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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 solution to this problem of collective action is that some form of positive assortment (due to kinship or spatial structure) or of enforcement (reward and punishment) is necessary for public-goods cooperation to evolve. 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, and we review the considerable empirical evidence for the existence and maintenance of nonlinear public goods in biology. We argue that it is time to move beyond discussions about assortment and enforcement in the study of cooperation in biology.

Keywords: positive assortment, public goods, collective action, common-pool resources, cooperation, game theory, group selection, kin selection, social dilemma

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* (Hardin 1968), one of the most widely cited publications in both the natural and social sciences (Barrett & Mabry 2002; van Laerhoven & Ostrom 2007). 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 distributed over all the herdsman, every 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 (Rankin, Bargum & Kokko 2007), 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 (Ostrom 1990; 2000) later shifted the focus to enforcement imposed by peers (social norms). In biology, cooperation traditionally (Dawkins 1976) is ascribed to kin selection (Hamilton 1963; 1964a; b) or to preferential interactions with cooperators, caused for instance by persistent spatial structure (Axelrod & Hamilton 1981; Axelrod 1984; Nowak 2006). These explanations are forms of positive assortment (Fletcher & Doebeli 2009). Biological explanations that invoke enforcement (punishment targeted at defectors and rewards to cooperators) (Nowak 2006; Ågren, Davies & Foster 2009) 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 but 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. There is a separate debate that 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 (Matessi & Karlin 1984; 1986; Matessi 1988) and has recently been revived (Van Veelen 2009; van Veelen 2011; van Veelen *et al.* 2017; van Veelen 2018). This is not our point though. 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 nonlinear 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 (Cornish-Bowden 2012; Zhang, Bhattacharya & Andersen 2013; Frank 2013; Archetti & Scheuring 2016). This is a well-established observation in microbiology (Chuang, Rivoire & Leibler 2010; Becker *et al.* 2018; Rosenthal *et al.* 2018) and cell biology (Archetti 2014; Archetti, Ferraro & Christofori 2015; Archetti & Pienta 2019). In social interactions, nonlinearities arise when just a portion of a group is large enough to successfully detect a predator (Pulliam et al. 1982; Creel 1997; Clutton-Brock 1999), take down a difficult prey item (Bednarz 1988; Stander 1992; Heinsohn and Packer 1995; Kim et al. 2005; Yip et al. 2008; MacNulty et al. 2011), or reproduce successfully (Rabenold 1984). In human society, herd immunity from vaccinations (Reluga & Galvani 2011) and voting in winner-take-all elections (Palfrey & Rosenthal 1985) 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 (Rockström et al. 2009; Rustagi et al. 2010; Ricke et al. 2016; Steffen et al. 2018). 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.

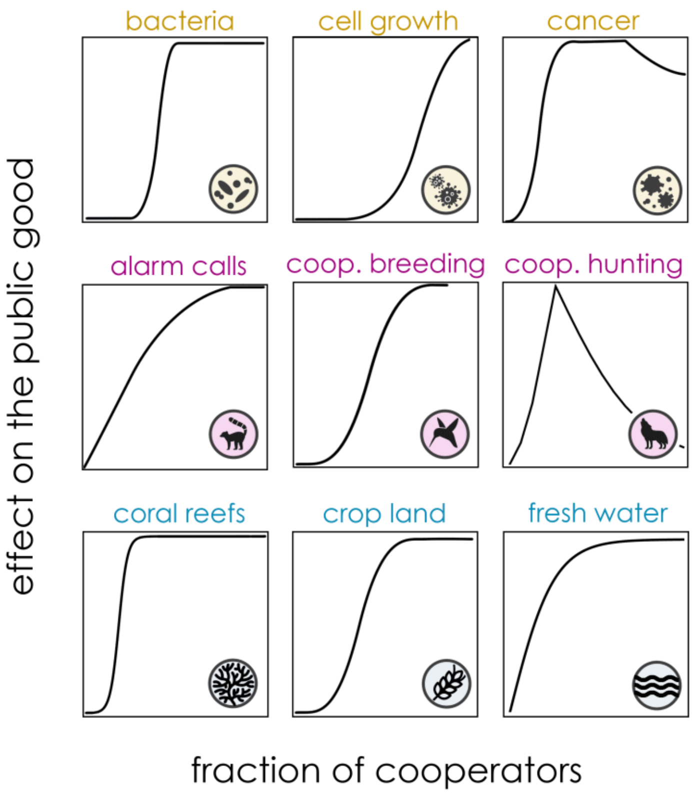

Fig. 1. **Public goods are nonlinear**. Top row (diffusible molecules): siderophore production in bacteria (Becker *et al.* 2018); growth factor production by eukaryotic cells (Archetti, Ferraro & Christofori 2015); the Warburg effect on cancer cells (Archetti 2014). Middle row (social behaviour in vertebrates): predator detection (Pulliam, Pyke & Caraco 1982); cooperative breeding (Rabenold 1984); cooperative hunting (MacNulty *et al.* 2011). Bottom row (environmental resources as a function of avoided global temperature increase) (Ricke *et al.* 2016): extension of coral reefs; availability of crop land; freshwater reserves.

The theory of nonlinear public goods

Linear public goods require 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) (Fox & Guyer 1978; Hamburger 2010), an extension to multiple players of the famous two-player *Prisoner's Dilemma* (Tucker 1950). 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, but the result 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

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 are not valid. As the examples in **Fig. 1** illustrate, biological public goods take a variety of nonlinear shapes, most of which can be modelled using a normalised 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 does 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.

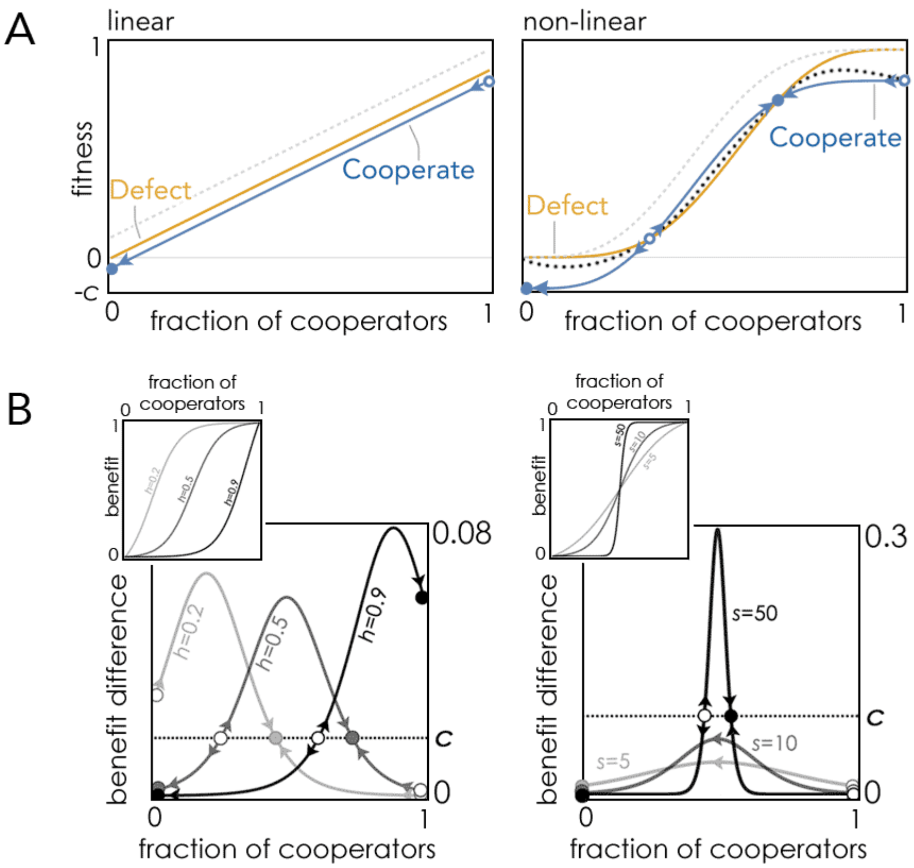

Fig. 2. **Dynamics of public goods.** (**A)** The fitness of cooperators (blue) and defectors (yellow) and the average fitness (black) as a function of the fraction of cooperators in the population, in the linear and nonlinear cases for the same group size *n*=10 and cost of cooperation *c*=0.15. The 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*→1 means that all individuals must be cooperators to achieve a high benefit, *h*→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*→0 gives the (linear) NPD; *s*→∞ gives a threshold-effect public goods game).

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A verbal explanation using a threshold-effect public good

Consider the simplest case of nonlinearity: a threshold-effect, or step-function, public good (a threshold is simply a very steep sigmoid function) in which a collective benefit is produced if and only if at least k group members cooperate by paying a cost c. We examine the fitness of a focal cooperator in a group of size n:

1. If there are fewer than k-1 cooperators in the rest of the group, adding one’s own contribution is worse than useless, because the threshold is not reached and no benefit is produced, but the cooperator has paid the cost c. The focal cooperator’s fitness is less than that of the defectors in the group, because the defectors did not pay the cost. Therefore, if the initial frequency of cooperators is too low, cooperation does not evolve.
2. If, however, there are exactly k-1 cooperators in the rest of the group, being the k-th cooperator not only results in the public good being produced, *it is also personally beneficial*, because the benefit received by the focal cooperator shoots up from 0 to b at k cooperators (provided of course that $b>c$). In other words, when the individual benefit of cooperation, weighted by the probability of being the k-th cooperator in a group, is higher than the cost of cooperation, cooperators have a higher fitness than do defectors and increase in frequency (**Fig. 2**).
3. Finally, if there are k or more cooperators in the rest of the group, adding one’s own contribution is a waste, because the threshold had already been reached, and while both cooperators and defectors enjoy the benefit of the public good, defectors have the higher fitness because they avoided the cost c. Therefore, cooperators decline in frequency, and cooperators never go to fixation because if their population frequency grows to be very high, defectors do better on average and increase in frequency.

The result is stable coexistence of cooperators and defectors, with no need for positive assortment or enforcement. In short, cooperation for nonlinear public goods is stabilised by frequency-dependent selection.

Sigmoidal public goods

The logic for sigmoidal benefit curves is similar, except that a cooperator can personally benefit over a broader set of conditions, both when there are exactly k-1 other cooperators in one’s group, where k is now the inflection point of the sigmoid benefit curve, and also with numbers of cooperators higher or lower than k, albeit to a declining extent. The dynamics depend on the shape of the benefit function, the cost c, and the group size n (**Fig. 2B**).

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Matching intuition, the production of public goods is easier when the cost is low and the groups are smaller. Less intuitively, increasing the inflection point increases the stable fraction of cooperators, while decreasing it can eliminate the internal unstable equilibrium and thus eliminate the origin problem (**Fig. 2B**). Increasing the steepness of the benefit 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**). Notice that while in the NPD, maximum benefit is achieved when all group members cooperate, 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 the public good (or most of it), having more cooperators in a group actually *reduces* the total fitness of the group, since all cooperators pay the cost of cooperation but produce no (or little) additional benefit (e.g. if everyone in a group stands guard against predators, no one gets to eat). This has been observed, and is sometimes misunderstood, in the form of maximal colony growth being achieved when cooperator cancer cells, bacteria, or yeast are at an intermediate frequency.

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 selection). But if nonlinearity holds, it is known that relatedness does not always improve cooperation(Matessi & Karlin 1984; Matessi 1988), a result that could apply more broadly, which implies that whether and how assortment helps or impairs public-goods cooperation remains an open question (Matessi & Karlin 1984; Matessi 1988; Van Veelen 2009; van Veelen 2011; van Veelen *et al.* 2017; van Veelen 2018) Enforcement (punishment for defectors and rewards for cooperators) (Nowak 2006; Ågren, Davies & Foster 2009) 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 (Korolev, Xavier & Gore 2014) 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 very few exceptions (Smith, Van Dyken & Zee 2010; Chuang, Rivoire & Leibler 2010), 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 (MacLean *et al.* 2010)). The fact that models of cooperation in bacteria and in cancer cells often incorrectly assume linear benefits has been pointed out (Cornforth, Sumpter & Brown 2012; Archetti 2018), 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* (Patel *et al.* 2019)). As one example, the secretion of growth factors by cancer cells has been manipulated (Archetti & Pienta 2019), and experiments have successfully shown both stable polymorphism and maximum growth at intermediate fraction of cooperators predicted by theory (Archetti, Ferraro & Christofori 2015).

Testing the theory in the field

However, 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 — 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 that however 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*.

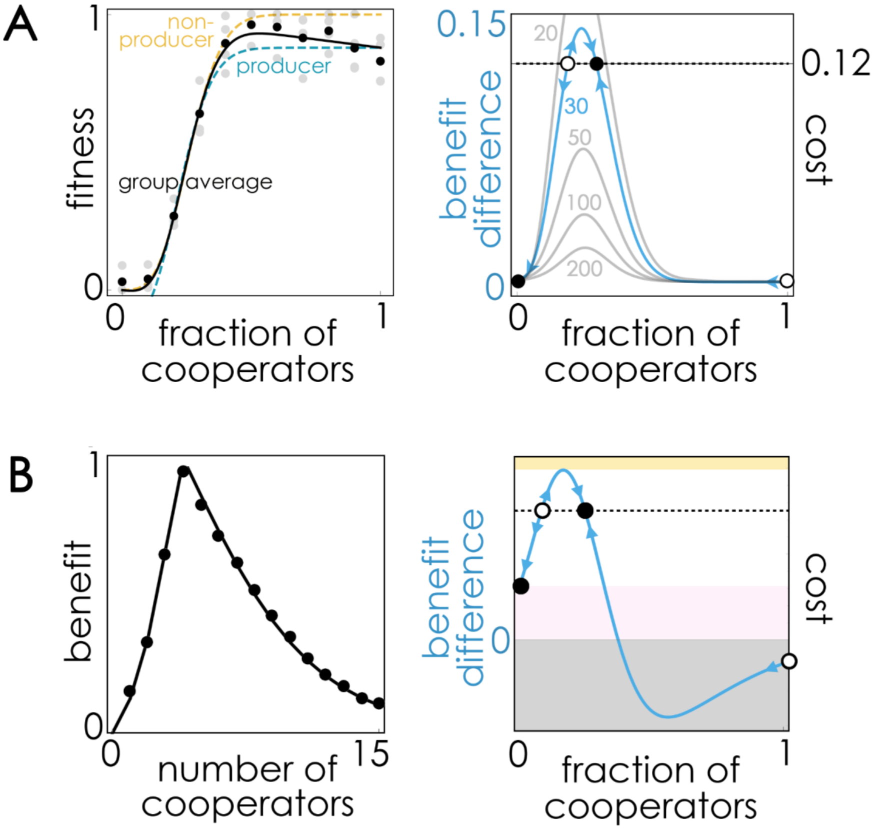

Fig. 3. Estimating parameters and predicting dynamics from mixed populations. **(A)** Cancer cells producing type 2-insulin-like growth factor (Archetti, Ferraro & Christofori 2015). The empirically measured fitnesses of polymorphic (producers and nonproducers) populations of cells as a function of the 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 (MacNulty *et al.* 2011). 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 (Archetti 2018). 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.

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Box 1: Models of public goods

An individual can be a cooperator or a defector. 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 $(n-1, x)$:

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

The fitnesses of cooperators and defectors are given therefore by

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

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

where *b*(*i*) is the benefit (payoff) for being in a group with *i* other cooperators. Being a cooperator in a group means that the focal cooperator enjoys the larger benefit $b(i+1)$ of having one more cooperator in its group (itself) compared to being a defector in the same group, $b(i)$. However, cooperators pay 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

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

The replicator dynamics of this system is

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

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

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

is the gradient of selection, with

$$\Delta b_i = b(i+1) - c - b(i) \qquad (7)$$

Linear public goods. — In the NPD, $b(i)$ is a linear function, and the fitnesses for a cooperator and a defector, respectively, are:

$$W_c(x) = \sum_{i=0}^{n-1} f_i(x) \cdot b(i+1) - c = \frac{rc(i+1)}{n} - c = \frac{rci}{n} + \frac{(r-n)c}{n} \tag{2b}$$

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

Only in the unlikely case that $r > n$ (*per capita* return on cooperation is larger than group size), is $W_C > W_D$, meaning that cooperation pays off and the social dilemma disappears. This case is unrealistic except for quite small groups (e.g. $n = 3$).

In the more likely case that $r < n$ (*per capita* return is smaller than group size), cooperators have a lower average fitness than do defectors, and defecting is the only stable strategy. Such an equilibrium is Pareto-inefficient: an alternative outcome is possible in which at least one player would have a higher payoff without reducing any other player's payoff (a Pareto improvement is possible, hence the inefficiency), but no one has an incentive to change their behaviour (hence the equilibrium).

The $r < n$ case is Hardin's Tragedy of the Commons: the rational behaviour of the individual contrasts with the optimal outcome for the group. The NPD game makes a crucial (and apparently innocuous) assumption: the individually provided benefits rc are multiplied by the number i of the group's cooperators to calculate the total benefit to the group: rci. In other words, the individual contributions have additive effects, and the size of the public good is just a linear function of the number of cooperators.

Non-linear public goods. — 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 $(n - 1)$ defectors is given by

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

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

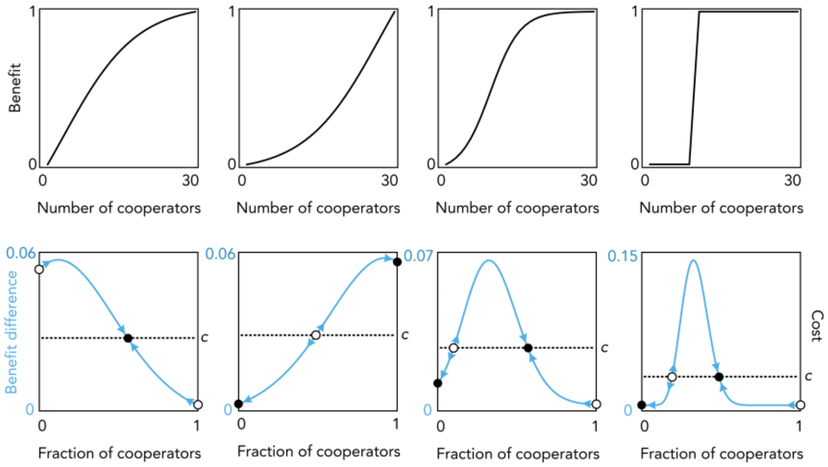
$$l(i) = \frac{1}{1 + e^{s(h-i/n)}} \tag{9}$$

The parameter h defines the position of the inflection point: $h \to 1$ gives increasing returns (convex) and $h \to 0$ diminishing returns (concave); s defines the steepness of the function

($s \to \infty$ models a threshold public goods game; $s \to 0$ models an NPD; the normalization in (9) prevents the logistic function (9) from becoming constant for $s \to 0$) (**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 (Cohen & Eshel 1976; Motro 1991; Foster 2004; Hauert *et al.* 2006; Frank 2010; Cornforth, Sumpter & Brown 2012): 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) (Maynard Smith 1965; Charnov & Krebs 1975; Matessi & Jayakar 1976; Tamachi 1987) or for the simple case of $n = 3$ with $k = 2$ (Bach *et al.* 2001; Bach, Helvik & Christiansen 2006). More general models require approximations for large n (Archetti 2009*a*; 2009*b*; Souza et al. 2009; Boza and Számadó 2010; Archetti and Scheuring 2011; 2012).

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 (Archetti 2013; 2018). 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 analysed using the same methods (Archetti 2018).



Different types of benefit functions (top panels) and their dynamics (bottom panels). From left to right: concave (*h*=0.1, *s*=4), convex (*h*=0.9, *s*=4), sigmoid (*h*=0.3, *s*=10), and step (*h*=0.3, *s*=10000). The circles show the equilibria (full: stable; empty; unstable); the arrows show the direction of the dynamics. The horizontal dotted line shows the cost (c=0.03); n=30.

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

1. Chuang et al. (2010) 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. (2018) 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. (2018) 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. (2010) 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. (2010) 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. (2009) 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. (2010) observed that maximum growth in yeast populations occurred at intermediate frequencies of cooperation.
8. Lindsay et al. (2016) 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 (Archetti, Ferraro & Christofori 2015), 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 (1990) Design Principles for common-pool resources also rely on nonlinear effects?

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