Stark, Oded; Jakubek, Marcin

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Is Population Growth Conducive to the Sustainability of Cooperation?

by

Oded Stark & Marcin Jakubek

Faculty of Economics and Social Sciences
www.wiwi.uni-tuebingen.de

Is population growth conducive to the sustainability of cooperation?

by

Oded Stark*

University of Bonn, Germany
University of Klagenfurt, Austria
University of Vienna, Austria
University of Tuebingen, Germany
Warsaw University, Poland
Warsaw School of Economics, Poland
e-mail: ostark@uni-bonn.de

and

Marcin Jakubek

University of Klagenfurt, Austria
e-mail: MarcinKacper.Jakubek@uni-klu.ac.at

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* Corresponding author

Abstract

This paper asks whether population growth is conducive to the sustainability of cooperation. A simple model is developed in which farmers who live around a circular lake engage in trade with their adjacent neighbors. The payoffs from this activity are governed by a prisoner's dilemma "rule of engagement." Every farmer has one son when the population is not growing, or two sons when it is growing. In the former case, the son takes over the farm when his father dies. In the latter case, one son stays on his father's farm, whereas the other son settles around another lake, along with the "other" sons of the other farmers. During his childhood, each son observes the strategies and the payoffs of his father and of the trading partners of his father, and imitates the most successful strategy when starting farming on his own. Then mutant defectors are introduced into an all-cooperator community. The defector strategy may spread. A comparison is drawn between the impact in terms of the sustainability of cooperation of the appearance of the mutants in a population that is not growing, and in one that is growing. It is shown that the ex-ante probability of sustaining the cooperation strategy is higher for a community that is growing than for a stagnant community.

Keywords: Population growth; Imitation; Sustainability of cooperation

JEL classification: C72; D01; D83; J19; J62; R12; R23

1 Introduction

In this paper we link together two strands of the literature: that on the evolution and sustainability of cooperative behavior, and that which has long sought to demonstrate that population growth is conducive to the wellbeing of societies and nations (Simon, 1977, 1996). The purpose of this paper is to inquire whether and under what circumstances population growth is conducive, or detrimental, to the sustainability of cooperative behavior in a population. Obviously, these questions are so broad that it is virtually impossible to address them in general terms. We therefore resort to an example. We delineate a specific setting in which two cases - one without population growth, the other with - can be compared in a well defined manner. In the setting developed and presented in this paper, we find that it is more likely that cooperation will be sustained when a population is growing than when it is not. Under a standard one-shot prisoner's dilemma payoff structure, cooperation is, on average, more conducive to survival than defection, as it confers a higher per capita payoff. Therefore, we are led to infer that in the specific setting studied by us, a growing population has some feature that better supports future population growth that a stagnant population does not have.

In section 2 we delineate our basic model: farmers who are located around a lake trade with their neighbors in a setting in which the returns to trade are governed by a prisoner's dilemma payoff structure, and where, to begin with, all the farmers are cooperators. In section 3 we tinker with the model by assuming that one or two defectors appear in a constant population of nine cooperators. We use nine farmers as our "canonical" example because nine is the smallest settlement size for which, in terms of the sustainability of cooperation, qualitative differences appear between the no population growth and the population growth case. We calculate the probability of the spread of the defector strategy in the farmers' community, and we show that the community has a significant chance of ending up as a pure defector community, which in turn has the lowest per capita payoff of all possible farmer-by-type configurations. In section 4 we replicate the analysis of section 3 for a situation in which the population is growing. Once again, we allow for the appearance of one or two defectors in the initial, all-cooperator population. For a settlement of nine farmers we calculate the probability that the population will end up consisting entirely of defectors. We find that with two initial defectors, the probability is *lower* than it would be with a constant population. This leads us to conjecture that in our model, population growth is conducive to the sustainability of cooperation. In section 5 we provide a generalization: stepping beyond the case of a settlement of nine farmers, we study a settlement of cooperators of any size in which a

random number of mutant defectors appear. We find that qualitatively our findings carry through also to this general case: the ex-ante probability of the survival of cooperation is higher for a growing population than for a stagnant population. Section 6 explains how our approach relates to and differs from writings in evolutionary biology that study the impact of demographic processes on the prevalence of altruism. Section 7 concludes. In the appendix we present an extension of our model, postulating that progeny depends positively on payoffs. We show that such a constellation too can give rise to the main result reported in the body of the paper.

2 The model

We base our model on the perception that, typically, the success or failure of an individual who makes an economic decision is influenced by the choices made by others in his economic sphere. Following Bergstrom and Stark (1993) and more recently Stark and Behrens (2010, 2011), we consider a population of n farmers, where $n \geq 3$ and is a natural number, who cultivate their plots which are arranged around a lake. Thus, every farmer has exactly two neighbors. Each of the n farmers trades with his immediate neighbors, one to his right, and one to his left.[1] We assume that trading is necessary for the proper functioning of a farm; every farmer thus has to engage in trade with his neighbors.

The payoffs to a farmer from a trade are governed by a prisoner's dilemma game in which he is either a cooperator, who plays *C*, or a defector, who plays *D*, with his two trading partners. The farmer's overall payoff is the sum of the payoffs from playing with his two trading partners, where the payoff from the play with each partner is given by the following matrix:

		Column player	
		C	D
Row player	C	R,R	S,T
	D	T,S	P,P

where

$$T > R > P > S . \tag{1}$$

[1] Obviously, three is the minimal number of farmers that allows an individual to have two neighbors to trade with.

Additionally, we assume that

$$2R > T + P, \tag{2}$$

namely that a cooperator surrounded by cooperators (thereby receiving a payoff of $2R$) is more successful (enjoys a higher total payoff) than a defector trading with a cooperator and a defector (thereby receiving a payoff of $T + P$).

Dynamics is introduced into the model in the form of learning and generational replacement. A farmer belongs to one generation t, $t = 0,1,2,\ldots$. Life is divided into two periods or phases: childhood, and farming-cum-trading. At the beginning of the second period, each farmer has one or two sons, depending on the population growth setting.

During childhood, a son learns from observing the effects of the practices pursued by his father and his father's trading partners. He finds out which practice (strategy) is the most successful (in terms of the sum of the payoffs) in the parental generation. When a son takes over the farming operations, he adopts the strategy that has yielded the highest payoff.

This highly stylized structure accords with evidence that farmers' decisions respond to the actions and outcomes of other farmers in their "geographic proximity." Conley and Udry (2010) present evidence that the intensity of fertilizer use by farmers in southern Ghana is strongly attributable to learning from their "information neighbors" and from their own experience.

We start with a population of farmers who are all cooperators. This implies that each farmer receives from each trading relationship a payoff of *R*.

To investigate the robustness or the sustainability of cooperation in the "ancestral" village community, we assume that in generation $t = 0$, there is a mutation of cooperators into defectors whose strategy could well spread into future generations. We track the consequences of the appearance of defector mutants in what otherwise is a pure cooperator population in two settings: one without population growth, the other with. We characterize population growth as a multiplication of farming settlements (ours is "a lake district"): when each farmer has two sons, one son takes over his father's farm whereas the other son, along with the second sons of all the other farmers, settles around another lake, choosing his farm placement randomly.

3 The sustainability of cooperation without population growth

In this section, we study the case in which there is no population growth: each farmer has only one son, who takes over his father's farm when the father passes away. We track the "history" of the farming community as of time $t=0$ when one or two cooperators mutate into defectors.

One mutant defector

In the ancestral village, let there be one random mutation into defection. In all the graphs that follow, farmers are represented by circles placed around the lake: a white circle stands for a cooperating farmer, a black circle - for a defector farmer. The letters *P*, *R*, *S*, *T* near the circles are the payoffs that a farmer gets from a trade with a neighbor.

The generation $t=0$ population is depicted in Figure 1.

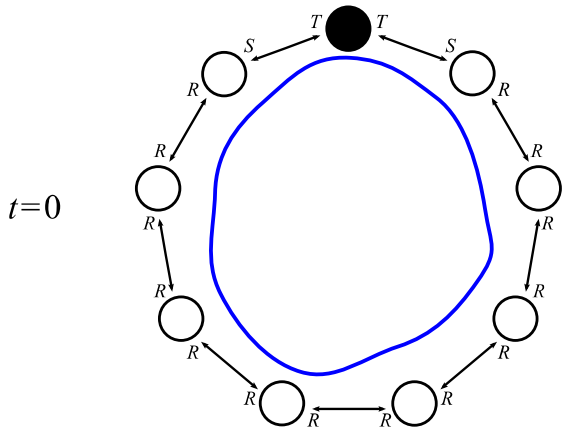

Figure 1. The strategies and the payoffs in a settlement of $n=9$ farmers, in generation $t=0$, and in the wake of one mutation.

From condition (1) it follows that the mutant's trait, which results in a total payoff of $2T$, will spread among the sons of the mutant's two immediate neighbors, as his trait will be the most successful example in their neighborhood. Thus, at time $t=1$, the configuration will be as in Figure 2.

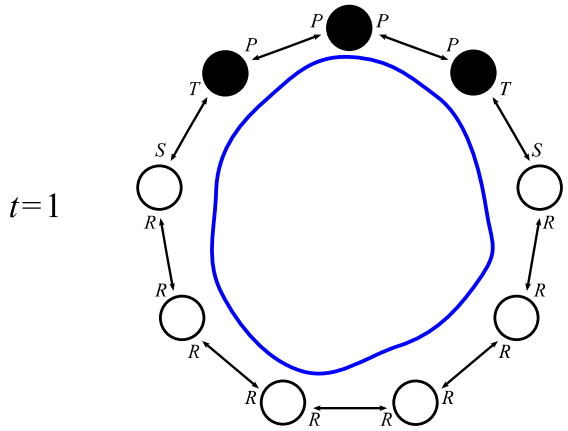

Figure 2. Strategies and payoffs in a settlement of $n=9$ farmers, in generation $t=1$, and in the wake of one mutation.

What happens in the next generation ($t=2$) depends on the prevalence of a "cooperator island" of sufficient size (cf. Stark and Behrens, 2011), namely on whether the population size is large enough ($n \geq 6$) to allow for at least one cooperator to be surrounded only by cooperators, resulting in him receiving a total payoff of $2R$. According to (2), the cooperator in the middle of a batch of cooperators will be more successful than a defector on the border of a cluster of two or more defectors who receives $(T+P)$, and therefore, the D trait will spread no more. Clearly, had the population size been less than 6, no successful "example" of playing C strategy would have been left, and the entire community would have ended up as a community of defectors.

It is worth noting that in the case of a single mutant defector, the community outcome does not depend on the defector's random placement; the spatial configuration is the same no matter in which farm the mutant happens to appear.

Two mutant defectors

The situation is more intricate when at $t=0$ there are two mutant defectors. To help us map the whereabouts of the defectors, we define a vector $D_t(n,k)=(d_1,...,d_k)$ that traces the number of cooperators among the k defectors in generation t.[2]

[2] For illustrative purposes, when presenting the configurations $D_t(n,k)=(d_1,...,d_k)$ we start enumerating the separating cooperators from the defector who is the first after "the 12 o'clock position" and proceed clockwise. Since the spread of the defection strategy depends only on the numbers of cooperators separating the k defectors, the configurations $D_t(n,k)=(d_1,...,d_k)$ are equivalent with respect to rotations and symmetric transformations. For example, the configuration $D_t(9,4)=(2,3,0,0)$ is qualitatively equivalent to the configuration $(0,2,3,0)$ or to the configuration $(0,0,3,2)$. We will use the term "probability of a configuration" synonymously with "the

There are $9\times 8 = 72$ possible initial placements of the two mutant defectors among the nine farmers. These placements can be pooled into four representative configurations that differ in substance one from the other, and occur each with probability $1/4$: $D_0^{\mathrm{I}}(9,2) = (7,0)$, $D_0^{\mathrm{II}}(9,2) = (6,1)$, $D_0^{\mathrm{III}}(9,2) = (5,2)$ and $D_0^{\mathrm{IV}}(9,2) = (4,3)$.

The four parts of Figure 3 depict the evolution of the community structure in these four configurations.

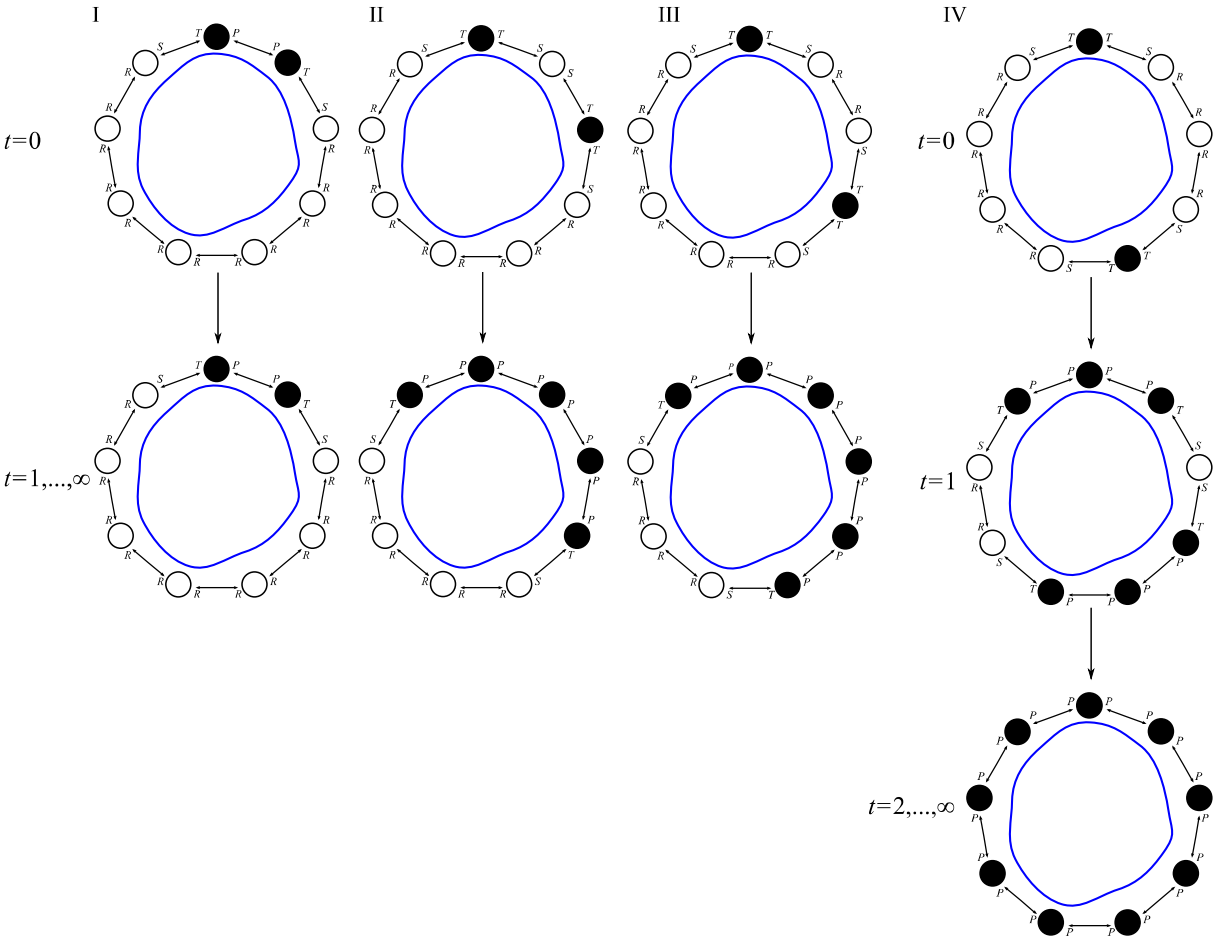

Figure 3. The evolution of strategies in a settlement of $n = 9$ farmers in the wake of two random mutations.

The repercussions of the spread of the defector strategy differ across the four cases, but they follow a simple general rule: when a defector is introduced into the population, his "momentary" success among neighboring cooperators is mimicked in the next generation by the sons of his immediate neighbors who learn from his example during their childhood. The repercussions depend on the relative placement of the two defectors in the community. We

probability of all of a configuration's qualitative/structural equivalents (with respect to rotations and symmetry)."

have two types of outcomes:

(i) when the mutant defectors are separated by at least one cooperator, the defector strategy spreads among all the trading partners of the defectors (configurations II through IV in Figure 3);

(ii) when the mutant defectors are placed one next to the other, condition (2) implies that their strategy will not be considered as successful by their neighbors if the size of the community is large enough for a successful cooperator to be left so as to serve as a good example (configuration I in Figure 3), and hence, the defector strategy does not spread among the defectors' neighboring cooperators.

In subsequent generations, the spread of the defector strategy stops in a manner akin to that of one mutant defector: when an "island of cooperation" of at least three cooperators is left, that is, when the configuration allows for at least one cooperator to trade with only cooperators, then the defector strategy does not appear as tempting to the sons of the cooperating farmers in the neighborhood of this successful cooperator. The spread of defection is halted.

In sum: considering the question of the survival of cooperation in a population of nine farmers and two mutant defectors, only in one initial case - configuration D_0^{IV} - is the result starkly "negative;" after two generations, the community becomes a pure defector community; the two clusters of cooperators in generation $t=1$ are too small for the *C* strategy to be successful in comparison with the *D* strategy in such a mixed population. Given this, we can state that in the current setup, the probability of sustaining cooperation in the wake of the mutation of two cooperators into defectors is $3/4$, since the probability of each of the three "positive" configurations that does not allow elimination of cooperators (configurations D_0^{I}, D_0^{II}, and D_0^{III}) is $1/4$.

In the next section we study the same setup but with population growth. We show that as long as only one mutant defector appears in the population, there are no distinct repercussions of population growth - compared to the case of no population growth - for the sustainability of cooperation in the farming population. However, when there are two mutant defectors, the probability of the spread of the defector strategy among the entire population is muted; it is *lower* than in the absence of population growth.

4 The sustainability of cooperation with population growth

In this section we inquire how the preceding results are affected when we allow the population to grow.

We introduce population growth by assuming that at the beginning of the second period of his life, every farmer has two sons. At the end of the farmer's life, one of the sons, the "stayer," takes over his father's farm, whereas the second son, the "settler," along with his peers, begins farming around a new lake. Therefore, after each generation, the population of active farmers as well as the number of settlements doubles.

We assume that when settling around the new lake, the settler sons are placed randomly, with uniform probabilities of each of the possible permutations.[3] As in the setting without population growth, during their childhood both sons learn from the experience (payoffs) of their father and his two adjacent neighbors. Consequently, at the time of the generational shift, both sons (the stayer and the settler) choose the same strategy, yet they end up playing it in different locales.

We could alternatively assume that the sons settle around the new lake not randomly, but rather by mimicking the neighborhood pattern that would have prevailed had they been the only sons taking over their fathers' farms in the ancestral village. It is immediately obvious that in such a case, population growth will not yield an outcome different from that of no population growth because the evolution of strategies in the descendant villages will be the same as in the ancestral village leading, in terms of the sustainability of cooperation, to the same outcome across all the settlements. Therefore, in the population growth setting, we attend only to a random placement of the settlers.

One mutant defector

To begin with, let there be a randomly placed mutant defector in the population. There are two possibilities: if $(3 \leq)n < 6$, then the batches of three next-generation defectors in each

[3] The possibility that on the way to the new lake some sort of a grouping of cooperators will be formed, aimed at forming a settlement pattern that is less random and more rewarding, does not align with our framework. This is so for two reasons. First, because the sons of a given father observe only the immediate neighbors of their father (they do not observe the payoffs of farmers farther away), they cannot foresee the strategies of the sons of neighbors of their father, because the information base for the choice of strategies of a neighbor's sons is not available to the sons of a given farmer. (Stark and Behrens, 2010, developed a theory of an evolutionary edge of knowing *less*; more information could well be a curse, not a reward.) Second, because the true strategies of settlers are not common knowledge, and because deviators have no incentive to reveal their true type, any exchange of information between the settlers about the strategy that they will adhere to is bound to end with all of them presenting themselves as cooperators, making the exchange useless. (For an example of model that in a prisoner's dilemma setting allows selection of counterparts by type, see Stark et al., 2009.)

of the communities are too "massive" to allow for an "island of cooperation" of a size of at least three to survive. Therefore, for such a low *n*, cooperation is doomed. If $n \geq 6$, however, then at least in the ancestral village cooperation is not "endangered;" as revealed by the analysis in the preceding section, the appearance of one mutant defector does not suffice to "convert" the ancestral village into a pure defector community. Cooperation will survive at least in this village. So in general, we can state that in the case of one mutant defector, *in terms of the sustainability of cooperation* the outcome for a population growth setting is the same as the outcome for a no population growth setting.

Two mutant defectors

When, for $n = 9$, in the ancestral settlement in generation $t = 0$ two defectors are randomly placed amongst the remaining seven cooperators, the evolution of strategies in the ancestral village will be the same as the evolution depicted in the preceding section for the no population growth setting. Even when we allow now for doubling of the number of settlements as described above, if in the ancestral village the two mutant defectors are placed according to configurations D_0^{I}, D_0^{II} or D_0^{III}, cooperation will surely survive at least in that village, no matter what will be the outcome of the random placements of the settlers in the newly-settled villages. Therefore, the only situation when the overall population has a chance of ending up as a pure defector community is the appearance of mutant defectors as in configuration D_0^{IV} (cf. part IV of Figure 3).

Because the mechanism of "learning" is the same for both settler sons and staying sons, we can infer that among the sons who in generation $t = 1$ look for a new place to settle, there will be six individuals who perceive defecting to be the more successful strategy - exactly the same number as that which we observed in $t = 1$ in the ancestral village (cf. the $t = 1$ depiction in part IV of Figure 3).

The question to address is whether the random placement of the individuals in the new village affects the fate of cooperation which in the ancestral settlement is "doomed."

As we know from the conditions discussed before, to "stop" the spread of the defector strategy we must have a cluster of at least three cooperators placed against possible clusters of defectors. For only three cooperators to be left in a population of nine individuals, this means that their placement must be of the form:

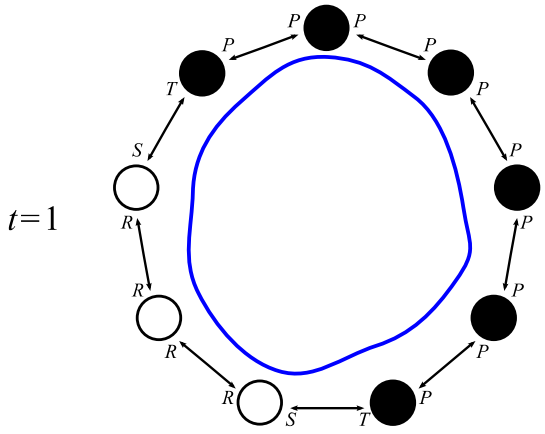

Figure 4. A configuration $D_1(9,6)=(0,0,0,3,0,0)$ allowing the survival of cooperation in the settlers' village after an appearance of mutant defectors in the ancestral village according to configuration D_0^{IV}.

The probability of the configuration $D_1(9,6)=(0,0,0,3,0,0)$ among nine individuals out of which six are defectors and three are cooperators, is:[4]

$$P\left(D_1(9,6)=(0,0,0,3,0,0)\right)=\frac{6!\times 3!\times 9}{9!}=\frac{3}{28}. \tag{3}$$

The remaining configurations with the complementary probability 25/28, lead to pure defector communities also in this new settlement (and in all of its descendant settlements).

Therefore, if we assume that the various configurations of settling around the new lake are independent of the placement of the mutant defectors around the ancestral lake, the probability of sustaining cooperation in the (overall) population goes up from 3/4 in the no population growth model, to

$$P\left(Cooperation\right)=\frac{3}{4}+\frac{1}{4}\times\frac{3}{28}=\frac{3}{4}+\frac{3}{112}. \tag{4}$$

In the case of a community of nine farmers who engage in trading activities with their closest neighbors, population growth has a distinct beneficial influence on the survival of cooperation. We next assess the implications of population growth for the sustainability of cooperation when the ancestral population can be of any size $n\geq 3$.

[4] We have $3!\times 6!$ possible arrangements of three cooperators and six defectors giving *exactly* the same configuration as in Figure 4, but this arrangement is equivalent with respect to nine possible permutations. Therefore $3!\times 6!\times 9$ arrangements out of a total $9!$ yields the configuration $D_1(9,6)=(0,0,0,3,0,0)$.

5 A generalization

Consider a probabilistic constellation of the size of the settlement, of the number of the initial mutant defectors, and of their placement among settlers; all for generation $t=0$. That is, we assume that the initial settlement size ($n \geq 3$) is first chosen according to a probability distribution $P=(p_3, p_4, p_5, ...)$ such that $p_i > 0$ for $i = 3,4,5,....$ Next, the number of mutant defectors k, $1 \leq k \leq n$, is chosen according to a probability distribution $Q_n = (q_1, ..., q_n)$ such that $q_i > 0$ for $i = 1,2,...,n$. And finally, for given n and k, the configuration in which the defectors appear in the ancestral village, $D_0(n,k)$, is chosen over the set of all possible configurations according to a distribution that assigns to each possible configuration a non-zero probability. Then, a village characterized by the triplet $(n, k, D_0(n,k))$ will be treated as the ancestral settlement. This settlement then experiences, or does not experience, population growth.[5] In the population growth setting, the random placement of the farmers in the newly-settled villages is governed by a uniform distribution over all possible configurations.

Since we are interested in the likely survival of cooperation, we will denote by $P_{growth}(Cooperation)$ the ex-ante (that is, before the choice of the settlement size n) probability of the event that cooperation will survive in the long run in at least one of the 2^t villages in generation t in the population growth setting,[6] and by $P_{static}(Cooperation)$ the ex-ante probability of the event that cooperation will survive in the long run in the ancestral village in the static no population growth setting.

We now state and prove the following claim.

Claim 1: $P_{growth}(Cooperation) > P_{static}(Cooperation)$.

Claim 1 tells us that the ex-ante probability of the survival of cooperation is strictly higher in the population growth setting than in the no population growth setting.

Proof: First, we note that

$$\forall_n \forall_{k \leq n} P_{growth}(Cooperation \mid n,k) \geq P_{static}(Cooperation \mid n,k). \quad (5)$$

[5] We assume that the (joint) distributions of n, k and $D_0(n,k)$ are the same for these two settings.

[6] "Long run" means any generation t which is beyond the moment in time at which the evolution of strategies in the ancestral village has reached a stable state.

This inequality arises from the assumption that the distribution of $D_0(n,k)$ is the same in the population growth setting as in the no population growth setting, and from the fact that in a given configuration $\left(n,k,D_0\left(n,k\right)\right)$, the occurrence of the *Cooperation* event in the no population growth setting implies occurrence of the *Cooperation* event also in the population growth setting, since in both settings the evolution of strategies in the ancestral villages is the same.

Moreover, from the example presented in section 4 we already know that there exists at least one combination $\left(n,k\right)$, namely $n=9$ and $k=2$ such that[7]

$$P_{growth}\left(Cooperation \mid n=9,k=2\right) > P_{static}\left(Cooperation \mid n=9,k=2\right). \tag{6}$$

Since it follows from our assumptions about distributions of n and k that $\forall_n \forall_{k\le n} P_{growth}\left(n,k\right) = P_{static}\left(n,k\right) > 0$, we can infer from using the law of total probability that for the ex-ante probabilities we have

$$P_{growth}\left(Cooperation\right) > P_{static}\left(Cooperation\right), \tag{7}$$

which concludes the proof. □

Furthermore, that the probability of the survival of cooperation is higher in the population growth setting than in the no population growth setting does not critically hinge on the configuration $n=9$ and $k=2$. To this end, we state and prove the following corollary.

Corollary 1: $\forall_{n\ge 12} P_{growth}\left(Cooperation \mid n\right) > P_{static}\left(Cooperation \mid n\right)$.

Corollary 1 tells us that the ex-ante probability of the survival of cooperation is always strictly higher in the population growth setting than in the no population growth setting when the community is large enough.

Proof: We have already noted (5). To prove the corollary, we only need to find for each $n \ge 12$ a k and an initial configuration $D_0(n,k)$ such that defection spreads in the ancestral

[7] The calculation, reported in equation (4), of the difference between the probabilities of sustaining cooperation in the two settings was for a uniform probability distribution of the $D_0\left(n,k\right)$ configurations. This quantitative result may no longer apply in the more general setting discussed here. Nonetheless, as long as we assume that every possible configuration $D_0\left(n,k\right)$ can be chosen with a non-zero probability, the qualitative result that the probability of sustaining cooperation is higher in the population growth setting than in the stagnant population setting carries through.

village, whereas in the newly-settled village cooperation survives with a non-zero probability. Let k be a natural number satisfying

$$5k \geq n\,, \tag{8}$$

and

$$n - 3k \geq 3\,. \tag{9}$$

It is easy to check that such a k exists for any $n \geq 12$.[8] We note that from condition (9) we get that

$$n - k \geq 3 + 2k \geq 2k\,. \tag{10}$$

Conditions (8) and (9) ensure that there is a non-zero probability that in the ancestral village a configuration $D_0(n,k)$ will arise such that there are k defectors, each surrounded by clusters of 2, 3, or 4 cooperators, since at least one in five individuals is a mutant defector (condition (8)), and at the same time there are more than $2k$ cooperators to form clusters between the mutants (condition (9) looked at through the prism of (10)). Then, there is no cluster of cooperators of sufficient size, namely 5, to sustain the cooperation strategy, and all farmers in the ancestral village will exhibit the trait D in the second generation after the appearance of mutants.

Additionally, in such a $D_0(n,k)$ configuration where each of k mutant defectors trades with two cooperators, there will be exactly $(n-k)-2k = n-3k$ cooperators among the settlers in the first generation after the mutation. Now, condition (9) ensures that there are at least three cooperators settling on the shores of the new lake. Since all possible configurations of farmers in the newly-settled village occur with a non-zero probability, it is possible that the settlers form two clusters, one of cooperators and one of defectors. And since the cluster of cooperators is at least of size 3, cooperation will survive in this descendant village. This concludes the proof. □

Two words of clarification are in order. First, our criterion for the survival of

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[8] This can be seen clearly upon rewriting conditions (8) and (9) as an interval $K_n = \left[\frac{n}{5}, \frac{n-3}{3}\right]$. A sufficient condition for the existence of a natural number k that jointly satisfies (8) and (9) is that the length of the interval K_n is at least one, that is, $\frac{n-3}{3} - \frac{n}{5} \geq 1$, which is equivalent to $n \geq 15$. (Obviously, because $\frac{n-3}{3} < n$, such a k also satisfies the requirement $k \leq n$.) Additionally, for $n = 12,13,14$ conditions (8) and (9) are jointly satisfied for $k = 3$.

cooperation (defined as the occurrence of the *Cooperation* event) does not tell us the prevalence or fraction of cooperating farmers in the total population of the settlements in a given generation. It may well be the case that in the setting of population growth with a random placement of the new farms, the expected ratio of cooperators to defectors is lower than in the no population growth setting. In addition, even the expected number of pure-defector settlements can be higher in the population growth setting than in the no population growth setting. Still, our interest is in the probability of survival of cooperation somewhere in the settlements and, as we have shown, this probability is higher in the population growth setting than in the no population growth setting.

Second, we do not address the question how population pressure or environmental carrying capacity might impact on the link between population growth and cooperation. There are good reasons for this. In our setting, the "fate" of cooperation is decided in a relatively short span of time.[9] Therefore, factors that may be associated with the depletion of resources and untenable farming space are unlikely to influence the rate of population growth or the payoffs from farming activities. Nor is it proven that population pressure depletes resources. Boserup (1981), Simon (1977, 1996), and others have persuasively argued that "necessity is the mother of invention," and marshaled powerful evidence that refutes the Malthusian theory. We thus elected to refrain from considering this issue within the confines of the present paper.

6 A link with evolutionary biology

The study of the relationship between demographic processes and the prevalence of altruism or the incidence of cooperative behavior has a long tradition in evolutionary biology.[10] However, in a number of respects our approach differs from that of evolutionary studies.

In his pioneering work, Hamilton (1964) modeled the influence of cooperative behavior between relatives, acting through so called *inclusive fitness* (a measure of fitness accounting for the "external" effects of the altruistic acts of relatives), on the spread of the

[9] This time span is given by the number of generations during which the defector strategy spreads in the ancestral village. This number of generations is smaller than the number of farmers in the ancestral village.
[10] For a comprehensive recent review see Lehmann and Rousset (2010).

gene that carries the predisposition of such behavior in the population.[11] The prevalence of cooperative behavior was connected to *viscosity*, that is, to the tendency of relatives to live in close proximity. Consequently, the success of the "cooperative gene" depends on the balance between losses from the competition for limited resources in the occupied area and gains from the altruistic behavior of relatives who share a similar genetic endowment.

Studies that followed the work of Hamilton (1964) looked more closely at viscosity and at different approaches to the spread of cooperating organisms (see, for example, Rogers, 1990; Taylor, 1992; and Gardner and West, 2006). However, the models in these studies did not account directly for population growth but rather assumed a constant or an infinite number of organisms, placing emphasis on the fraction of the organisms in the population that possess the "altruistic" gene.

More closely related to the population growth theme are the models of van Baalen and Rand (1998), Lehman et al. (2006), and Lion and Gandon (2009), who show that allowing a cluster of altruistic individuals to grow increases the probability of the spread of altruism. However, this positive effect on the prevalence of altruism is not brought about by growth of the overall population but is rather the result of the expansion of the local cooperating group; by dimming the competition between relatives the expansion unshackles the advantages of cooperative behavior.

The choice of strategy in our model does not emanate from a genetic endowment nor from a predisposition of the individual; rather, it is an outcome of rational choice based on information garnered through observation of the environment: individuals optimize subject to an informational constraint. A strategy of a parent does not translate automatically into the strategy of the offspring.

In our setting, although the procedure of settlement of the offspring might be reminiscent of the "budding dispersal" model of Gardner and West (2006), the payoff from cooperation and the choice of the cooperative strategy itself do not depend on a counterpart being a relative nor, for that matter, on any measure of family relatedness.

In sum, our approach is more suitable to analyze traits among human populations where strategies are selected on the basis of decisions, rather than being implanted as a consequence of a genetic endowment. In a way, we could say that our model "takes over"

[11] For a derivation of "Hamilton's rule" in a game-theory setting similar to the payoff structure used in the current paper, see Stark and Wang (2004).

altruistic individuals whose characteristics could have been formed in some evolutionary process, and studies the fate of cooperation in a growing population from a point in time at which the individuals' development allows a conscious choice of behavior that may just as well constitute a break with genetic predisposition.

7 Conclusions

Drawing on a simple setting of a community of farmers who live around a lake and who trade each with his two adjacent neighbors, we studied the consequences for the sustainability of cooperation of two scenarios: no population growth, and population growth. We found that population growth that results in the formation of new settlements strictly increases the probability that a defector strategy, introduced initially by mutations, will not spread to the entire community. That population growth is positively correlated with the sustainability of the cooperative habit in a community provides a new explanation for the advantages enjoyed by a growing population over a stagnant population. And indeed, since under a standard one-shot prisoner's dilemma payoff structure as employed by us a pure-defector community has the lowest per-capita payoff of all cooperator-defector configurations, we infer that in the specific environment studied by us, a growing population has some feature that supports future population growth prospects which is missing in a stagnant population.

We note that population growth will not impact differentially on the evolution of cooperation when the new settlements are mere replicas of the existing settlement, yet that it will be conducive to the evolution of cooperation when the pattern of settling "around the new lakes" is random. A fascinating topic of historical research would be a comparative study of the pattern of settlement of the first, "cloning" type, for example that of the medieval German settlements in Eastern Europe - the *Ostsiedlung* (Dickinson, 1945; Higounet, 1990) - replicating the structures of the towns of origin, and of the essentially second, random type, for example that of the British colonization of new lands in North America's Great Plains and Australia.[12] On a more abstract level, a study of the correlation between a measure of cooperation in societies and the rate of population growth of societies will be just as intriguing: is it the case that populations that were for some exogenous reason able to grow

[12] We thank Doris A. Behrens for drawing our attention to the German experience of settlement in Eastern Europe during medieval times.

faster developed norms of cooperation? What can be learned from a study of the historical developments of mankind? From anthropological accounts?

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Appendix: Payoffs and progeny

In this appendix, we attend to the possibility of a link between payoffs and reproductive outcomes; progeny could plausibly be increasing in payoffs, entailing a pattern of differential population growth rather than a uniform population growth.

Let *m*, the number of sons that a farmer has, be a function of the farmer's payoff: $m(\omega) \in \mathbf{N}$ for $\omega \in \Omega$, where $\Omega \in \{2S, 2P, S+R, T+P, 2R, 2T\}$ is the set of possible payoffs from farming-cum-trading for which assumptions (1) and (2) hold,[13] and let

$$m(\omega_2) \geq m(\omega_1) \text{ for } \omega_2 > \omega_1.$$

We assume (i) that each farmer has at least one son, that is, $m(2S) \geq 1$; (ii) that if a farmer has exactly one son, this son takes over his father's farm; and (iii) that a cooperator farmer surrounded by two cooperators has at least two sons, that is, $m(2R) \geq 2$.

Since the number of settler sons can be different from (or may not be a multiple of) the number of farms in the ancestral village, we need to specify further the process of settling around the new lake(s). Let then the number of farms in the ancestral village, *n*, also denote the maximal number of farms around a lake, namely *n* delineates the "carrying capacity" of a single lake. Then, a generation of sons from a single ancestral village settles around the minimal number of lakes that is sufficient to accommodate them all. The process of settlement around the new lake(s) takes place in a uniformly random fashion, namely, all the settlers have equal probability of occupying every available farm.[14]

When a lake is settled by fewer farmers than the maximal "carrying capacity" of the lake, each farmer fences up the additional space for his farm, such that future generations of settlers cannot join an already-settled lake. Since farming-cum-trading requires contact between neighbors, larger farms imply also longer distances, on average, to be covered during the joint activities of neighbors. Since the advantage of larger farms is offset by the disadvantage of higher costs of communication/cooperation between the farmers, the payoffs can be held the same as in the preceding settings.

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[13] We note that assumptions (1) and (2) do not yield a complete ordering of the Ω set; only that $2S < 2P < T+P < 2R < 2T$, that $2S < S+R$, and that $S+R < T+P$. This incompleteness has no bearing, however, on the discussion that follows.

[14] We do not specify in additional detail how the space around the newly-settled lakes is organized into farms because this is not crucial for our argument. For example, settlement could take place so as to fill all lakes but one to their "carrying capacity" or, alternatively, such that the number of farms around each settled lake is the same.

The remaining specification of the model (the choice of $\left(n, k, D_0(n,k)\right)$, the independence of random distributions, and so on) is the same as in section 4.

In this revamped setting, the results presented in section 4 continue to apply. To see this, note, first, that assumptions (i) and (ii) ensure that the evolution of strategies in the ancestral village is the same in the differential fertility setting as in the no population growth setting. Therefore, if cooperation is preserved in the no population growth setting, it will also be preserved in the population growth setting, at least in the ancestral village. Second, if $n=9$, $k=2$, and the initial placement of mutant defectors is as per configuration D_0^{IV} (cf. Figure 3), assumption (iii) ensures that there will be at least three settlers who will choose the cooperation strategy, and at least two settlers who will choose the defection strategy. Then, in the course of the settlement of the new village(s), there is a strictly positive probability that the settling arrangement will yield an "island" of at least three cooperators, surrounded by defectors who receive a payoff of $T+P$ from trading with a cooperator and with a defector, a configuration that serves to guarantee sustainability of the cooperation strategy in the new settlement, even if in the ancestral village cooperation is "doomed." It follows then that in the differentiated population growth setting, the probability of occurrence of the *Cooperation* event (survival of cooperation) is higher than in the no population growth setting.

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