



Harsh environments and the evolution of multi-player cooperation

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ABSTRACT

The game-theoretic model in this paper provides micro-foundations for the effect a harsher environment on the probability of cooperation among multiple players. The harshness of the environment is alternatively measured by the degree of complementarity between the players' cooperative efforts in producing a public good, and by the number of attacks on an existing public good that the players can collectively defend, where it is shown that these two measures of the degree of adversity facing the players operate in a similar fashion. We show that the effect of the degree of adversity on the probability of cooperation is monotonous, and has an opposite sign for smaller and for larger cooperation costs. For intermediate cooperation costs, we show that the effect of a harsher environment on the probability of cooperation is hill-shaped.

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1. Introduction

Among several evolutionary explanations of cooperation (Dugatkin, 2002; Sachs et al., 2004; Lehmann and Keller, 2006; Nowak, 2006), a particular simple explanation is found in *by-product mutualism* (West Eberhard, 1975; Brown, 1983): players cooperate because it is in their individual interests to do so, and any benefit that this produces for other players is a mere by-product. Mesterton-Gibbons and Dugatkin (1992, 1997) argue that by-product mutualism arises particularly in harsh environments, leading to the so-called common-enemy hypothesis of by-product mutualism. The purpose of this paper is to provide micro-foundations for this common-enemy hypothesis in the setting of cooperation between multiple players.

Mesterton-Gibbons and Dugatkin (1992, 1997) formalize the common-enemy hypothesis by means of a two-player game where each player can either cooperate, or defect. Define R as the reward from jointly cooperating, T as the temptation payoff of unilaterally deviating from joint cooperation, S as the sucker payoff obtained when unilaterally cooperating, and P as the punishment payoff of joint defection. Let it be the case that the harshness of the environment can be reflected by a single measure, referred to as the degree of adversity. Mesterton-Gibbons and Dugatkin assume that the degree of adversity positively affects both $(R - T)$ (i.e., the added payoff of cooperating jointly) and $(S - P)$ (i.e., the added payoff of cooperating alone), and that $(R - T) > (S - P)$. The consequence is that, as the degree of adversity is increased, one

moves from a game where joint defection is the only evolutionary stable state (henceforth ESS; Maynard Smith and Price, 1973), to a game where both joint defection and joint cooperation are ESS's, to finally a game where joint cooperation is the only ESS, illustrating the common-enemy hypothesis. Yet, micro-foundations of how the degree of adversity affects the payoffs are not provided. At a more general level, in literature linking cooperation to harsh environments, the mechanism by which the degree of adversity affects cooperation is not clear (Sandoval and Wilson, 2012), and theoretical underpinnings are missing (Smaldino et al., 2013).

For the two-player case, De Jaegher and Hoyer (2016a) provide micro-foundations for the effect of the degree of adversity by modeling cooperation in two ways. In their first model, cooperation consists of the production of a public good, and a higher degree of adversity is linked to a higher degree of complementarity between players' contributions to the public good. For instance, in a cooperative hunt (see, e.g., Scheel and Packer, 1991 on cooperative hunting by lions), when facing the harsher environment of a larger prey (Mesterton-Gibbons and Dugatkin, 1992; Dugatkin, 2002), each predator's effort may become more pivotal in ensuring a successful hunt. In particular, a division of labor may be needed where each predator takes on a specific role (see e.g. Stander, 1992; Leimar and Connor, 2003). What Mesterton-Gibbons and Dugatkin (1992, 1997) call the *boomerang effect* now applies, where a player who unilaterally deviates from joint cooperation is the victim of his own cheating: as he takes on a specific, pivotal role in the cooperative group, unilateral deviation means that little of the public good is produced. One would therefore expect the common-enemy hypothesis to apply. Yet, as argued by De Jaegher and Hoyer (2016a), the harsher environment of, e.g., a larger prey, and the attached

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higher degree of complementarity between players' contributions, also make the added payoff of cooperating alone decrease. A *sucker effect* applies, where unilateral deviation from joint defection is unattractive; if every player takes on a specific role in the cooperative group, then unilaterally cooperating does not produce much value of the public good. Looking at the sucker effect in isolation, rather than the common-enemy hypothesis applying, one would expect a competing hypothesis to apply, where a harsher environment makes cooperation less likely.

The same mechanisms apply in the second model treated in De Jaegher and Hoyer, where cooperation consists of the defense of an existing public good, and where a harsher environment is measured by a larger number of attacks on the players. For instance, male lions defend territories in order to keep exclusive access to females (Grinnell et al., 1995; other possible examples of territorial defense include Gese, 2001, and Rubenstein and Nuñez, 2009; see Port et al., 2011 for a more general treatment). Also, prey collectively defend against predators (Mesterton-Gibbons and Dugatkin, 1992, p. 274; Spieler, 2003). In De Jaegher and Hoyer's (2016a) model of collective defense, as long as players' contributions to collective defense are complementary to a sufficient extent, a harsher environment also causes a boomerang and a sucker effect: a larger number of attacks on the one hand makes it less attractive to deviate from joint cooperation (as a unilaterally defecting player is more likely to be attacked), and on the other hand makes it less attractive to deviate from joint defection (as a unilaterally cooperating player is less likely to make a difference).

For both models, De Jaegher and Hoyer show that the boomerang effect is the dominant effect for large cooperation costs, in which case the common-enemy hypothesis applies. For small cooperation costs, the competing hypothesis applies instead. Yet, a weakness of their model is that it only considers two players, and not the empirically more relevant case of multiple players. It is not clear then, first, whether similar results apply in the case of multiple players (in general, as pointed out by e.g. Peña et al., 2014, Gokhale and Traulsen, 2014, and Broom and Rychtář, 2016 having more than two players makes the selection gradient non-linear and may change the number of fixed points); second, whether the cases of large and small cooperation costs both remain equally relevant in the case of multiple players. The present paper analyzes the multi-player case, and not only identifies similarities to, but also critical differences with, the two-player case.

2. General setting

We start with a general setting for public goods games, which fits both a public goods game where players produce a public good (Section 3), and a public goods game where players defend an existing public good (Section 4). The public goods games we consider are one-shot, have n players ($n \geq 2$), are binary, and have constant costs. Our players face the binary choice of either investing in the public good (= cooperate), or not investing (= defect). We assume an infinitely large, well-mixed population that reproduces asexually. At any given point of time, the population contains a fraction x of cooperators, and a fraction $(1 - x)$ of defectors. The population is repeatedly and randomly matched in groups of n players. In line with these assumptions, the change in the fraction of cooperators x follows the continuous replicator dynamics (Hofbauer and Sigmund, 1998), and is determined by the performance of cooperators relative to defectors:

$$\dot{x} = x(1 - x)[f_C(x) - f_D(x)], \quad (1)$$

where $[f_C(x) - f_D(x)]$ is the gain function of cooperating rather than defecting, and where $f_C(x)$ denotes the average fitness of cooperating and $f_D(x)$ denotes the average fitness of defecting, as a function

of the fraction of cooperators x . These fitnesses equal respectively

$$f_C(x) = \sum_{k=0}^{n-1} \binom{n-1}{k} x^k (1-x)^{n-1-k} b_{k+1} - c \quad (2)$$

$$f_D(x) = \sum_{k=0}^{n-1} \binom{n-1}{k} x^k (1-x)^{n-1-k} b_k. \quad (3)$$

Eqs. (2) and (3) can be understood as follows. First, when exactly k other players cooperate in a group, this generates a benefit b_k to the focal player in this group who defects, and a benefit b_{k+1} to the focal player in this group who cooperates. These benefits constitute a public good to the given group, as they are non-excludable (Dionisio and Gordo, 2006): each player in a group always obtains the same benefit. As we limit ourselves to constant cost games, cooperating comes at a constant cost c . Second, players in the population are randomly matched in groups of size n , with $n \geq 2$. It follows that from the perspective of a focal player, the number k of cooperators among the $(n - 1)$ other players in his current group follows a binomial distribution (cf. Archetti and Scheuring, 2012; Peña et al., 2014). The individual cooperator will have at least one cooperator (namely himself) in his group, so that the number of cooperators ranges from 1 to n . The individual defector will have at most $(n - 1)$ cooperators in his group, so that the number of cooperators ranges from 0 to $(n - 1)$.

We now use concepts introduced in Peña et al. (2014), which allow for a simple characterization. The benefit sequence is the sequence of all benefits, $\mathbf{b} = (b_0, b_1, \dots, b_n)$. For k such that $0 \leq k \leq (n - 1)$, denote the first forward difference of b_k as $\Delta b_k = b_{k+1} - b_k$ (which is the equivalent of the first derivative of a real function). For k such that $0 \leq k \leq (n - 2)$, denote the second forward difference of b_k as $\Delta^2 b_k = \Delta b_{k+1} - \Delta b_k$ (which is the equivalent of the second derivative of a real function). Δb_k is the added benefit (or incremental benefit) of cooperating rather than defecting in a group where k other players cooperate, where the added benefit sequence is the sequence $\Delta \mathbf{b} = (\Delta b_0, \Delta b_1, \dots, \Delta b_{n-1})$. The shape of \mathbf{b} and $\Delta \mathbf{b}$ together characterizes the "technology" through which players' investments get turned into value of the public good (a taxonomy of extreme cases of such technologies is found in Hirschleifer, 1983). We limit ourselves to technologies where \mathbf{b} is an increasing sequence, meaning $\Delta \mathbf{b} > \mathbf{0}$; simply, the value of the public good generated increases in the number of investing players.

The technologies we consider are distinguished by the sign of $\Delta^2 \mathbf{b}$ (i.e., the sign of $\Delta^2 b_k$, for k such that $0 \leq k \leq (n - 2)$; cf. Motro, 1991). First, with a convex technology, it is the case that $\Delta^2 \mathbf{b} > \mathbf{0}$, meaning that \mathbf{b} is convex (and that $\Delta \mathbf{b}$ is increasing). Starting from a situation with only defectors in a group, if one consecutively adds cooperators to the group, each additional cooperator adds more and more value to the public good. A limit case of the convex technology is the weakest-link technology, where $b_0 = b_1 = \dots = b_{n-1} = 0$, and $b_n > 0$ (meaning that $\Delta b_0 = \Delta b_1 = \dots = \Delta b_{n-2} = 0$, $\Delta b_{n-1} > 0$), so that benefits are only obtained in case all players in a group cooperate; as soon as at least one player defects, zero benefits are obtained. In this limit case, the public goods game is a *weakest-link game* (Hirschleifer, 1983).

Second, with a concave technology, it is the case that $\Delta^2 \mathbf{b} < \mathbf{0}$, meaning that \mathbf{b} is concave (and that $\Delta \mathbf{b}$ is decreasing). Starting from a situation with only defectors in a group, if one consecutively adds cooperators to the group, each additional cooperator adds less and less to the value of the public good. A limit case of the concave technology is the best-shot technology, where $b_1 = b_2 = \dots = b_n > 0$, and $b_0 = 0$ (meaning that $\Delta b_1 = \Delta b_2 = \dots = \Delta b_{n-1} = 0$, $\Delta b_0 > 0$), so that maximal benefits of the public good are obtained as soon as at least one player in a group cooperates. In this limit case, the public goods game is a so-called *volunteer's dilemma* (Diekmann, 1985).

Exactly in between convex and concave technologies is the limit case where $\Delta^2 \mathbf{b} = \mathbf{0}$. In this case, each additional cooperator adds exactly the same to the public good, meaning that $\Delta b_0 = \Delta b_1 = \Delta b_2 = \dots = \Delta b_{n-1} > 0$. In this limit case, the game is a *linear public goods game* (Archetti and Scheuring, 2012).

Public goods games can be distinguished according to the number and types of ESS's. The following types of public goods games are possible in our analysis, where we follow taxonomies of games found in, e.g., Doebeli and Hauert (2005), Archetti et al. (2011), and Archetti and Scheuring (2012). A *Prisoner's Dilemma* (Tucker, 1950) has a single ESS where all players defect ($x = 0$). A *Harmony game* has a single ESS where all players cooperate ($x = 1$). A *Stag Hunt* (Skyrms, 2004) has both an ESS where all players cooperate and an ESS where all players defect (both $x = 0$ and $x = 1$ are ESS's, or so-called bistability). Finally, a *Snowdrift game* (Sugden, 1986; also called Chicken game Russell, 1959, or Hawk–Dove game Maynard Smith and Price, 1973) has a single ESS where a fraction of the players cooperate, and a fraction defects (an x^* with $0 < x^* < 1$ exists such that x^* is an ESS, or so-called co-existence).¹

As noted by Peña et al. (2014), the gain function contained in (1) is a polynomial in Bernstein form (Farouki, 2012). From this fact follows a direct link between, on the one hand, the shape of the benefit sequence \mathbf{b} (concave or convex technology) and the relation of the added benefit of cooperating alone (Δb_0) and the added benefit of cooperating jointly (Δb_{n-1}) to the cooperation cost (c); and, on the other hand, the type of the public goods game. Indeed, Proposition 1 follows directly from Result 4 in Peña et al. (2014). Note now that for the two-player case ($n = 2$), Δb_0 and Δb_{n-1} together constitute the entire added benefit sequence, and therefore their relation to c automatically determines the type of the game. As Proposition 1 shows, even though for $n > 2$ the added benefit sequence $\Delta \mathbf{b}$ consists of additional intermediate added benefits, when limiting ourselves to technologies that are either concave or convex, it continues to be true that only the relation of Δb_0 and Δb_{n-1} to c determines the game type. Thus, applying the notation typically used for the two-player game (see the Introduction), it continues to be true in the multi-player game that the type of the game is determined by the sign of $(R - T) = \Delta b_{n-1} - c$ and of $(S - P) = \Delta b_0 - c$.

Proposition 1. *Types of public goods games:*

- (1) *With a convex technology ($\Delta^2 \mathbf{b} > \mathbf{0}$), if cooperation costs*
 - (a) *exceed both the benefit of cooperating alone and of cooperating jointly ($\Delta b_0 < \Delta b_{n-1} < c$): Prisoner's Dilemma;*
 - (b) *lie in between the benefit of cooperating alone and of cooperating jointly ($\Delta b_0 < c < \Delta b_{n-1}$): Stag Hunt;*
 - (c) *are exceeded by both the benefit of cooperating alone and of cooperating jointly ($c < \Delta b_0 < \Delta b_{n-1}$): Harmony game.*
- (2) *With a concave technology ($\Delta^2 \mathbf{b} < \mathbf{0}$), if cooperation costs*
 - (a) *exceed both the benefit of cooperating alone and of cooperating jointly ($\Delta b_{n-1} < \Delta b_0 < c$): Prisoner's Dilemma;*
 - (b) *lie in between the benefit of cooperating jointly and of cooperating alone ($\Delta b_{n-1} < c < \Delta b_0$): Snowdrift game;*
 - (c) *are exceeded by both the benefit of cooperating alone and of cooperating jointly ($\Delta b_{n-1} < \Delta b_0 < c$): Harmony game.*

As our interest lies in the manner in which the probability of cooperation is affected by the degree of adversity, we here develop measures for the probability of cooperation. When the game is a Prisoner's Dilemma or Harmony game, the probability

of cooperation trivially is 0 or 1. For the Snowdrift game and the Stag Hunt, consider the fraction of cooperators x^* such that the gain function contained in (1) equals zero, i.e. x^* such that $[f_c(x^*) - f_D(x^*)] = 0$. This fraction is represented for these respective games in the phase diagrams in Fig. 1. When the game is a Snowdrift game, the probability of cooperation, denoted as q , is simply measured by the fraction of cooperators in the unique mixed-population ESS, meaning that $q = x^*$. For the Stag Hunt, two pure-strategy ESS's exist, and it is at first sight not clear how the probability of cooperation can be measured. In this case, we measure the probability of cooperation by the size of the basin of attraction of the ESS where $x = 1$, which equals $(1 - x^*)$. The underlying reasoning is that, when each initial population is equally likely, the joint cooperation ESS will evolve with probability $(1 - x^*)$. Denoting by Q the probability that the joint cooperation ESS evolves, it is the case that $Q = (1 - x^*)$.

In the next two sections, we treat two public goods games fitting this general setting, and we investigate how the degree of adversity facing the players affects the probability of cooperation. In Section 3, investing means contributing to the production of a public good, and the degree of adversity is proxied by the degree of complementarity between the players' cooperative efforts. In Section 4, investing in the public good means investing in the maintenance of a public good, in that players defend an existing public good against attacks, and the degree of adversity is measured by the number of attacks facing the players.

3. Production of a public good, degree of complementarity as degree of adversity

3.1. Model and basic analysis

In the public goods game we consider here, cooperating means investing in the production of the public good, and defecting means not investing. Our interest lies in the manner in which the degree of adversity facing the players affects the probability that they cooperate. We reason that the harsher the environment the players face, the more pivotal each player's investment in the public good in a group becomes. For instance, the group of n players may be predators who together can produce the benefit of catching a prey that is a non-excludable public good to the group. The degree of adversity may now be measured by the size of the prey (Mesterton-Gibbons and Dugatkin, 1992; Dugatkin, 2002). While we consider the degree of adversity as a continuum, the effect of the degree of adversity is best understood by looking at some extreme cases. When the degree of adversity is very low (small prey), a single predator chasing the prey may suffice to catch it; in this case, the game played by the predators approaches a volunteer's dilemma, and the benefit sequence is extremely concave. For an intermediate degree of adversity (medium-size prey), each additional predator in a group who joins the chase, may increase the probability of catching the prey linearly; in this case predators play a linear public goods game, and the benefit sequence is linear. Finally, for a very high degree of adversity (large prey), each predator's participation in the chase may be pivotal for catching the prey, and a single predator who does not participate may mean that the prey escapes; in this case, the game played by the predators approaches a weakest-link game, and the benefit sequence is extremely convex.

This suggests that the degree of adversity facing the players can be proxied by the degree of convexity of the technology through which the players' investments get turned into value of the public good. It is precisely the degree of convexity that gets varied in the model of synergy and discounting in public goods by Hauert et al. (2006). In this model, the added benefit sequence $\Delta \mathbf{b}$ takes the form $((V/n), (V/n)w, (V/n)w^2, \dots, (V/n)w^{n-1})$, so that $b_k = (V/n)(1 + w + w^2 + \dots + w^{k-1})$ for $k \geq 1$ (with $b_0 = 0$),

¹ As Peña et al. (2014, p. 25) note, public goods games where players either cooperate or defect can also be re-interpreted such that players choose from a continuum of mixed strategies. In this case, in the ESS of the Snowdrift game, all players mix between cooperating and defecting.

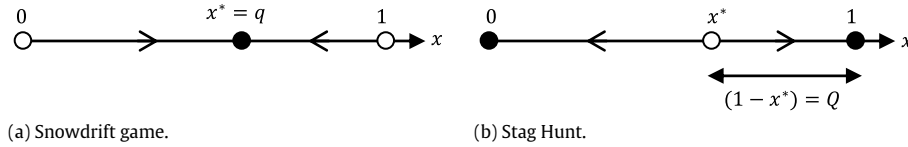


Fig. 1. Axes representing phase portraits for the Snowdrift game and the Stag Hunt, with the fraction of cooperators ranging from 0 to 1. A filled dot indicates a stable fixed point, a non-filled dot a non-stable fixed point; the arrows on the axes indicate the direction in which the population evolves. x^* denotes the fraction of cooperators in the interior fixed point, where the gain function equals zero ($[f_C(x^*) - f_D(x^*)] = 0$). (a) In the Snowdrift game, the probability of cooperation, denoted q , is the fraction of cooperators in the unique mixed-population ESS, where $q = x^*$. (b) In the Stag Hunt, the probability of cooperation, denoted Q , is the size of the basin of attraction of the joint cooperation ESS, where $Q = (1 - x^*)$.

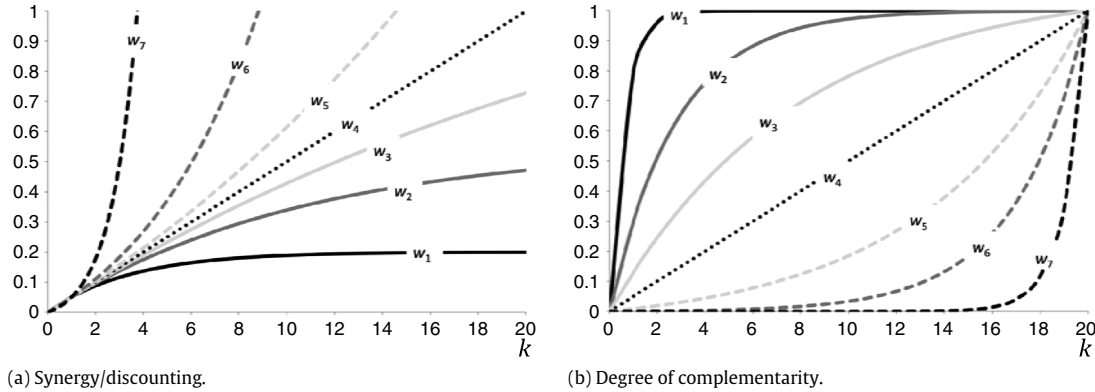


Fig. 2. Value of the public good as a function of the number of cooperators for (a) several levels of synergy/discounting; (b) several degrees of complementarity, where $w_1 < w_2 < w_3 < w_4 < w_5 < w_6 < w_7$. The example represents the case $n = 20$, $V = 1$.

where (V/n) is the fixed value which a first investing player adds to the public good; in Peña et al., 2015, this is referred to as the geometric production function. Fig. 2(a) represents b_k (represented for clarity as a real function) for different levels of w in the model of synergy/discounting. For $w < 1$, the benefit sequence \mathbf{b} is concave (in Peña et al., 2015 referred to as a decelerating production function, or as diminishing returns to scale); for $w = 1$, \mathbf{b} is linear (linear production function, constant returns to scale); for $w > 1$, \mathbf{b} is convex (accelerating production function, increasing returns to scale). The idea here is that a first cooperating player always contributes the same; yet as there is more synergy between (respectively more discounting of) players' investments, additional investing players add more and more (respectively less and less) to the public good. While w can be seen as measuring the degree of convexity, for our purposes, the problem with this specification is that b_k increases in w for any given k . Yet, for w to reflect the degree of adversity, quite oppositely, it must be the case that higher w , while being a measure of the degree of convexity, also decreases any b_k ; the reasoning here is that a higher degree of adversity means that for any fixed number k of cooperators, a lower value of the public good is achieved. For w to reflect the degree of adversity, we modify b_k to take the form:

$$b_0 = 0, \quad b_k = \frac{V(w + w^2 + \dots + w^k)}{w + w^2 + \dots + w^n} \quad \text{for } 1 \leq k \leq n. \quad (4)$$

Eq. (4) can be written as:

$$b_k = \frac{V(1 - w^k)}{1 - w^n} \quad \text{for } w \neq 1, \\ b_k = \frac{kV}{n} \quad \text{for } w = 1 (\text{with } 0 \leq k \leq n). \quad (5)$$

Furthermore, it follows from (5) that

$$\Delta b_k = \frac{Vw^k(1 - w)}{1 - w^n} \quad \text{for } w \neq 1, \\ \Delta b_k = \frac{V}{n} \quad \text{for } w = 1 (\text{with } 0 \leq k \leq (n - 1)). \quad (6)$$

Using (6) to look at how Δb_k changes as a function of k , it is clear that the benefit sequence is concave for $w < 1$ ($\Delta^2 \mathbf{b} < \mathbf{0}$), linear for $w = 1$ ($\Delta^2 \mathbf{b} = \mathbf{0}$) and convex for $w > 1$ ($\Delta^2 \mathbf{b} > \mathbf{0}$), so that w continues to measure the degree of convexity of the benefit sequence. At the same time, from (4) it is clear that if all players invest, value V of the public good always gets produced, whatever w . Furthermore, it can be checked from (4) that $\partial b_k / \partial w < 0$, meaning that all else equal higher w means a lower benefit. We refer to w as the *degree of complementarity* between the players' investments in the public good, measuring how pivotal each player's investment is in producing the maximal possible value V of the public good.² This degree of complementarity proxies for the degree of adversity, where we reason that a harsher environment makes each player's investment more pivotal. For w approaching zero, the game approaches a volunteer's dilemma; for w equal to one, it is a linear public goods game; for w approaching infinity, the game approaches a weakest-link game.

As we know from Proposition 1, the type of the public goods game depends only on whether the benefit sequence is concave or convex (i.e. on the sign of $\Delta^2 \mathbf{b}$), and on the size of the added benefit of cooperating jointly (Δb_{n-1}) and the added benefit of cooperating alone (Δb_0) relative to the cooperation cost (c). An initial and rudimentary way of looking at the manner in which the degree of adversity affects the probability of cooperation, is to look at increases in the degree of complementarity large enough to change the type

² In economics, the standard way to represent a production function in which one can continuously vary the degree of complementarity is the so-called constant-elasticity-of-substitution (CES) production function (Solow, 1956), which applied to our model can be written down as $V \left\{ \left[\frac{1}{n} \sum_{i=1}^n (y_i + 1)^\pi \right]^{1/\pi} - 1 \right\}$ (De Jaegher and Hoyer, 2016b), where $y_i = 1$ ($y_i = 0$) means that player i invests (does not invest). Indeed, for π approaching minus infinity, one approaches the weakest-link technology, for π approaching one, one approaches the summation technology, and for π approaching plus infinity, one approaches the best-shot technology, making π an inverse measure of the degree of complementarity (Ray et al., 2007). We employ an alternative production function with the same properties as the CES production function, because this makes our calculations tractable.

of game played, which we refer to as a game-changing increase in the degree of complementarity. To see how w affects the type of game played, we need to know how w affects Δb_0 and Δb_{n-1} . As shown in [Appendix A](#), Δb_0 decreases, and Δb_{n-1} increases in w . Intuitively, for a degree of complementarity approaching zero (best-shot technology, volunteer's dilemma), the added benefit of cooperating alone approaches the maximal value V and the added benefit of cooperating jointly approaches zero. For w equal to 1 (summation technology, linear public goods game), both added benefits equal V/n , as each additional cooperator then adds the same to the public good. Finally, for a degree of complementarity approaching infinity (weakest-link technology/game), the added benefit of cooperating alone approaches zero and the added benefit of cooperating jointly approaches the maximal value V . In general, it is the case that $\Delta b_0 > \Delta b_{n-1}$ when $w < 1$ (as with concave benefits, the first cooperating defender adds more than the n th cooperating defender), and $\Delta b_0 < \Delta b_{n-1}$ when $w > 1$ (as with convex benefits, the first cooperating defender adds less than the n th cooperating defender).

[Proposition 1](#) can now directly be applied to determine the type of the game as a function of w and c , where four different types of games are obtained, as represented in [Fig. 3\(a\)](#).³ Using [Fig. 3\(a\)](#), the effect of a game-changing increase in the degree of complementarity becomes immediately clear. As represented in [Fig. 3\(b\)](#), and as listed in [Result 1](#), four cases are possible, which are exactly the same as in the two-player game. The intuition for [Result 1](#) is the following. Start from a linear public goods game ($w = 1$), where the added benefit of cooperating alone and of cooperating jointly are equal, and let cooperation costs be large, such that the game is a Prisoner's Dilemma. When the degree of complementarity increases, as can be seen in [Fig. 3\(a\)](#), the added benefit of cooperating jointly increases, and the added benefit of cooperating alone decreases. It follows that the former increases to exceed the cooperation cost (causing the boomerang effect mentioned in the Introduction to become operative), while the latter remains smaller than cooperation cost (meaning that the sucker effect mentioned in the Introduction continues to apply), so that the game becomes a Stag Hunt. When the degree of complementarity instead decreases, the added benefit of cooperating jointly instead decreases and the added benefit of cooperating alone increases. It follows that the latter increases to exceed the cooperation cost (causing the sucker effect to disappear), while the former remains smaller than the cooperation cost (meaning that it continues to be the case that the boomerang effect does not apply), so that the game becomes a Snowdrift game. A similar intuition applies starting from a linear public goods game when cooperation costs are small; the difference then is that the starting point is a Harmony game, instead of a Prisoner's Dilemma.

Result 1 (Effect of a Game-changing Increase in the Degree of Complementarity). **Case 1.** Large cooperation costs ($c > (V/n)$).

Case 1.1. Low degree of complementarity ($w < 1$): change from a Snowdrift game into a Prisoner's Dilemma, and decrease in the fraction of cooperating players (q). **Case 1.2.** High degree of complementarity ($w > 1$): change from a Prisoner's Dilemma into a Stag Hunt, and increase in the basin of attraction of the joint cooperation ESS (Q).

Case 2. Small cooperation costs ($c < (V/n)$).

Case 2.1. Low degree of complementarity ($w < 1$): change from a Snowdrift game into a Harmony game, and increase of the fraction of cooperating players (q).

Case 2.2. High degree of complementarity ($w > 1$): change from a Harmony game into a Stag Hunt, and decrease in the basin of attraction of the joint cooperation ESS (Q).

As the cases depend only on the relation of Δb_0 and Δb_{n-1} to c , these cases are the same as in the two-player analysis of [De Jaegher and Hoyer \(2016a\)](#). Yet, it should be stressed that the stated results apply for a change in the degree of complementarity large enough to literally be a “game changer”, in causing a change in the type of game played. As we now go on to show, if we instead look at the effect of small changes in the degree of complementarity, this effect is non-monotonous in specific cases.

3.2. Detailed analysis

Given the fact that in [\(4\)](#) we adopted a specific functional form for the benefits, a detailed analysis is possible for the effect of the degree of adversity on the probability of cooperation. We then not only look at the effect of the degree of complementarity on the type of the game that is played, as in [Result 1](#), but also at the manner in which the fraction of cooperators q in the Snowdrift game, and the probability Q that the joint cooperation ESS evolves in the Stag Hunt (see [Fig. 1](#)), are affected by the degree of complementarity w .

As shown in [Appendix B](#), the x^* such that the gain function contained in [\(1\)](#) equals zero (i.e., $[f_C(x^*) - f_D(x^*)] = 0$) is given by

$$x^* = \frac{1}{1-w} - \frac{1}{1-w} \left[\frac{c(1-w^n)}{V(1-w)} \right]^{1/(n-1)}. \quad (7)$$

[Appendix B](#) further shows that $\frac{\partial x^*}{\partial w} > 0$ when $c > c^*(w, n)$, and that $\frac{\partial x^*}{\partial w} < 0$ when $c < c^*(w, n)$, where

$$c^*(w, n) = V \left[\frac{1-w}{1-w^n} \right] \left[\frac{(n-1)(1-w^n)}{n(1-w^{n-1})} \right]^{n-1}. \quad (8)$$

It follows that the effect of a small change in the degree of complementarity broadly confirms [Result 1](#): for relatively large cooperation costs ($c > c^*(w, n)$), an increase in the degree of complementarity causes a decrease in the fraction of cooperators in the Snowdrift game, and an increase in the basin of attraction of the joint cooperation ESS in the Stag Hunt game; the opposite is true for relatively small cooperation costs. Yet, the problem is that what defines large and small cooperation costs now depends on the degree of complementarity itself, as reflected by the function $c^*(w, n)$. The shape of $c^*(w, n)$, and its position relative to the added benefit of cooperating alone (Δb_0) and to the added benefit of cooperating jointly (Δb_{n-1}) is derived in [Appendix B](#), and represented in [Fig. 4\(a\)](#). As illustrated, $c^*(w, n)$ is a U-shaped function of w , which approaches $V \left[\frac{(n-1)}{n} \right]^{n-1}$ both for w approaching zero and approaching plus infinity,⁴ and which approaches V/n for w approaching 1, where $\frac{V}{n} < V \left[\frac{(n-1)}{n} \right]^{n-1} < V$.

The different cases for the effect of a small change in the degree of complementarity now immediately follow, and are listed in [Result 2](#), and represented in [Fig. 4\(b\)](#). For the upper range of large cooperation costs, such that it is the case for all w that $c > c^*(w, n)$

³ Because we have concave benefits for $0 < w < 1$ and convex benefits for $w > 1$, the range of w with concave benefits is vanishingly small compared to the range with convex benefits. To make the different cases visible, [Fig. 3](#) only considers the range $w \leq 3$. It should be noted that Δb_{n-1} approaches V for w approaching infinity. Also, the fact that in the model there is a wider range of w with convex benefits, is not meant to imply that concave benefits are less important.

⁴ This fact is not immediately clear from [Fig. 4\(a\)](#), as we only represent the range $w \leq 3$ on the X-axis. See also Footnote 3.

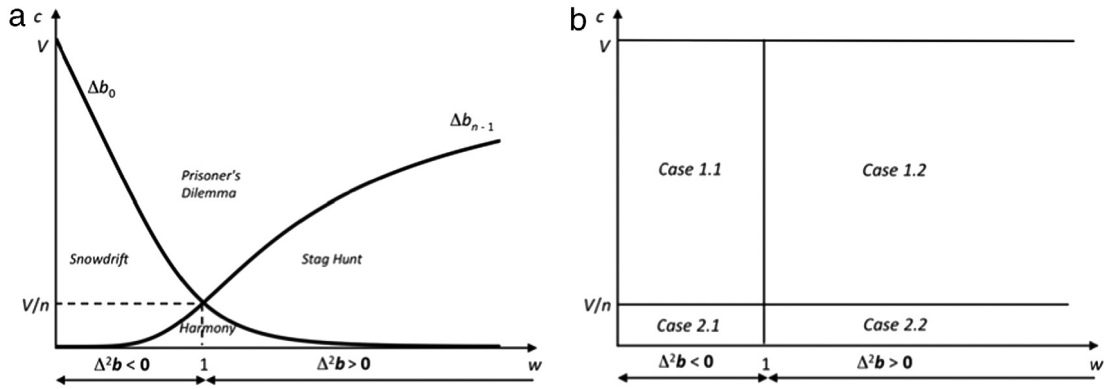


Fig. 3. (a) Type of game played as a function of the cooperation cost (c) and the degree of complementarity (w). The games are delineated by the curves where the added benefit of cooperating jointly (Δb_{n-1}) and the added benefit of cooperating alone (Δb_0) equal the cooperation cost. For $w < 1$, the benefit sequence is concave ($\Delta^2 b < 0$), for $w > 1$, it is convex ($\Delta^2 b > 0$). The case represented is the one where $n = 7$, $V = 1$, where the figure only represents the range $0 \leq w \leq 3$. (b) Corresponding cases, as listed in [Result 1](#), for the effect of a game-changing increase in the degree of complementarity on the probability of cooperation.

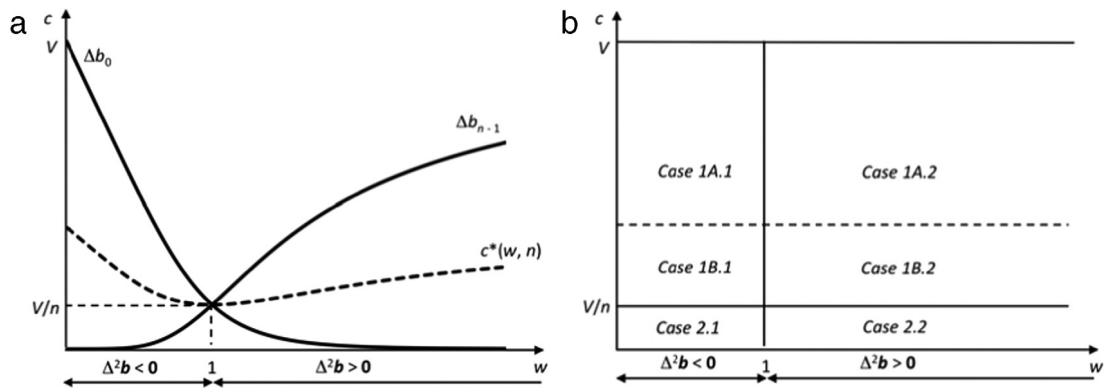


Fig. 4. (a) Identical to [Fig. 3\(a\)](#), but with the curve $c^*(w, n)$ added. On this curve, the effect of the degree of complementarity on the probability of cooperation undergoes a sign change. (b) Corresponding cases, as listed in [Result 2](#), for the effect of small changes in the degree of complementarity on the probability of cooperation.

(meaning that $c > V \left[\frac{(n-1)}{n} \right]^{n-1}$), the direction of the effect of a game-changing increase and of a small increase in the degree of complementarity, is the same; thus, Case 1A in [Result 2](#) is analogous to Case 1 in [Result 1](#). For small cooperation costs, such that it is the case for all w that $c < c^*(w, n)$, it is also the case that the direction of the effect of a game-changing increase and of a small increase in the degree of complementarity is the same; therefore, Cases 2 in [Result 2](#) and in [Result 1](#) are also analogous.

However, for the bottom range of large cooperation costs ($V/n < c < V \left[\frac{(n-1)}{n} \right]^{n-1}$), as the degree of complementarity is increased, the position of the given c with respect to $c^*(w, n)$ changes. The results for the bottom range of large cooperation costs (Case 1B in [Result 2](#)) are now best stated by defining $w^*(c, n)$ as the inverse function of $c^*(w, n)$, where this inverse function is implicitly defined by (8). For low degrees of complementarity ($w < 1$), we already know from Case 1.1 in [Result 1](#) that game-changing increases in the degree of complementarity change the game from a Snowdrift game into a Prisoner's Dilemma, decreasing the fraction of cooperators. As [Fig. 4\(a\)](#) makes clear, small changes in the degree of complementarity in the Snowdrift game have an effect in the same direction, as long as $w > w^*(c, n)$. Yet, for $w < w^*(c, n)$, a small change in the degree of complementarity instead increases the fraction of cooperators in the Snowdrift game, meaning that the fraction of cooperators is overall a hill-shaped function of the degree of complementarity (Case 1B.1 in [Result 2](#)).

In the same way, for high degrees of complementarity ($w > 1$), by Case 1.2 in [Result 1](#) we already know that game-changing

increases in the degree of complementarity change the game from a Prisoner's Dilemma into a Stag Hunt, increasing the probability that the joint cooperation ESS is played. As is clear from [Fig. 4\(a\)](#), in the Stag Hunt small changes in the degree of complementarity have an effect in the same direction, as long as $w < w^*(c, n)$. Yet, for $w > w^*(c, n)$, a small change in the degree of complementarity instead decreases the probability that the joint cooperation ESS is played, meaning that this probability overall is a hill-shaped function of the degree of complementarity (Case 1B.2 in [Result 2](#)).

Thus, broadly speaking, for degrees of complementarity close to the linear public goods game, the effect of a game-changing increase in the degree of complementarity, and of a marginal increase in the degree of complementarity go in the same direction, as is intuitive. Yet, because of the non-linearity of multi-player public goods games, for the bottom range of large cooperation costs, at the extremes on both sides of the linear public goods game, the effect of a small increase in the degree of complementarity has the opposite sign of the effect of a game-changing increase in the degree of complementarity. The interested reader will find a detailed intuition for this result in [Appendix C](#).

Result 2 (Effect of a Marginal Increase in the Degree of Complementarity). **Case 1A.** Upper range of large cooperation costs ($c > V \left[\frac{(n-1)}{n} \right]^{n-1}$):

Case 1A.1. Low degree of complementarity ($w < 1$): in the Snowdrift game, decrease in the fraction of cooperators ($\frac{\partial q}{\partial w} = \frac{\partial x^*}{\partial w} < 0$);

Case 1A.2. High degree of complementarity ($w > 1$): in the Stag Hunt, increase in the probability that the joint cooperation ESS is played ($\frac{\partial Q}{\partial w} = \frac{\partial (1-x^*)}{\partial w} > 0$);

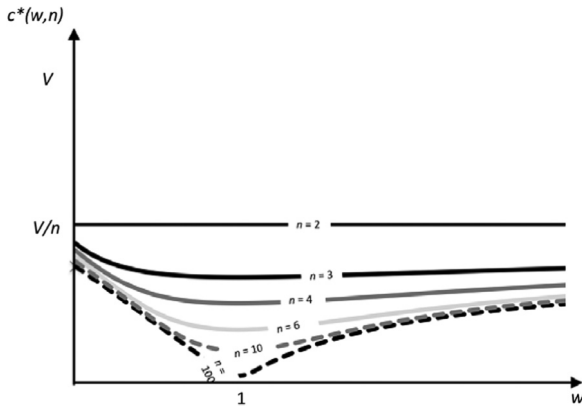


Fig. 5. For $w < 1$, curve above which the ESS fraction of cooperators decreases in the degree of complementarity w , and below which the opposite is the case; for $w > 1$, curve above which the basin of attraction of the joint cooperation ESS increases in w , and below which the opposite is the case. The curve is represented for several numbers of players n in a cooperating group (where in the represented example, $V = 1$).

Case 1B. Bottom range of large cooperation costs ($V/n < c < V \left[\frac{(n-1)}{n} \right]^{(n-1)}$):

Case 1B.1. Low degree of complementarity ($w < 1$): in the Snowdrift game, hill-shaped effect on the fraction of cooperators ($\frac{\partial q}{\partial w} = \frac{\partial x^*}{\partial w} \geq 0$ for $w \leq w^*(c, n)$).

Case 1B.2. High degree of complementarity ($w > 1$): in the Stag Hunt, hill-shaped effect on the probability that the joint cooperation ESS is played ($\frac{\partial Q}{\partial w} = \frac{\partial (1-x^*)}{\partial w} \geq 0$ for $w \leq w^*(c, n)$).

Case 2. Small cooperation costs ($c < V/n$):

Case 2.1. Low degree of complementarity ($w < 1$): in the Snowdrift game, increase in the fraction of cooperators ($\frac{\partial q}{\partial w} = \frac{\partial x^*}{\partial w} > 0$).

Case 2.2. High degree of complementarity ($w > 1$): in the Stag Hunt, decrease in the probability that the joint cooperation ESS is played ($\frac{\partial Q}{\partial w} = \frac{\partial (1-x^*)}{\partial w} < 0$).

3.3. Effect of the number of players

As can be checked from (8), with two players, $c^*(w, 2) = V/2$ and Case 1B vanishes, so that the effect of a game-changing increase and of a marginal increase in the degree of complementarity always goes in the same direction (see De Jaegher and Hoyer, 2016a). Also, considering the range $[0, V]$ as the relevant range for the cooperation costs, with two players Cases 1 and 2 in Result 2 each cover half of the relevant range. As public goods games may typically involve more than two players, it is important to see how the relative importance of these cases is affected by the number of players.

Fig. 5 depicts $c^*(w, n)$ for several levels of n . This shows that the range of cooperation costs for which Case 1B in Result 2 is relevant increases in n , while the range of cooperation costs for which Case 2 applies vanishes. It is the case that $c^*(0, n) = V \left[\frac{(n-1)}{n} \right]^{(n-1)}$ approaches $(1/e) \approx 0.37$ for n approaching infinity, whereas V/n approaches zero. Yet, at the same time, it can be checked from the expression for x^* in (7) that the probability of cooperation approaches zero as the number of players becomes very large, both when the probability of cooperation is measured as the size of the basin of attraction of the joint cooperation ESS in the Stag Hunt ($w > 1$), or as the fraction of cooperators in the Snowdrift game ($w < 1$). Thus, while Case 2 vanishes as the number of players becomes large, the fraction of cooperators vanishes as well.

4. Defense of a public good, number of attacks as degree of adversity

In the second public goods game we consider, rather than producing a public good, every group of n players that is formed can defend an existing public good against attacks. Cooperating means defending the public good, defecting means not defending the public good. The players face a number A of random attacks, where each attack draws a random player from the n players. As attacks are random, players who cooperate are equally likely to be attacked as players who do not cooperate; moreover, when there is more than one random attack, the same player may be attacked more than once. A player i who cooperates always provides an input with value $y_i = 1$ to the maintenance of the public good. A player i who defects, but is not drawn during the random attacks, still contributes $y_i = 1$ to the maintenance of the public good. Only a player i who defects, and is attacked at least one, contributes $y_i = 0$ to the value of the public good. We focus here on the case where the value of the public good is given by $V * \min(y_1, y_2, \dots, y_n)$; therefore, as a function of inputs $y_i = 0, 1$, the maintenance of the public good is based on the weakest-link technology.

Following the notation of Section 2, the benefit b_k as a function of the number k of cooperators now simply takes the form $b_k = V \left[\frac{k}{n} \right]^A$. The gain function therefore becomes:

$$f_C(x) - f_D(x) = V \sum_{k=0}^{n-1} \binom{n-1}{k} x^k (1-x)^{n-1-k} \times \left\{ \left[\frac{k+1}{n} \right]^A - \left[\frac{k}{n} \right]^A \right\} - c. \quad (9)$$

While the maintenance of the public good as a function of the number of players who contribute to the maintenance (i.e., who either cooperate, or defect but are not attacked) follows a weakest-link technology, as shown in Appendix D, the maintenance of the public good as a function of the number of cooperators follows a convex technology for an intermediate number of attacks ($\Delta^2 b > 0$). For $A = 1$ we have a summation technology as a function of the number of cooperators (linear public goods game), and for A approaching infinity we approach the weakest-link technology (weakest-link game). It follows that Proposition 1(1) directly applies, meaning that, depending on the position of the added benefit of cooperating alone (Δb_0) and the added benefit of cooperating jointly (Δb_{n-1}) relative to the cooperation cost (c), the game is either a Prisoner's Dilemma, a Stag Hunt, or a Harmony game. Intuitively, for a very large number of attacks, not defending almost automatically means that one does not contribute to the maintenance of the public good, meaning that the technology as a function of the number of cooperators, and as a function of the number of players that contributes to the maintenance of the public good, is the same. For a low number of attacks, however, not cooperating does not automatically mean that one fails to contribute to the maintenance of the public good, as one may not be attacked.

As further shown in Appendix D, $\Delta b_0 = \Delta b_{n-1} = (V/n)$ for $A = 1$, and Δb_0 decreases in A , whereas Δb_{n-1} increases in A . It follows that we obtain the same pattern as for $w \geq 1$ in Fig. 3(a), with A taking the place of w . As summarized in Result 3, a game-changing increase in the number of attacks therefore has the same effect as a game-changing increase in the degree of complementarity in Cases 1.2 and 2.2 of Result 1, where for $c > (V/n)$ a game-changing increase in A turns the game from a Prisoner's Dilemma into a Stag Hunt, and for $c < (V/n)$ a game-changing increase in A turns the game from a Harmony game into a Stag Hunt. Intuitively, in the current model, the players may be seen as producing

the collective defense of their public good. A larger number of attacks makes each player's defensive effort more pivotal, explaining the analogue between an increase in the number of attacks and an increase in the degree of complementarity. To highlight the analogue, for the difference cases in [Result 3](#), we use the same labels as for the corresponding cases in [Result 1](#).

Result 3 (Effect of a Game-Changing Increase in the Number of Attacks). **Case 1.2** Large cooperation costs ($c > (V/n)$): change from a Prisoner's Dilemma into a Stag Hunt, and increase in the basin of attraction of the joint cooperation ESS; (Q).

Case 2.2 Small cooperation costs ($c < (V/n)$): change from a Harmony game into a Stag Hunt, and decrease in the basin of attraction of the joint cooperation ESS (Q).

To confirm the intuition that the effect of an increase in the number of attacks resembles the effect of an increase in the degree of complementarity, we check whether marginal increases in the number of attacks have the same effect as in [Result 3](#). Here, we hit upon the problem that (9) does not allow us to solve $f_c(x^*) - f_D(x^*) = 0$ for x^* analytically. Yet, by applying implicit differentiation and exploiting properties of Bernstein polynomials, we show in [Appendix D](#) that small increases in the number of attacks have a similar effect as small increases in the degree of complementarity in the production model of [Section 3](#) when the starting point is a high degree of complementarity. The results are summarized in [Result 4](#), where for the cases obtained, we use the same labels as for the analogous cases in [Result 2](#). We were not able to establish whether there is a corresponding case to Case 1A.2 in [Result 2](#), where a higher number of attacks always increases the probability of cooperating, and therefore it is not clear whether or not the cost level \bar{c} delineating Case 1B.2 in [Result 4](#), is strictly smaller than V . Yet, in an analogous way as in [Fig. 4](#) to the right of $w = 1$ (high complementarity), the larger the cooperation costs, the larger the range of A for which the probability of cooperation increases in the number of attacks. An intuition for [Result 4](#) analogous to [Appendix C](#) can be constructed—an exercise we do not undertake here.

Result 4 (Effect of a Marginal Increase in the Number of Attacks). **Case 1B.2**. For a range of large cooperation costs ($V/n < c < \bar{c}$): in the Stag Hunt, hill-shaped effect on the probability that the joint cooperation ESS is played (an $A^*(c, n)$ exists such that $\frac{\partial Q}{\partial A} = \frac{\partial(1-x^*)}{\partial A} \geq 0$ for $A \leq A^*(c, n)$).

Case 2.2 For small cooperation costs ($c < V/n$), in the Stag Hunt, decrease in the probability that the joint cooperation ESS is played ($\frac{\partial Q}{\partial A} = \frac{\partial(1-x^*)}{\partial A} < 0$).

[Results 3](#) and [4](#) both apply to the specific case where the underlying technology as a function of the number of players who contribute (by cooperating, or by defecting but not being attacked) takes the form of a weakest link technology. [Appendix E](#) explores other underlying technologies, and shows that the analogue between an increase in the number of attacks in the defense model, and an increase in the degree of complementarity in the production model (with $w > 1$), applies as long as the underlying technology is a convex technology.

5. Discussion

For the two-player case, [De Jaegher and Hoyer \(2016a\)](#) provide a model where the effect of a harsher environment on the probability of cooperation in a public goods game depends on the context, in that the effect is different for large and for small cooperation costs. The current paper shows that in the multi-player case, the results are largely in line with those of the two-player case. Yet, at the

same time, the results for the multi-player predict further ways in which the direction of the effect of a harsher environment on the probability of cooperation is context-dependent, where we show both the number of players, and the degree of adversity itself, to matter.

We now look at manners in which the model could be extended. First, we have assumed that the degree of complementarity between players' cooperative efforts can change independently of the number of cooperating players, whereas in reality the degree of complementarity may itself depend on the number of cooperating players. Indeed, the division of labor associated with a high degree of complementarity may be most plausible for a small number of players (see e.g. [Maynard Smith, 1983](#), p. 448, and [Nunn and Lewis, 2001](#), p. 60 for this argument), meaning that in larger groups of cooperating players, the degree of complementarity may be lower. The model may be extended to include this fact, and this may lead to a reassessment of the relative importance of the different cases obtained.

Second, the model focuses exclusively on a harsh environment as a possible rationale for cooperation, and ignores relatedness between potential cooperators and structured populations as alternative rationales. Following the framework of [Peña et al. \(2015\)](#), it is straightforward to add both relatedness and structured populations to the model, by rescaling the cooperation costs. In this sense, our result that the direction of the effect of a harsher environment on the probability of cooperation depends on the level of the cooperation costs, can also be interpreted as relatedness, or a parameter reflecting population structure, affecting the direction of the effect. For instance, a high degree of relatedness means a small rescaled cooperation cost, and therefore fits the case of small cooperation costs in our model, which in such an extension may therefore receive more weight.

Third, in our model, the harshness of the environment is exogenously given; yet, it may not only be the case that the harshness of the environment affects the probability of cooperation, but the probability of cooperation may in turn affect the harshness of the environment. This creates an eco-evolutionary feedback, which may be integrated into a game-theoretic setting (cf. [Hauert et al., 2008](#); [Gokhale and Hauert, 2016](#)). Moreover, the harshness of the environment may itself be set by a strategic player (such as a prey in the case of collective hunting, or a predator in the case of collective defense); the common enemy may thus be a player who evolves to set the harshness of the environment, in response to how this environment affects the probability of cooperation.

Even with such extensions, the model will continue to be highly stylized, and the use of game theory to model cooperation is not without its critics. In an overview of cooperation, [West et al. \(2009\)](#) argue that game theory was useful to the cooperation literature in the 1970s and 1980s, for producing the basic insight that the fact that it is in the common interest of organisms to cooperate, does not necessarily mean that they will cooperate in equilibrium. But now that we have this basic insight, the argument continues, further game-theoretic modeling of cooperation is not of interest because it is often hard to relate the abstract payoffs in the model to any empirical setting. An argument for still using game-theoretic modeling in spite of this criticism, is that when it comes to the effect of adversity on the probability of cooperation, we are still at the level of gaining basic insights into micro-foundations, and that game-theoretic modeling can provide such insights. Moreover, one may directly replicate stylized public-good games in experiments, such as, e.g., [Clements and Stephens \(1995\)](#). Paraphrased to our context, while such experiments would not reflect any real-life situation of adversity, the underlying reasoning is that evolution has equipped organisms to recognize situations of environmental adversity, including novel ones, and to respond

to them in appropriate ways. Additionally, it has recently been argued that public goods production in microbial populations fits stylized games quite well (Doebeli and Hauert, 2005; Archetti et al., 2011). We hope that future research will show closer links between real-world instances of cooperation, and game-theoretic models of multi-player cooperation.

Acknowledgments

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Appendix A. Added benefits of cooperating jointly and alone as a function of the degree of complementarity

By (4), Δb_k can be written as $\frac{V w^{k+1}}{w + w^2 + \dots + w^n}$. Looking at the derivative of this expression with respect to w :

$$\begin{aligned} \frac{\partial \Delta b_k}{\partial w} &= V \frac{(k+1) w^k (w + w^2 + \dots + w^n) - w^{k+1} (1 + 2w + \dots + n w^{n-1})}{(w + w^2 + \dots + w^n)^2} \\ &= V \frac{k w^{k+1} + (k-1) w^{k+2} + \dots + (k+1-n) w^{k+n}}{(w + w^2 + \dots + w^n)^2} \\ &= V w^{k+1} \frac{k + (k-1) w + \dots + (k+1-n) w^{n-1}}{(w + w^2 + \dots + w^n)^2}. \end{aligned} \quad (\text{A.1})$$

It follows that for $k = 0$, Δb_0 is decreasing, and for $k = (n-1)$, Δb_{n-1} is increasing in w .

Appendix B. Derivation of x^* , and position and shape of $c^*(w, n)$

Exploiting the structure of (5), the average fitnesses (2) and (3) can be rewritten as:

$$f_C(x) = \frac{V}{1-w^n} [1 - w \{wx + (1-x)\}^{n-1}] - c \quad (\text{B.1})$$

$$f_D(x) = \frac{V}{1-w^n} [1 - \{wx + (1-x)\}^{n-1}]. \quad (\text{B.2})$$

Using (B.1) and (B.2), the difference between the gain function becomes:

$$f_C(x) - f_D(x) = \frac{V(1-w) [wx + (1-x)]^{n-1}}{1-w^n} - c. \quad (\text{B.3})$$

It can be checked now that x^* such that $f_C(x^*) - f_D(x^*) = 0$ is given by (7). The derivative of x^* with respect to w can be calculated as:

$$\begin{aligned} \frac{\partial x^*}{\partial w} &= \frac{1}{(1-w)^2} \\ &\quad - \frac{n(1-w^{n-1})}{(1-w)^3(n-1)} \left[\frac{c}{V} \right]^{1/(n-1)} \left[\frac{(1-w^n)}{(1-w)} \right]^{\frac{1}{n-1}-1}. \end{aligned} \quad (\text{B.4})$$

It can further be checked that $\frac{\partial x^*}{\partial w} \geq 0$ depending on whether

$$c \geq V \left[\frac{1-w}{1-w^n} \right] \left[\frac{(n-1)(1-w^n)}{n(1-w^{n-1})} \right]^{n-1} = c^*(w, n). \quad (\text{B.5})$$

The limit of the right-hand side of (B.5) for w approaching 0 is obtained by plugging in $w = 0$ in $c^*(w, n)$, yielding $V \left[\frac{(n-1)}{n} \right]^{(n-1)}$. The limit for w approaching plus infinity is obtained by rewriting

$c^*(w, n)$ in (B.5) as $V \left[\frac{w-1}{w^{n-1}} \right] \left[\frac{(n-1)(w^n-1)}{n(w^{n-1}-1)} \right]^{n-1}$, and noting that the limit of this expression for w approaching plus infinity equals $V \left[\frac{(n-1)}{n} \right]^{(n-1)}$. Finally, to obtain the limit for w approaching 1, note

that $c^*(w, n)$ can be rewritten as $V \frac{[1+w+w^2+\dots+w^{n-1}]^{n-2}}{[1+w+w^2+\dots+w^{n-2}]^{n-1}} \left[\frac{(n-1)}{n} \right]^{n-1}$; plugging in $w = 1$, one obtains (V/n) .

We now show the relation between the added benefit of cooperating jointly/alone, and $c^*(w, n)$. Using (6) to express Δb_{n-1} ,

$$\begin{aligned} \frac{V w^{n-1}(1-w)}{1-w^n} &\geq V \left[\frac{1-w}{1-w^n} \right] \left[\frac{(n-1)(1-w^n)}{n(1-w^{n-1})} \right]^{n-1} \\ &\Leftrightarrow \\ 0 &\geq w^n - nw + (n-1). \end{aligned} \quad (\text{B.6})$$

The right-hand side of (B.6) is zero for $w = 1$, and decreasing in w for $w < 1$, but increasing in w for $w > 1$. It follows that Δb_{n-1} is smaller than $c^*(w, n)$ for $w < 1$, but is the larger than $c^*(w, n)$ for $w > 1$. In the same way, using (6) to express Δb_0 ,

$$\begin{aligned} \frac{V(1-w)}{1-w^n} &\geq V \left[\frac{1-w}{1-w^n} \right] \left[\frac{(n-1)(1-w^n)}{n(1-w^{n-1})} \right]^{n-1} \\ &\Leftrightarrow \\ (n-1)w^n - nw^{n-1} + 1 &\geq 0. \end{aligned} \quad (\text{B.7})$$

The left-hand side of (B.7) is zero for $w = 1$, and increasing in w for $w < 1$, but decreasing in w for $w > 1$. It follows that Δb_0 is larger than $c^*(w, n)$ for $w < 1$, but is smaller than $c^*(w, n)$ for $w > 1$.

Appendix C. Intuition for non-monotonicity of effect of w on x^*

In order to get an intuition about the non-monotonicity in Case 1B of Result 2, it is instructive to look at the effect of w not just on Δb_0 and Δb_{n-1} , but on Δb_k for $1 \leq k \leq (n-2)$. Any k_0 such that Δb_{k_0} lies close to c now suggests an ESS where a fraction close to k_0/n players cooperate if players play a Snowdrift game, and where the basin of attraction of the joint cooperation ESS is close to $(n-k_0)/n$ if players play a Stag Hunt. When looking at the effect of w on k_0 for given c , we then see how play in the Snowdrift game or Stag Hunt is affected by w . Such a simplified analysis neglects the fact that each group of n players drawn from the population consists of a finite number of players, and need not contain the same fraction of cooperating players as the entire population. Yet, the conclusions of the simplified analysis are in line with Result 2, and such a simplified analysis is instructive as an intuition for the formal results.

We first establish the following results about the shape of $\Delta b_k(w)$ (i.e., Δb_k expressed as a function of w) for $1 \leq k \leq (n-2)$:

Result C.1. (i) $\Delta b_k(w)$ is a hill-shaped function of w , reaching its maximum for a finite value $w_{\max}(k)$ above zero;
(ii) $\partial w_{\max}(k)/\partial k > 0$, and $\partial (\Delta b_k(w_{\max})) / \partial k$ is smaller than zero for $w < 1$, and larger than zero for $w > 1$, where for odd n , $\Delta b_{(n-1)/2}(w_{\max}) = (V/n)$.

Proof. In (A.1), for $1 \leq k \leq (n-2)$, the first terms of the numerator are positive, and the last terms negative. Given that each of the expressions $k, (k-1), \dots, (k+1-n)$ gets weights w^0, w^1, \dots, w^{n-1} , this indicates that for each k with $1 \leq k \leq (n-2)$, $\Delta b_k(w)$ is hill-shaped.

For k such that $1 \leq k \leq (n-2)$, the level $w_{\max}(k)$ that maximizes Δb_k can be found by maximizing:

$$\max_w \frac{V w^k (1-w)}{1-w^n}$$

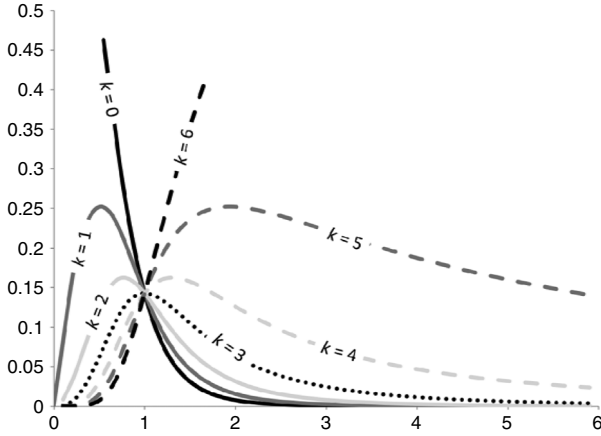


Fig. C.6. Added benefits of cooperating as a function of the degree of complementarity w , for several numbers of cooperators. When indicating the level of the cooperation costs as a horizontal line, for $w < 1$ (respectively $w > 1$), the intersection of the horizontal line with an added benefit of cooperating Δb_k suggests an ESS where about (k/n) players cooperate (respectively, suggests a cutoff point at k cooperators between the basin of attraction of the joint defection ESS and the joint cooperation ESS). The case represented is the one where $n = 7$, $V = 1$.

yielding the first-order condition:

$$\begin{aligned} V \frac{[kw^{k-1} - (k+1)w^k](1-w^n) - nw^{n-1}w^k(1-w)}{(1-w^n)^2} &= 0 \\ \Leftrightarrow \\ Vw^{k-1} \frac{[k - (k+1)w](1-w^n) - nw^n(1-w)}{(1-w^n)^2} &= 0. \end{aligned} \quad (\text{C.1})$$

Consider $w_{\max}(k)$ that solves (C.1), and denote by SD the second derivative of the right-hand side of (C.1). Then using implicit differentiation, it is the case that $\partial w_{\max}(k)/\partial k = -[Vw^{k-1} \frac{(1-w)(1-w^n)}{(1-w^n)^2}] / SD$. Given that by the second-order condition, $SD < 0$, it follows that $\partial w_{\max}(k)/\partial k > 0$. Using (4) to rewrite Δb_k as $\frac{Vw^{k+1}}{w+w^2+\dots+w^n}$, (C.1) can also be written as $Vw^{k+1} \frac{k+(k-1)w+\dots+(k+1-n)w^{n-1}}{w+w^2+\dots+w^n} = 0$. Plugging in $w = 1$ and solving for k , we see that the k for which $w_{\max}(k) = 1$ is $k = 0.5(n-1)$ (assuming odd n). Plugging in $w = 1$ into $\frac{Vw^{k+1}}{w+w^2+\dots+w^n}$, it follows that $\Delta b_{(n-1)/2}(w_{\max}(n-1)/2) = V/n$, where we note that at $w = 1$, all Δb_k are equal to V/n .

By the fact that the benefit sequence is concave for $w < 1$ and convex for $w > 1$, it follows that Δb_k decreases in k for $w < 1$, and increases in k for $w > 1$. From this fact, and from the fact that $\partial w_{\max}(k)/\partial k > 0$, it follows that $\partial(\Delta b_k(w_{\max}))/\partial k$ is smaller than zero for $w < 1$, and larger than zero for $w > 1$.

Result C.1 is illustrated for the case $n = 7$ in Fig. C.6, which represents the seven added benefits of cooperating for this case as a function of the degree of complementarity w . The result can be understood as follows. All added benefits of cooperation are equal to (V/n) when $w = 1$, as each additional cooperator then always contributes the same to the value of the public good. As already established in Appendix A, Δb_0 decreases in w , and Δb_{n-1} increases in w . Any intermediate Δb_k must be zero for $w = 0$ (as one cooperator then suffices to produce the full value of the public good), and must be zero for w approaching infinity as well (as all players must then cooperate to produce any value of the public good), explaining why Δb_k is hill-shaped in w . Furthermore, intuitively, for a small (large) number of cooperators, the corresponding added benefit of cooperating reaches a maximum for a low (high) degree of complementarity.

Finally, note that in Fig. C.6, for given w , the added benefit sequence decreases (increases) in w for $w < 1$ ($w > 1$), in line with a concave (convex) benefit sequence.

In Fig. C.6, let us now consider a fixed cooperation c , and look at the effect of a change in the degree of complementarity. For $w < 1$, a point where $\Delta b_k = c$ suggests a mixed-population ESS where a fraction of about (k/n) players cooperate in the Snowdrift game. We can now see how this fraction changes as we increase w . When we fix c such that $c < (V/n)$, we can see that as we increase w , $\Delta b_k = c$ first for $k = 1$, $k = 2$, ..., and finally $k = 6$, upon which all added benefits exceed c and the game becomes a Harmony game. This explains Case 2.1 in Result 2. Yet, for $c > (V/n)$, as long as c is smaller than the maximum of Δb_2 , as we increase w , $\Delta b_k = c$ first for $k = 1$, then for $k = 2$, but then again for $k = 1$. This suggests that, while eventually the effect of w on the ESS fraction of cooperators becomes negative, for small w the effect is positive, explaining Case 1B.1 in Result 2.

For $w > 1$, a point where $\Delta b_k = c$ suggests that the basin of attraction of the joint defection ESS takes on the size (k/n) . When we fix c such that $c < (V/n)$, we can see that as we increase w , at first all added benefits exceed c and the game is a Harmony game, after which Δb_k becomes equal to c first for $k = 0$, $k = 1$, ..., This explains Case 2.2 in Result 2. Yet, when we fix c such that $c > (V/n)$, as long as c is smaller than Δb_{n-2} , as w is increased the game is first a Prisoner's Dilemma, after which $\Delta b_k = c$ first for $k = 6$, then for $k = 5$, but then again for $k = 6$. This suggests that, while a higher degree of complementarity first increases the size of the basin of attraction of joint cooperation, this size eventually decreases again, explaining Case 1B.2 in Result 2.

Appendix D. Derivations for the defense model

(i) Given that $\Delta b_k = V \left\{ \left[\frac{k+1}{n} \right]^A - \left[\frac{k}{n} \right]^A \right\}$, for $A = 1$ we have $\Delta b_k = V/n$ for all k such that $0 \leq k \leq (n-1)$, meaning that $\Delta^2 \mathbf{b} = \mathbf{0}$. For A approaching infinity, Δb_k approaches 0 for $k < (n-1)$, and approaches V for $k = (n-1)$, so that $\Delta \mathbf{b}$ takes on the form $(0, \dots, 0, V)$, meaning that $\Delta^2 \mathbf{b} \geq \mathbf{0}$. For intermediate A , as $\frac{\partial(\Delta b_k)}{\partial k} = V \left\{ \frac{A}{n} \left[\frac{k+1}{n} \right]^{A-1} - \frac{A}{n} \left[\frac{k}{n} \right]^{A-1} \right\} > 0$, it follows that $\Delta^2 \mathbf{b} > \mathbf{0}$.

(ii) It is the case that $\Delta b_0 = V \left[\frac{1}{n} \right]^A$, which is increasing in A . Furthermore, $\Delta b_{n-1} = V \left\{ 1 - \left[\frac{n-1}{n} \right]^A \right\}$, which is decreasing in A .

(iii) Applying implicit differentiation to the condition $f_C(x^*) - f_D(x^*) = 0$, we obtain:

$$\frac{\partial x^*}{\partial A} = - \frac{\partial [f_C(x^*) - f_D(x^*)] / \partial A}{\partial [f_C(x^*) - f_D(x^*)] / \partial x}. \quad (\text{D.1})$$

As pointed out by Peña et al. (2014), in a Bernstein polynomial of the form $\mathcal{B}(n, \mathbf{d}) = \sum_{k=0}^{n-1} \binom{n-1}{k} x^k (1-x)^{n-1-k} d_k$, all the properties of the sequence $\mathbf{d} = (d_0, d_1, \dots, d_{n-1})$ are inherited by $\mathcal{B}(n, \mathbf{d})$. Thus, if \mathbf{d} is an increasing sequence, then $\partial \mathcal{B}(n, \mathbf{d}) / \partial x > 0$. Applying this result, as (9) is a Bernstein polynomial, and as $\partial \left\{ \left[\frac{k+1}{n} \right]^A - \left[\frac{k}{n} \right]^A \right\} / \partial k > 0$ (meaning that $\Delta \mathbf{b}$ is an increasing sequence), it follows that $\partial [f_C(x^*) - f_D(x^*)] / \partial x > 0$.

(iv) By (9), it follows that:

$$\begin{aligned} \frac{\partial [f_C(x^*) - f_D(x^*)]}{\partial A} &= V \sum_{k=0}^{n-1} \binom{n-1}{k} x^k (1-x)^{n-1-k} d_k - c \\ &= V \sum_{k=0}^{n-1} \binom{n-1}{k} x^k (1-x)^{n-1-k} d_k - c \end{aligned} \quad (\text{D.2})$$

where

$$d_k = \partial \left\{ \left[\frac{k+1}{n} \right]^A - \left[\frac{k}{n} \right]^A \right\} / \partial A$$

$$= V \left\{ \left(- \left[\frac{k}{n} \right]^A \ln \left[\frac{k}{n} \right] \right) - \left(- \left[\frac{k+1}{n} \right]^A \ln \left[\frac{k+1}{n} \right] \right) \right\}. \quad (\text{D.3})$$

This means that $\frac{\partial [f_C(x^*) - f_D(x^*)]}{\partial A}$ is itself a Bernstein polynomial. It can be checked that d_0 is negative and d_{n-1} positive, and that the sequence $\mathbf{d} = (d_0, d_1, \dots, d_{n-1})$ as defined by (D.3) undergoes one sign change. By the *variation diminishing property* of Bernstein polynomials (see Peña et al., 2015), it follows that $\frac{\partial [f_C(x_0) - f_D(x_0)]}{\partial A}$ also undergoes one sign change, and has the same sign pattern as \mathbf{d} , so that there exists an x_0 implicitly defined by $\frac{\partial [f_C(x_0) - f_D(x_0)]}{\partial A} = 0$, such that $\frac{\partial [f_C(x^*) - f_D(x^*)]}{\partial A} < 0$ for $x^* < x_0$, and $\frac{\partial [f_C(x^*) - f_D(x^*)]}{\partial A} > 0$ for $x^* > x_0$. By the fact that $\partial [f_C(x^*) - f_D(x^*)] / \partial x > 0$ (see (iii)) and by (D.1), this means that for $x^* < x_0$, it is the case that $dx^*/dA > 0$, meaning that $dQ/dA < 0$; for $x^* > x_0$, it is the case that $dx^*/dA < 0$, meaning that $dQ/dA > 0$. As x^* is increasing in cooperation costs, this in turn means that there exists a critical cost level c^* such that for $c > c^*$, $dQ/dA > 0$ (common enemy effect), and such that for $c < c^*$, $dQ/dA < 0$ (competing hypothesis).

(v) We here show that the c^* itself depends on A . To show this, we derive the effect of A on x_0 . As x_0 is given by $\frac{\partial [f_C(x_0) - f_D(x_0)]}{\partial A} = 0$, using implicit differentiation, we have

$$\frac{\partial x_0}{\partial A} = - \frac{\frac{\partial^2 [f_C(x_0) - f_D(x_0)]}{\partial A^2}}{\frac{\partial^2 [f_C(x_0) - f_D(x_0)]}{\partial A \partial x}}. \quad (\text{D.4})$$

Given that, as previously established, $\frac{\partial [f_C(x^*) - f_D(x^*)]}{\partial A} < 0$ for $x^* < x_0$, and $\frac{\partial [f_C(x^*) - f_D(x^*)]}{\partial A} > 0$ for $x^* > x_0$, it follows that $\frac{\partial^2 [f_C(x_0) - f_D(x_0)]}{\partial A \partial x} > 0$. $\frac{\partial^2 [f_C(x_0) - f_D(x_0)]}{\partial A^2}$ equals

$$V \sum_{k=0}^{n-1} \binom{n-1}{k} x^k (1-x)^{n-1-k} \times \left\{ \left[\frac{k+1}{n} \right]^A \left(\ln \left[\frac{k+1}{n} \right] \right)^2 - \left[\frac{k}{n} \right]^A \left(\ln \left[\frac{k}{n} \right] \right)^2 \right\}. \quad (\text{D.5})$$

To see that (D.5) is negative, note that the condition $\frac{\partial [f_C(x_0) - f_D(x_0)]}{\partial A} = 0$ can be written as:

$$V \sum_{k=0}^{n-1} \binom{n-1}{k} x^k (1-x)^{n-1-k} \times \left\{ \left[\frac{k+1}{n} \right]^A \left| \ln \left[\frac{k+1}{n} \right] \right| - \left[\frac{k}{n} \right]^A \left| \ln \left[\frac{k}{n} \right] \right| \right\} = 0. \quad (\text{D.6})$$

As $|\ln \left[\frac{k+1}{n} \right]| < |\ln \left[\frac{k}{n} \right]|$, given (D.6), it follows that (D.5) is smaller than zero, so that $\frac{\partial^2 [f_C(x_0) - f_D(x_0)]}{\partial A^2} < 0$. By (D.4), this means that $\frac{\partial x_0}{\partial A} > 0$. As higher x^* is associated with larger c , it follows that the critical cost level c^* dividing the cases where the common enemy hypothesis applies, and the competing hypothesis applies, is an increasing function $c^*(A)$ of A . As such a critical c^* also exists around $A = 1$, and as $c^*(A)$ is an increasing function of A , it follows that for c below the critical c^* for $A = 1$, the competing hypothesis always applies. The critical c^* for $A = 1$ equals exactly (V/n) , as this divides the area where one moves from a Prisoner's Dilemma to a Stag Hunt, and from a Harmony game to a Stag Hunt. Finally, we note that in Result 4, to state the results we make use of the function $A^*(c)$, which is the inverse function of $c^*(A)$.

Appendix E. Defense model beyond the weakest-link technology

For $A = 1$, we have:

$$\Delta b(A = 1) = \frac{V w^{n-1} (1-w)}{n(1-w^n)} \quad (\text{E.1})$$

where we suppress k in the subscript, as for given w , the added benefit of cooperating does not depend on the number of players who are currently cooperating. This means that, whatever the technology (given by w) as a function of the number of players who contribute to the maintenance of the public good (by cooperating, or by not cooperating and not being attacked), when $A = 1$ the technology as a function of the number of cooperating players is always a summation technology. It can be checked that $\Delta b(A = 1)$ approaches (V/n) for w approaching plus infinity, approaches (V/n^2) for w approaching 1, and approaches 0 for w approaching 0.

For A approaching plus infinity, as a player who defects is attacked with probability approaching one, the technology as a function of the number of players contributing to the maintenance of the public good, and as a function of the number of cooperating player is the same. In this case, by (6) we have:

$$\Delta b_k(A \rightarrow \infty) = \frac{V w^k (1-w)}{1-w^n}. \quad (\text{E.2})$$

It follows that $\Delta b_{n-1}(A \rightarrow \infty)$ approaches V for w approaching plus infinity, approaches (V/n) for w approaching 1, and approaches 0 for w approaching 0. Furthermore, $\Delta b_0(A \rightarrow \infty)$ approaches 0 for w approaching plus infinity, approaches (V/n) for w approaching 1, and approaches V for w approaching 0. Also, $\Delta b_{n-1}(A \rightarrow \infty) > \Delta b(A = 1)$ for $w > 0$, and $\Delta b_{n-1}(A \rightarrow \infty) = \Delta b(A = 1)$ for $w = 0$. Moreover, $\Delta b_0(A \rightarrow \infty) \leq \Delta b(A = 1)$ for $w \geq n^{1/(n-1)}$. Finally, $\Delta b_{n-1}(A \rightarrow \infty) \geq \Delta b_0(A \rightarrow \infty)$ for $w \geq 1$.

The following cases are now obtained. For $w > n^{1/(n-1)}$, a game-changing increase in the number of attacks either changes the game from a Harmony game into a Stag Hunt (relatively small cooperation costs), or from a Prisoner's Dilemma into a Stag Hunt (relatively large cooperation costs); this case is in line with Result 3. For $1 < w < n^{1/(n-1)}$, a game-changing increase in the number of attacks changes the game from a Prisoner's Dilemma into a Stag Hunt; this case is in line with Case 1.2 in Result 3. In general, for $w > 1$, an increase in the number of attacks changes the technology as a function of the number of cooperating players from a summation technology for $A = 1$, to a convex technology for large A , explaining the link to Result 3.

For $w < 1$, a game-changing increase in the number of attacks changes the game from a Prisoner's Dilemma into a Snowdrift game. The technology as a function of the number of cooperating players changes from a summation technology for $A = 1$, into a concave technology for large A . The effect of a game-changing increase in the number of attacks is here to make the players' efforts less, rather than more complementary.

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