frequencies, most groups have few or many cooperators, respectively, and adding one more cooperator has little effect on public goods production. The cost of cooperation then dominates the dynamics, cooperators have lower fitness than do defectors, and defectors increase in frequency.

Taken together, cooperators increase when they are at intermediate population frequencies, until such point that cooperators are so frequent that defectors have the higher fitness. More technically, under a wide range of parameter values, there are two interior equilibrium points (**Fig. 2A**), one of which is polymorphic and stable, meaning that cooperators and defectors coexist stably without the need for positive assortment or enforcement. The other point is also polymorphic but unstable, which creates an origin problem for public-goods production.

The existence and positions of the equilibrium points depend on the shape of the benefit function, the cost c, and the group size n (**Fig. 2B**). Matching intuition, the production of public goods is easier (the stable point is more likely to exist) when cost is lower and groups are smaller. For instance, Mielke et al. (53) have reported that sooty mangabey monkeys are more likely to issue an alarm call for snakes when surrounded by fewer individuals, whereas caller sex or the presence of grooming partners, kin, and potential mates all have no effect on call probability. Given that alarm calling is likely to incur a

small-to-moderate cost (the caller might attract other predators, draw in competing foragers, or have had reduced foraging success by having been more vigilant), Mielke et al. conclude that these calls are likely to be a nonlinear public good.

Less intuitively, increasing the inflection point increases the stable fraction of cooperators, while decreasing it can eliminate the unstable equilibrium point and thus eliminate the origin problem (**Fig. 2B**). Increasing the steepness of the benefit curve allows the polymorphic equilibrium to be achieved at higher costs of cooperation, which makes cooperation easier to maintain, but also brings the stable and unstable equilibria closer together, which makes cooperation less robust to random fluctuations (**Fig. 2B**).

Note that in the NPD, maximum benefit is only achieved when all group members cooperate, but this is not necessarily the case with nonlinear benefits, where the presence of free-riders can improve average group fitness. Once there are enough cooperators to produce most of the public good, adding cooperators to a group can *reduce* the total fitness of the group, since all cooperators pay the cost of cooperation but produce no (or little) additional benefit (if everyone in a group volunteers to stand guard, no one gets to eat). This has been observed in the form of maximal colony growth being achieved when cooperator cancer cells, bacteria, or yeast are at an intermediate frequency (**Box 2**) and is a marker of a public good being nonlinear.

Assortment and enforcement are not necessary

We certainly agree that positive assortment exists in nature, but our argument is that it is not necessary for the evolutionary stability of nonlinear public goods. This does not mean that positive assortment is unimportant or even that nonlinear benefits are always sufficient to stabilize cooperation. For instance, when the cost/benefit ratio of cooperation is too high, there can be no polymorphic equilibrium in a well-mixed population, and positive assortment can instead lead to the maintenance of cooperation (sometimes referred to as 'altruism' rather than 'cooperation'). The evolution of sterile workers in eusocial insects is a clear example; the extreme cost of cooperation and immense group size requires positive assortment (kin-directed altruism). But if nonlinearity holds, it is known that relatedness does not always improve cooperation (17, 19, 22), a result that could apply more broadly, which implies that whether and how assortment helps or impairs public-goods cooperation remains an open question (17, 19–23) Enforcement (punishment for defectors and rewards for cooperators) (13, 16) can also help cooperation, but enforcement mechanisms are not possible in many biological systems.

Private benefits for cooperators (when cooperators benefit more than do defectors from the public good they produce) are another type of payoff asymmetry that has been proposed to select for public-goods production. It stands to reason that no pure public good exists in nature — cells secreting diffusible molecules, for instance, are likely to benefit more from their own molecules than are neighbouring cells. However, claiming that private benefits alone stabilize public goods (54) is incorrect; a private benefit is simply a reduction in the cost paid by the producer, and if the cost remains above zero, then public-goods production continues to require explanation. If, on the other

hand, the private cost is outweighed by a private benefit, the public-goods problem is solved merely by defining it away.

Empirical evidence

Empirical observations are in line with the predictions (but sometimes misunderstood)

Some of the strongest evidence for nonlinear public-goods games has been found in cell populations (we describe nine examples in **Box 2**). However, with few exceptions (28, 55), these results have *not* been interpreted as examples of nonlinear public goods, even though they did not fit the predictions of the linear NPD (notably, observations that maximum growth was achieved at intermediate frequencies of cooperators (56)). The fact that models of cooperation in bacteria and in cancer cells often incorrectly assume linear benefits has been pointed out (57, 58), but the disconnect between observation and theory persists.

Testing the theory in the lab

Deliberate experimental tests of the theory are challenging. However, the tools of molecular biology can be applied to cellular systems, and in **Box 2** we describe nine *in-vitro* studies that have manipulated model parameters and achieve a stable polymorphism with a nonlinear public good (plus the example of crystal toxins produced by *Bacillus thuringiensis* (59)). As one example, the secretion of growth factors by cancer cells has been manipulated (33), and experiments have successfully shown both stable polymorphism and maximum growth at intermediate fraction of cooperators predicted by theory (32).

Testing the theory in the field

While experiments with cells allow one to manipulate and measure costs and benefits, it is difficult to estimate group size, because the diffusion ranges of molecules are difficult to measure; hence, predictions of the dynamics of cell populations producing public goods must currently be made for a range of group sizes (**Fig. 3A**). In contrast, for populations of social vertebrates, it is often possible to measure both group size and the benefit of collective action as a function of the number of cooperators — as can be seen with cooperative hunting in wolves (42) and alarm calling in monkeys (53) — but the relative cost of cooperation is difficult to quantify. In these cases, it is possible to predict the existence and disappearance of the polymorphic equilibrium for a range of cost/benefit ratios (**Fig. 3B**).

What should we focus on in cooperation research?

Social scientists and biologists have long had the intuition that nonlinearities are important for the stability of cooperation, an intuition, however, that has not been widely recognised nor applied to empirical systems. Part of the reason has been the power of Hardin's essay, which galvanised research by arguing that society needed to apply an exogenous mechanism (enforcement) to ensure the supply of public goods. In biology, research on cooperation has correspondingly focused on finding exogenous mechanisms (positive assortment and enforcement) to stabilize cooperation,

glossing over the oversimplified assumption of linearity. Recent clear evidence of nonlinear effects, experimental studies with cellular systems, and theoretical advances together show that public goods can be stable without positive assortment or enforcement, helping us explain cooperation in well-mixed populations of unrelated individuals, from single cells to sentient multicellular organisms.

We urge that empirical work on public goods in biology should move on from linear thinking and focus instead on measuring, and if possible manipulating, group sizes and the nonlinear effects of cooperation, testing for stable coexistence, the existence of critical thresholds, and maximum fitness at intermediate levels of cooperation (**Box 3**). This new direction should result in deeper insights and also be more likely to result in practical ways to enhance or impair cooperation in biological systems, with implications for problems ranging from antibiotic resistance and anti-cancer therapies to ecosystem management. Fifty years after Hardin published the Tragedy of the Commons, it is past time to study the *Non-Tragedy of the Non-Linear Commons*.

Box 1: Models of public goods

First consider the simplest case of a single group of n individuals in which a public good is produced (conferring a benefit equal to 1 on each group member) if at least k=1 individual cooperates (this is known as the Volunteer's Dilemma). Cooperating costs c and receives a benefit of 1, hence an average payoff equal to 1-c. Defecting receives a benefit equal to 0 if no one cooperates but receives a benefit equal to 1 if at least one *other* individual cooperates, which happens with probability $1-(1-x)^{n-1}$, where x is the probability of one individual volunteering. (Note that this is also the average payoff to defecting since the value of the benefit equals 1.) When these two payoffs are equal, at $x=1-c^{1/(n-1)}$, we have a mixed equilibrium: some individuals cooperate and some do not. The equilibrium is stable because if we inspect the average payoff to defecting $(1-(1-x)^{(n-1)})$, we see that as the probability of an individual cooperating x increases, the payoff to defecting increases, whereas as x decreases, the payoff to defecting decreases. As long as the cost of cooperating c is low enough, the payoff to cooperating will sometimes be higher than the payoff to defecting (see figure).

When the threshold of public-goods production is k>1, the calculations are more complex (60), but the result is similar. The intuitive explanation is that if there are at least k cooperators in the rest of the group, cooperating yields the same benefit as defecting, but at an extra cost c; if there are fewer than k-1 cooperators, cooperating yields no benefit anyway, again at an extra cost c; hence cooperation is selected against in both cases. The only case in which cooperation has a selective advantage is when there are exactly k-1 cooperators in the rest of the group (which happens with a probability that depends on group size, see below). Therefore, cooperation has an advantage at intermediate frequencies of cooperators.

When we replace the threshold (a step function) with a sigmoid function, the logic is similar, except that cooperation has a selective advantage not just when the cooperator is pivotal in producing the public good (as in the threshold public goods game above), but also for a wider range of number of cooperators. However, the critical cost that enables the existence of a mixed equilibrium decreases, see main text.

Finally, when there are multiple groups formed at random, the analysis is even more complex, but using the properties of Bernstein polynomials (58) (see below), we can characterize the dynamics (the number and type of equilibria) just by looking at the difference in benefit between cooperators and defectors — that is, essentially, by looking at what happens in a single group.
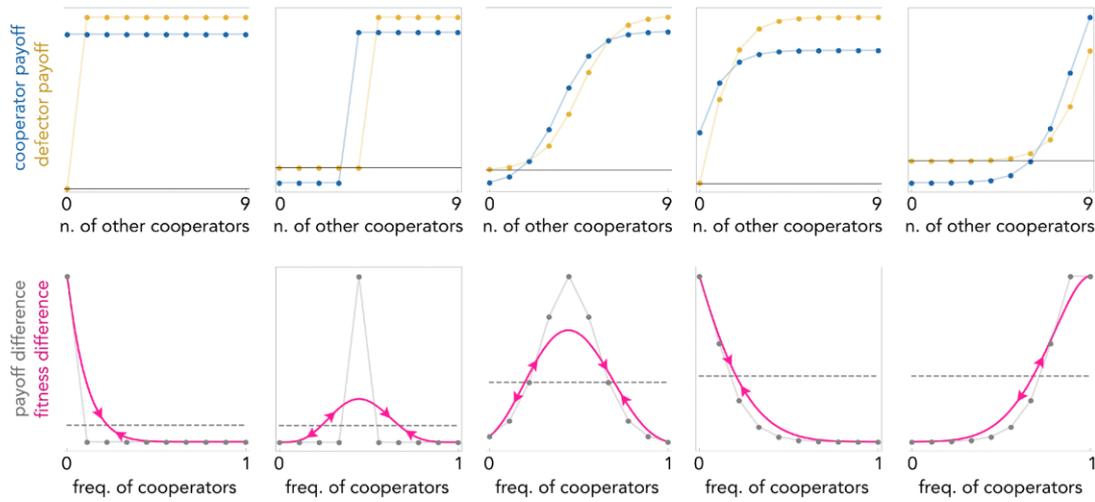
Figure. Top: Payoffs for different types of benefit functions in a single group. From left to right: a threshold of 1; a threshold of 5; concave (h=0, s=10), convex (h=1, s=10), sigmoid (h=0.4, s=10). **Bottom**: the payoff difference (cooperator - defector, grey dots) and the dynamics in large, well-mixed populations (pink curves; the arrows show the direction of the dynamics); the horizontal dotted line shows the cost (c=0.1); group size n=10.

In a large population with random group formation (of size n) at each generation, one's probability of having i cooperators among the other group members, given a frequency x of cooperators in the population, is given by the probability mass function of a binomially distributed random variable i with parameters ($n − 1$, x):

$$p_{i,n-1}(x) = \binom{n-1}{i} x^i (1-x)^{n-1-i} \tag{1}$$

The fitnesses of cooperators and defectors are given therefore by

$$W_C = \sum_{i=0}^{n-1} p_{i,n-1}(x) \cdot b(i+1) - c \tag{2}$$

$$W_D = \sum_{i=0}^{n-1} p_{i,n-1}(x) \cdot b(i) \tag{3}$$

where $b(i)$ is the benefit (payoff) for being in a group with i other cooperators; a cooperator has one cooperator more in a group (itself), compared to a defector in the same group, but the cooperator pays a cost c ($0 < c < 1$), if we assume that the maximum benefit is 1 and c is the cost/benefit ratio of cooperation. The average fitness of a mixed population is

$$\underline{W} \ = \ x \cdot W_C + (1 - x) \cdot W_D \tag{4}$$

The replicator dynamics of this system is

$$\dot{x} \ = \ x \, (1 - x) \, \beta(x) \tag{5}$$

where the fitness difference W_C-W_D is written in the form $\beta(x)$, and

$$\beta(x) = \sum_{i=0}^{n-1} \quad p_{i,n-1}(x) \cdot \Delta b_i \tag{6}$$

is the gradient of selection, with

$$\Delta b_i \ = \ b(i+1) - c - b(i) \tag{7}$$

When $b(i)$ is a linear function (that is, in the case of the NPD (50, 51)), (5) can be easily solved analytically, since $b(i)=rci/n$ (where r is the reward factor), unless $r>n$ (which implies unrealistically small groups and high rewards) the only stable equilibrium is $x=0$ (no cooperation — Hardin's *Tragedy of the Commons*).

Most cases of nonlinear benefits can be modelled using the following function. The benefit $b(i)$ for an individual in a group with i cooperators and $(n - i)$ defectors is given by

$$b(i) \ = \ \frac{[l(i) - l(0)]}{[l(n) - l(0)]} \tag{8}$$

the normalized version of a logistic function $l(i)$ with inflection h and steepness s:

$$l(i) \ = \ \frac{1}{1 + e^{s(h-i/n)}} \tag{9}$$

The parameter h defines the position of the inflection point: $h{\rightarrow}1$ gives increasing returns (convex) and $h{\rightarrow}0$ diminishing returns (concave); s defines the steepness of the function ($s{\rightarrow}\infty$ models a threshold public goods game; $s{\rightarrow}0$ models an NPD; the normalization in (9) prevents the logistic function (9) from becoming constant for $s{\rightarrow}0$) (**Fig. 2**).

Beyond the two trivial rest points $x = 0$ and $x = 1$, further interior equilibria are given by $\beta(x)=0$. With nonlinear benefits, an analytical solution is not possible, with the exception of concave and convex benefits (57, 61–64): games with concave or convex benefits can have at most one interior equilibrium, either stable or unstable. Threshold public goods games can be solved for $k=1$ (for example, in the case of alarm calls) (65–68) or for the simple case $n=3$ with $k=2$ (69, 70). More general models (60, 71–74) require approximations for large n.

With sigmoid or more complex benefit functions, a recent advance in the theory using the properties of Bernstein polynomials has made it possible to characterise the dynamics and approximate the equilibria (58, 75). Games with sigmoid benefits (or any benefit function with only one inflection point) can have two internal equilibria, one of which stable, and two pure equilibria (unstable pure cooperation; stable pure defection). More complex nonlinearities can be analyzed using the same methods (58).

Box 2. Examples of nonlinear public-goods production in cell populations

1. Chuang et al. (28) repeatedly and randomly subdivided an engineered *Escherichia coli* bacterial population into small groups that varied in the proportions of bacteria that did and did not export a costly antibiotic-resistance inducer molecule. Although the producer genotype had the slower growth rate, colony growth rate increased sigmoidally with the producer proportion, leading to coexistence of producers and nonproducers. The authors correctly argued that nonlinearity is a sufficient explanation for coexistence, which they explained in terms of Simpson's Paradox.

2. Becker et al. (29) reported that the export of iron-scavenging pyoverdine molecules by *Pseudomonas putida* bacteria reduced individual growth rate, but colony growth rate increased asymptotically (concave down) with pyoverdine concentration. Again, producers and nonproducers coexisted.

3. Rosenthal et al. (30) showed that *Bacillus subtilis* individuals stochastically switch on and off the costly enzymatic transformation of toxic acetate to nontoxic acetoin, regulated by a noise-excitable gene circuit. Acetate is a by-product of sugar metabolism, and <15% of a colony's cells were enough to eliminate acetate from the environment. Here, the bacteria were exhibiting a mixed strategy, equivalent to polymorphic equilibrium of producer and nonproducer coexistence.

4. Lee et al. (76) reported that antibiotic resistance in well-mixed populations of *E. coli* was due to a tiny minority of antibiotic-resistant cells that constitutively exported costly indole molecules, which induced drug efflux and oxidative stress protection in non-resistant cells. Producers and nonproducers coexisted, and maximum growth was achieved at intermediate fractions of producers.

5. Smith et al. (55) showed nonlinear effects in sporulation efficiency of *Myxococcus xanthus*, resulting in fitness functions that led to coexistence of cooperators and defectors without assortment.

6. Gore et al. (77) showed that in the yeast *Saccharomyces cerevisiae*, in which sucrose is digested extracellularly by the enzyme invertase, and ~99% of the product diffuses away, colony growth rate was asymptotic on glucose concentration, which allowed a small number of cooperators to supply sufficient invertase to the whole group. Invertase producers and nonproducers coexisted, despite producers having a lower growth rate, and maximum growth was observed at an intermediate frequency of cooperators.

7. MacLean et al. (56) observed that maximum growth in yeast populations occurred at intermediate frequencies of cooperation.

8. Lindsay et al. (78) reported a similar observation in a fungal pathogen population.

9. Experiments with cancer cells have been used to test the predictions of nonlinear public goods games (32), showing that a stable coexistence of cooperators and defectors depends on the cost/benefit ratio of cooperation and that growth rates peak at intermediate frequencies of cooperators, as predicted by the theory.

Box 3. Outstanding Questions

- Is there any example of a linear biological public good?

- How does assortment affect the origin and maintenance of cooperation for nonlinear public goods?

- How can we intervene in real systems to improve (e.g. for conserving natural resources) or impair cooperation (e.g. in anti-cancer therapies)?

- While we do not discuss public goods in human economic behavior, we note that similar concepts apply to common-pool resources (**Fig. 1**), where cooperation takes the form of paying an opportunity cost ('leaving fish in the sea'). Do Ostrom's (5) Design Principles for common-pool resources also rely on nonlinear effects?

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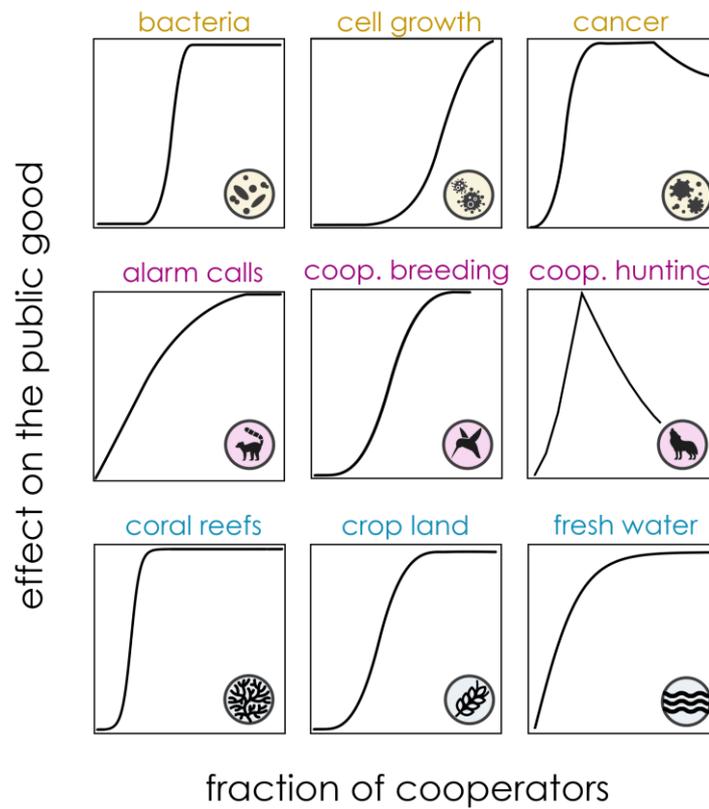
Figures and Tables

Figure. 1. **Public goods are nonlinear**. Top row (diffusible molecules): siderophore production in bacteria (29); growth factor production by eukaryotic cells (32); the Warburg effect on cancer cells (31). Middle row (social behaviour in vertebrates): predator detection (34); cooperative breeding (43); cooperative hunting (42). Bottom row (environmental resources as a function of avoided global temperature increase) (48): extension of coral reefs; availability of crop land; freshwater reserves.
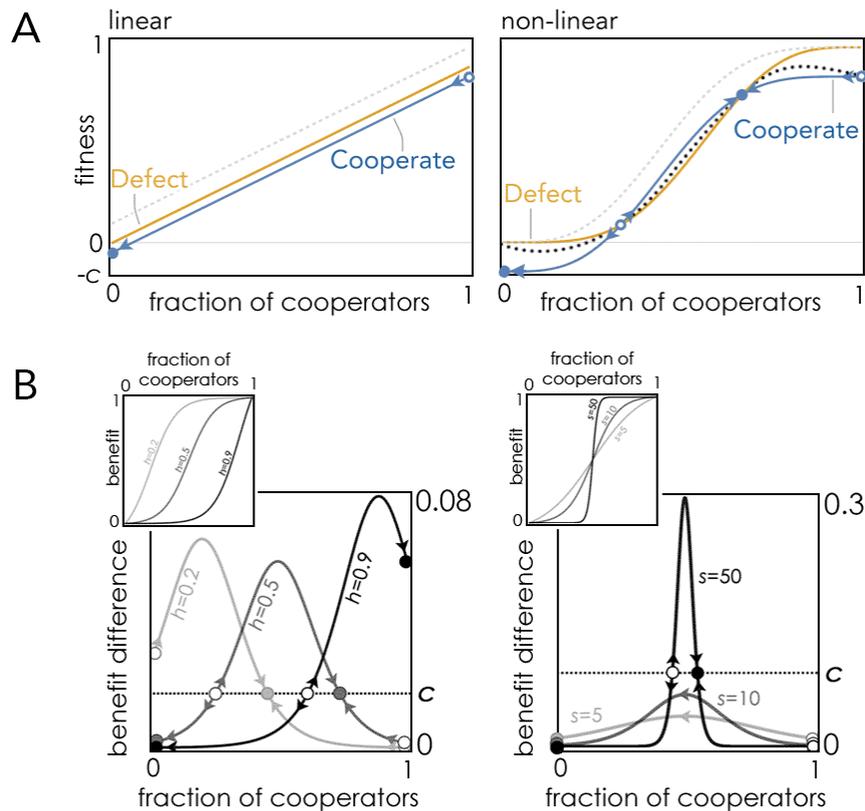
Figure. 2. **Dynamics of public goods.** (**A)** The fitness of cooperators (blue) and defectors (yellow) and the average fitness (black) as a function of the fraction of cooperators in the population, in the linear and nonlinear cases for the same group size n=10 and cost of cooperation c=0.15. The cooperator curve is shifted to the left of the defector curve by $1/n$ (the grey dotted curve) because a cooperator requires exactly one fewer cooperator among the other group members to obtain the same benefit as a defector, since the cooperator is itself contributing), and down by an amount c (the fitness cost of cooperation). Cooperation increases in frequency in the population when the cooperator fitness curve is above the defector curve. Thus, if the frequency of cooperators in the population starts between the two unstable equilibria (open circles, nonlinear case), the frequency evolves to the stable equilibrium (filled circle). (**B)** The dynamics can be observed more easily by plotting, instead of the fitnesses of the two types, the difference in benefit (that is, fitness without the cost) between a cooperator and a defector; equilibria are found where this difference intersects the horizontal line corresponding to the cost of cooperation. Arrows show the direction of the dynamics; circles show the equilibria (filled: stable; open: unstable). The dynamics shown are for three different values of the inflection point h (left, with s=10) and three different values of steepness s (right, with h=0.5), where h and s are parameters of the logistic function (**Box 1**, Eq. 9). A higher value of h means a higher proportion of cooperators is needed to achieve a given benefit ($h \rightarrow 1$ means that all individuals must be cooperators to achieve a high benefit, $h \rightarrow 0$ means that only one cooperator is needed to achieve a high benefit). A higher value of s means a steeper increase in the benefit of the public good ($s \rightarrow 0$ gives the (linear) NPD; $s \rightarrow \infty$ gives a threshold-effect public goods game).
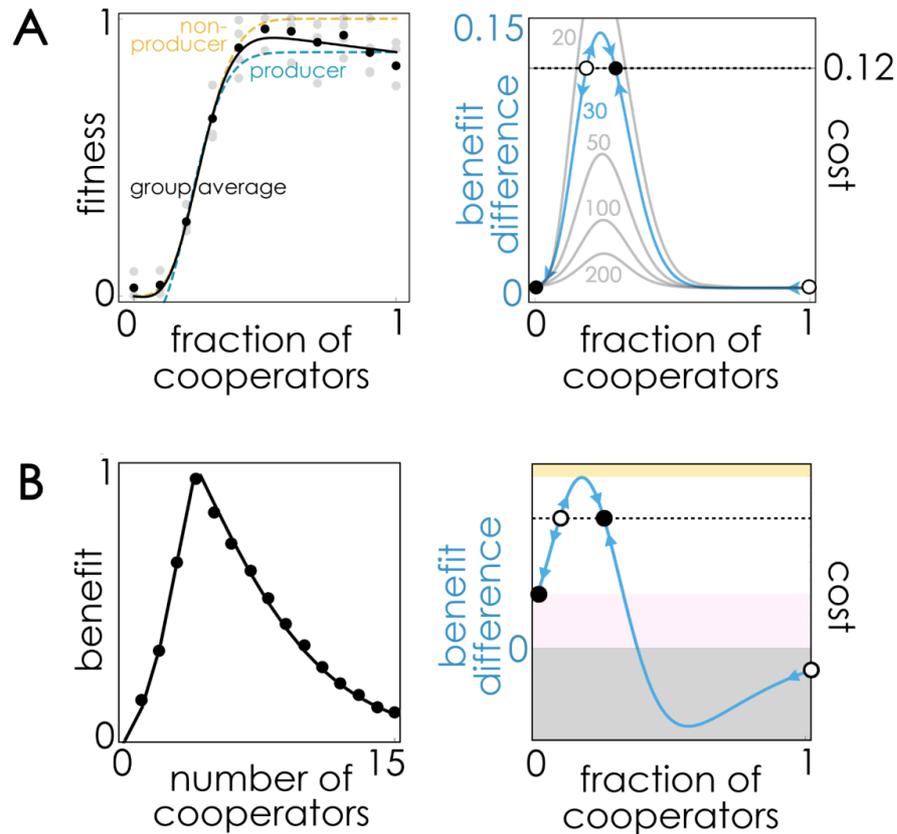
Figure. 3. Estimating parameters and predicting dynamics from mixed populations. **(A)** Cancer cells producing type 2-insulin-like growth factor (32). The empirically measured fitnesses of polymorphic (producers and nonproducers) populations of cells as a function of the fraction of producer cells (grey dots: individual measurements; black dots: mean); the black curve is the best fit to the average fitness; the dashed curves are the corresponding fitness functions for producers (blue) and non-producers (yellow). The difference in benefit between producers and non-producers is shown for different values of group size n (grey curves); the dynamics are shown for n=30 (blue curve) and c=0.12 (horizontal dotted line): the arrows show the direction of the dynamics (producer cells increase in frequency when the gradient of selection is positive; and decline otherwise), and the circles show the equilibria (white: unstable; black: stable). **(B)** Cooperative hunting in wolves (42). The benefit (probability of hunting success) is shown as a function of the number of individuals cooperating in the collective hunt; the black curve is the best fit to a double sigmoid function (58). The dynamics are shown for a hypothetical cost (c=0.15; horizontal dotted line). If the cost were above a critical threshold (approximately 0.2; yellow area) the fraction of cooperators would decrease until it reaches zero; with a cost below approximately 0.08 (pink area), the interior unstable equilibrium would disappear.