Multilevel selection in causal models: the multiplicative nature of evolutionary and probabilistic selection processes as the general driver for the irreversible emergence of cooperation and specialization.*

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Abstract

To explain why major evolutionary transitions are so common in the history of life we need to find the causes that systematically generate the irreversible emergence of cooperation and specialization. For this purpose it is necessary to consider selection at both the individual and group level. The co-author of the concept of major evolutionary transitions (Szathmáry) recently proposed to analyze the evolution of populations subject to multilevel selection by means of Bayesian hierarchical models, making use of the isomorphism between evolutionary theory and Bayesian inference. However, the proposal remains open.

In this paper we specify a probabilistic causal model, in which individuals are affected by the environment and by the social behaviors of cooperation and defection of their context. Even under this minimal set of hypotheses, where we consider *unconditionally* cooperative individuals who generate a common good that can be exploited by defecting individuals without receiving some kind of punishment in return (e.g. end of cooperation), probabilistic inference shows that cooperative individuals are favored by multilevel selection. In addition, we show that as soon as cooperation emerges, an advantage in favor of specialist strategies appears. Since the specialist strategies are individually poorly adapted to the environment, an irreversibility of the evolutionary transition is created.

The reason why an advantage in favor of cooperation and specialization arises in our simple causal model is due to the multiplicative (non-ergodic) nature of probability theory and its isomorphism with evolutionary theory.

1 Introduction

In the last third of the history of the Universe, sometime around 4 billion years ago, a simple form of matter organization capable of self-replication appeared on Earth. The growth of these lineages followed multiplicative and noisy processes: sequences of survival and reproduction rates. The errors produced during replication diversified the life forms, and the growth rates of the different strategies favored those better adapted to the environment. From that moment until now, life has acquired an extraordinary complexity, both in terms of cooperation and specialization.

The current complexity of life is the consequence of a series of evolutionary transitions in which entities capable of self-replication after the transition become part of higher level cooperative units [2–4]. Some of the paradigmatic transitions are: from prokaryotic to eukaryotic cells; from protozoa to animals, plants and fungi (cell differentiation and emergence of multicellular organisms); and from solitary individuals to societies. How to explain this permanent tendency of life in favor of cooperative and specialization?

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*`https://github.com/glandfried/transitions/releases/download/doc1.0.1/landfried-transitions.pdf`
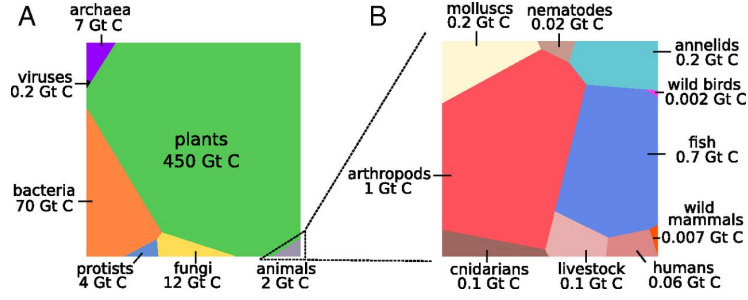
Figure 1: Distribution of biomass on Earth estimated by Bar-On et al. [1].

In evolution it is said that the growth of a lineage over time, $\omega(t)$, is governed by a stochastic sequence of survival and reproduction rates $f(\cdot)$ dependent on a random environment e,

$$\omega(T) = \prod_t^T f(e(t)) \approx g^T \tag{1}$$

where $e(t)$ represents the state of the environment at time t and g represents the characteristic growth rate when T is sufficiently large. For example, suppose nature flips a coin, if it comes up heads the population reproduces 50% and if it comes up tails it survives 60%.

$$f(e) = \begin{cases} 1.5 & e = \text{ Head} \\ 0.6 & e = \text{ Tail} \end{cases} \tag{2}$$

A similar example was proposed by Lewontin and Cohen (1969) [5], in which the population reproduces 70% or survives 50%. Different strategies s can be described with different functions $f_s(e)$. According to the standard model of evolution, known as *replicator dynamic* [6], the change in the proportion of a strategy in the population, x_s, is determined by its characteristic growth rate g_s,

$$x'_s = \frac{x_s g_s}{\sum_i x_i g_i} \qquad \text{(Replicator dynamic)}$$

where the denominator acts as a normalization constant. But, which is the characteristic growth rate g? Much of the evolutionary literature bases its analysis on populations of infinite size and considers that the correct estimate is obtained by the expected value, $g^t = \langle \omega \rangle_t$.

$$\langle \omega \rangle_t = \sum_{\omega \in \Omega_t} \omega \cdot P(\omega) \tag{3}$$

Where Ω_t is the set of all possible resource trajectories at time t, and $P(\omega)$ is the probability that the resource state ω occurs. In the coin example, the expected value in the first two time steps is,

$$
\begin{aligned}
\langle \omega_e \rangle_1 &= 1.5 \cdot \frac{1}{2} + 0.6 \cdot \frac{1}{2} = 1.05 \\
\langle \omega_e \rangle_2 &= 1.5^2 \cdot \frac{1}{4} + 2(0.6 \cdot 1.5 \cdot \frac{1}{4}) + 0.6^2 \cdot \frac{1}{4} = 1.05^2
\end{aligned}
\tag{4}
$$

That is, the estimated growth rate according to the expected value is 5% for each time step, $\langle \omega \rangle_t = 1.05^t$. And indeed that is what happens with the average of several individual trajectories, $\omega(t)$.
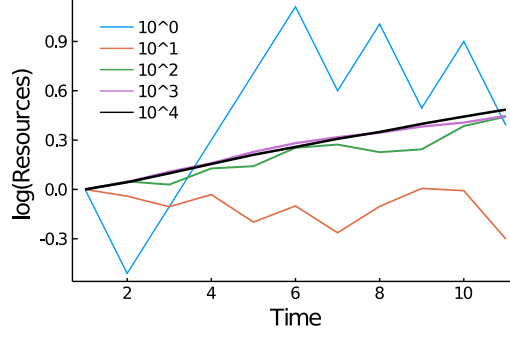
Figure 2: Average of individual resources over time for different population sizes, in log scale. As we increase the size of the population, the average approaches the expected value of 1.05^t.

However, the expected value does not represent what happens to the agents over time. Individually, all the trajectories lose in the long term at a rate close to 5%. The trajectories observed in figure 3a are variable, but the longer we observe the system the smoother these lines become (figure 3b).
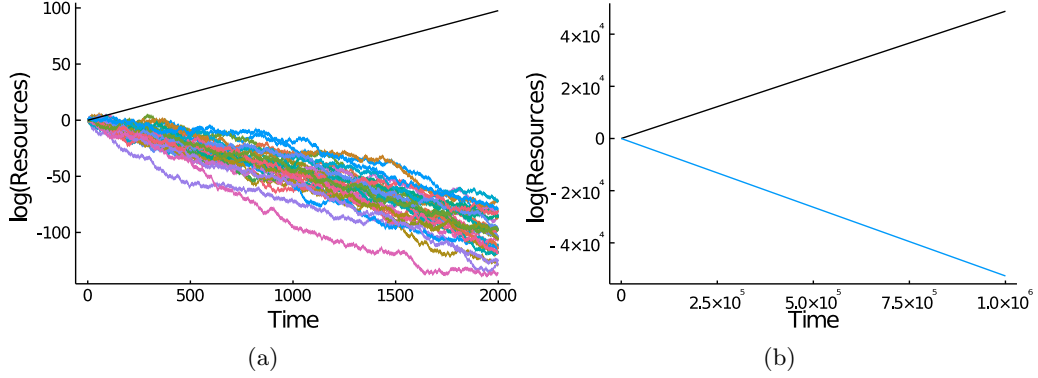

(a)

(b)

Figure 3: The black line represents the expected value. Figure 3a: size of individual resources over time, $\log(\omega(t))$. Figure 3b: given enough time, all individual trajectories stick to the blue line.

When the individual trajectories can be described by the expected value of the system states, then the process is said to be ergodic [7]. However, the conditions are very restrictive, and are not fulfilled in the case of multiplicative processes. To compute the growth rate g, we first express the product as follows,

$$\omega(T) = \prod_{t=1}^{T} f(e(t)) = f(\text{head})^{n_1} f(\text{tail})^{n_2} \tag{5}$$

where n_1 and n_2 represents the number of occurrences of $f(\text{head})$ and $f(\text{tail})$, with $n_1 + n_2 = T$. In the limit, $T \to \infty$ all individual trajectories will be determined by the same growth rate g.

$$\lim_{T \to \infty} \omega_e(T) = g^T$$

$$\left(\lim_{T \to \infty} \omega_e(T) \right)^{1/T} = g \tag{6}$$

$$\lim_{T \to \infty} f(\text{head})^{n_1/T} f(\text{tail})^{n_2/T}$$

Where the frequencies $\frac{n_1}{T}$ and $\frac{n_2}{T}$ in the limit $T \to \infty$ are equal to the probabilities of the environmental states p. Therefore, the growth rate is,

$$g = (1.5 \cdot 0.6)^{1/2} \approx 0.95 \tag{7}$$

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This formula, which allows computing the long-term growth rate of individual trajectories, has previously been used in the evolution literature under the name *geometric mean* [8]. The geometric mean is always less than the arithmetic mean (or expected value). This is because in multiplicative processes the physical impacts of losses are usually stronger than those of gains. In an extreme case, a single zero in the product is enough to generate an extinction.

1.1 Cooperation

As a consequence of the non-ergodicity of multiplicative processes, fluctuations have a negative effect on individual growth rates. Yaari-Solomon [9] and Peters-Adamou [10] (hereinafter Yaari and Peters) study the consequences that the following cooperative strategy has on the agents' growth rate.
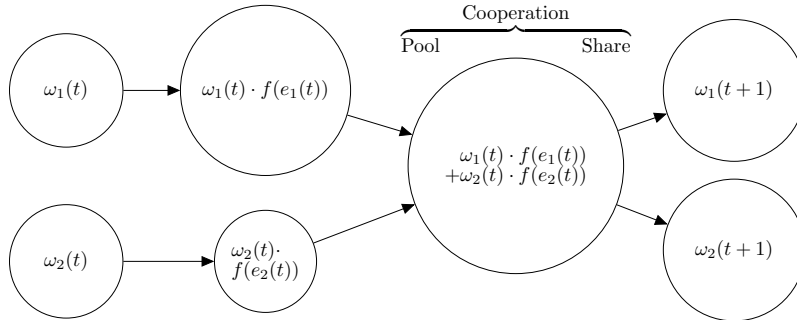

Figure 4: The agents start with the same initial resources, update them independently according to the equation 2, and finally redistribute it in equal parts.

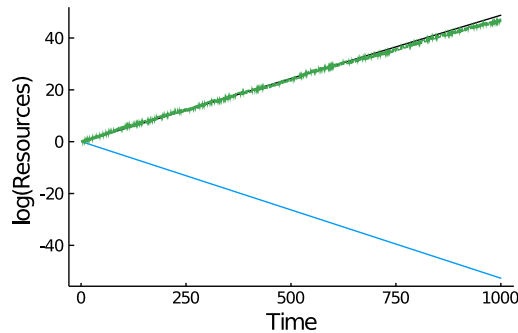In Figure 5 we show the trajectory of an agent in a cooperating group of size 33. Fully

Figure 5: The resources of an individual in a cooperative group of size 33 (green line) approaches the arithmetic mean (the black line below the green line). As a visual reference we show the geometric mean that drives the growth rate of individuals (blue line).

cooperative groups reduce their fluctuations, generating an increase in the growth rate of all their members.

Multilevel selection   To demonstrate the evolutionary advantage of cooperation in the presence of defection it is necessary to consider selection at both the individual and group level. The co-author of the concept of evolutionary transitions (Szathmáry [3, 4]) recently proposed to analyze the evolution of populations subject to multilevel selection by means of Bayesian hierarchical models [11], making use of the isomorphism between evolutionary theory and Bayesian inference [12, 13]. However, this work does not provide any model that performs multilevel selection, so the proposal remains open. In this paper we demonstrate the evolutionary advantage of

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cooperation in the presence of defection using a probabilitic causal model representing evolution under multilevel selection. To the best of our knowledge, our work would be the first to develop a Bayesian hierarchical model to solve an evolution problem under multilevel selection.

2 Methodology

In this section we present the isomorphism between probabilitic and evolutionary theory. In section "Results" we will prove the evolutionary advantage of cooperation, specialization and their irreversibility using a Bayesian hierarchical model with a causal interpretation representing evolution under multilevel selection.

2.1 Probability theory and causal models

Probability theory is currently the most widely used approach for computing uncertainty. Its rules have been derived from several axiomatic systems, conceptually distinct and independent of each other [14], which is one of the strong points in its favor. But perhaps more importantly, its strict application ensures maximization of uncertainty given empirical and formal information (data and causal models) [15], source of validation for empirical propositions.

Probability theory can be summarized in two rules: the sum rule and the product rule. The product rule allows describing multidimensional models through causal mechanisms: belief distributions on each effect, given the hidden values of its causes (conditional probabilities). The sum rule, on the other hand, predicts the behavior of a variable (marginal probabilities) with the contribution of all the hypotheses of the multidimensional causal model. Graphical models are a well-established tool in probability because they: 1. provide an intuitive language to unambiguously express all hypotheses, 2. reduce the dimensionality of the joint probability distribution, 3. and allows to perform inference efficiently through the sum-product algorithm [16]. To use the graphical models no causal interpretation is required, in fact the conditional probabilities can be expressed in any order.

There are several advantages when conditional probabilities are defined on the basis of causal interpretations [17]. Science elaborates its theories on the basis of causal stories: stable and autonomous mechanisms that induce conditional probabilities between causes and effects. In this sense, justifying conditional probabilities on the basis of a causal story is a more natural way of expressing what we know or believe about the world. In addition, causal interpretation also modularizes conditional probabilities: eventual changes in any of the causal mechanisms locally affect the topology of the Bayesian network, allowing the effect of external interventions to be predicted with a minimum of additional information. For these reasons, in this paper we will express the graphical models in terms of causal relationships.

2.2 Isomorphism between evolutionary and probability theories

From the product rule, we immediately obtain the Bayes' theorem, with which we can compute the uncertainty about the hidden hypothesis space given the data and the model:

$$\underbrace{P(\overbrace{\text{Hypothesis}_i}^{\text{Hidden}} | \overbrace{\text{Data}}^{\text{Observed}})}_{\text{Posterior}} = \frac{\overbrace{P(\text{Data} | \text{Hypothesis}_i)}^{\text{Likelihood}} \overbrace{P(\text{Hypothesis}_i)}^{\text{Prior}}}{\underbrace{P(\text{Data})}_{\text{Evidence or prior prediction}}} \tag{8}$$

where the only free variable is the hypothesis i. The data and the model are fixed. The likelihood and the evidence are both probabilities of the data , so they can be seen as predictions. When the data is a discrete variable, predictions always take values between 0 and 1. Unlike the likelihood, which makes a different prediction for each hypothesis, the evidence averages all the predictions,

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weighted by the prior probability of the hypotheses,

$$P(\text{Data}) = \sum_i P(\text{ Data } | \text{ Hypothesis}_i) P(\text{Hypothesis}_i) \tag{9}$$

The evidence then functions as a normalization constant. Therefore, the likelihood is the only factor that updates the probability distribution of the hypothesis, so the posterior is just the prior probability that is not filtered by the likelihood.

Recently, an isomorphism has been identified between the fundamental equations of evolutionary theory (replicator dynamic) and probability theory (Bayes theorem) [12,13]. The isomorphism is obvious when we link the probability of the hypotheses to the proportion of the strategies in the population and the likelihood to their fitnesses,

Bayes theorem	Replicator dynamic
Prior $P(H)$	Old distribution of strategies x_s
Likelihood $P(D|H)$	Fitness $f_s(e)$
Posterior $P(H|D)$	New distribution of strategies x'_s
Evidence $P(D)$	Population mean fitness $\sum_s x_s f_s(e)$

Based on this isomorphism, Czégel, Zachar and Szathmáry recently proposed to analyze the evolution of a population subject to multilevel selection through hierarchical Bayesian modeling [11]. To do so, they display a series of graphical models without specifying the conditional probabilities.
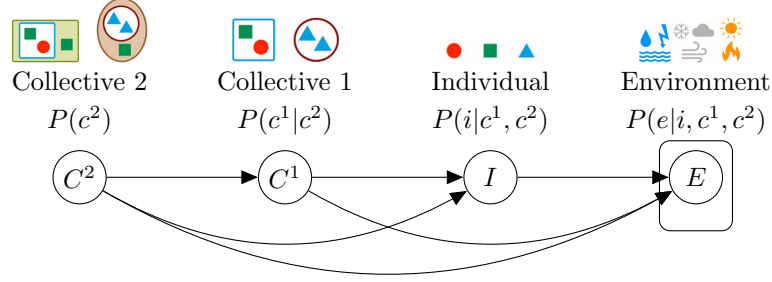

Figure 6: Model proposed by Czégel, Zachar and Szathmáry [11] to represent multilevel selection. The box represents repetition of the variable. Usually uppercase letters are variable names, and the lowercase letters are specific values.

The validity of this model is trivial as the product rule always allows the following decomposition,

$$P(e, i, c^1, c^2) = P(e|i, c^1, c^2)P(i|c^1, c^2)P(c^1|c^2)P(c^2) \tag{10}$$

However, the model does not express the causal relationship between the variables. This is evident in all conditional probability distributions. At one extreme, the level 2 collective C^2, which is composed of both the level 1 collective and individuals, appears in the model as an independent variable. At the other extreme, the environment E, which is usually considered in evolutionary causal models as an independent random variable, appears in this model as dependent on individuals and collectives. Conversely, all collectives and individuals appear independent of the environment.

2.3 A basic causal model: advantage for generalist individuals

The basic causal model we present here serves to introduce the methodology we will use in section "Results", and the conclusion we will draw from it will be of interest later on. In them, the binary environmental states depend on a probability p (for example p is the probability of the coin coming up heads).

$$P(e) = p^e(1-p)^{(1-e)} \tag{11}$$

While we are free to propose any set of strategies, we will consider only those that allocate a limited resource R among the binary states of the environment, with $0 \le s \le R$. The strategy proposed by Lewontin-Cohen is $s = 1.7$ with $R = 2.2$, and the strategy proposed by Peters is $s = 1.5$ with $R = 2.1$. To express all this strategies with a single parameter, we will work only with the family of fitnesses in which $R = 1$, $f(s, e)$.

$$f(s, e) = \begin{cases} s & e = 1 \\ 1 - s & e = 0 \end{cases} \tag{12}$$

Now, all strategies lie between 0 and 1: the strategy $s = 1.5/2.1 \approx 0.71$ is the one proposed by Peters, and the strategy $s = 1.7/2.2 \approx 0.77$ is the one proposed by Lewontin-Cohen. For other ways of defining this same function, see Yaari-Solomon equation 11 [9]. To define the probability of the strategies given the environment, $P(s|e)$, we need the set of strategies to integrate 1. Let's say, for now, that the probability of the strategy is proportional to its fitness,

$$P(s|e) \propto s^e (1-s)^{1-e} = f(s, e) \tag{13}$$

This allows us to partially define a graphical model with a causal interpretation, in which the

Environment: $\boxed{E_t}$ $P(e) = p^e(1-p)^{(1-e)}$
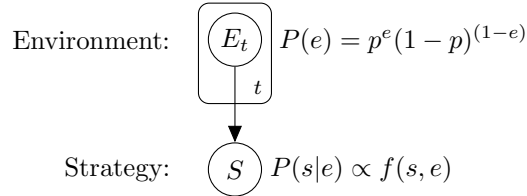
Strategy: $\bigcirc{S}$ $P(s|e) \propto f(s, e)$

Figure 7: Causal model in which the environment affects individuals.

environment is an independent random variable and the strategies depends on the observed states of the environment. The result of the posterior will indicate the evolutionary stability of the strategies.

Suppose that the environmental states are generated with probabilities $P(E = 1) = 0.71$ and $P(E = 0) = 0.29$. In Figure 8 we show how the posterior of the strategies changes as we add observations to the model.

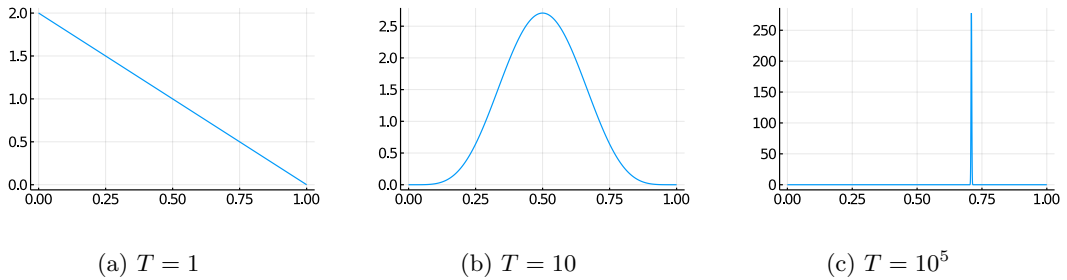(a) $T = 1$ (b) $T = 10$ (c) $T = 10^5$

Figure 8: Posterior probability of strategies as time progresses ($T = 1$, $T = 10$, $T = 10^5$).

The evolutionary process selects the most generalist individual strategy of all, the one that distributes resources in the same proportion as the states of the environment are generated. When the environment generates the states with probability $p = 0.71$, then the best adapted strategy is $s = 0.71$. The selection of individual strategies, now intuitive, will be different and perhaps counter-intuitive when we incorporate the possibility of cooperation and defection into the model.

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3 Results

In this section we will extend the causal model proposed in section "Methodology" by incorporating unconditionally cooperative behaviors, such as the one presented in the "Introduction" section, including defecting behaviors (which receive the benefit of cooperation without contributing to it).

3.1 Extended causal model

Individuals are spatially distributed and can interact only with members of the same region. Suppose we have regions of N individuals in which n are cooperators and $N - n$ defectors. Then, there are $N + 1$ types of possible regions, from $n = 0$ (all defectors) to $n = N$ (all cooperators). Then, if each individual belongs to a single region we need $M = N(N + 1)$ total individuals, $i \in \{1, \ldots, M\}$. Individuals i are characterized by three attributes: the region to which it belongs, $\texttt{region}(i) = i \texttt{ div } N$; and if their social behavior is cooperative, $\texttt{coop}(i) = i \bmod N < \texttt{region}(i)$ (the first n individuals in the region are cooperators and the rest defectors); and the strategy s_i they use to allocate resources $f(s, e)$ (equation 12). By combinatorics, it will be more likely a priori that individuals will inhabit mixed regions.

$$P(i) = \frac{1}{N} \mathcal{B}(\texttt{region}(i) | N, 0.5) \tag{14}$$

where the binomial distribution $\mathcal{B}$ gives more weight to individuals from mixed regions, the parameter 0.5 indicates a uniform prior between cooperating and defecting social behaviors, and the factor $\frac{1}{N}$ indicates that all individuals in the same region start with the same initial resources. As we have seen in the section "Methodology", the probability of the environmental states is,

$$P(e) = p^e (1 - p)^{1-e} \tag{15}$$

but now at each time t we have a vector $\vec{e}$, in which the $i-$th environmental state influences the $i-$th individual,

$$P(i | \vec{e}) = \frac{s_i^{e_i} (1 - s_i)^{1-e_i}}{\sum_j s_j^{e_j} (1 - s_j)^{1-e_j}} \propto s_i^{e_i} (1 - s_i)^{1-e_i} \tag{16}$$

Now, however, the agents are also influenced by the resources of the other agents at the previous time,

$$P(i^{t+1} | i^t) = \begin{cases} 1/N & \texttt{coop}(i^t) \wedge (\texttt{region}(i^{t+1}) = \texttt{region}(i^t)) \\ 1 & \neg\texttt{coop}(i^t) \wedge i^{t+1} = i^t \\ 0 & \texttt{else} \end{cases} \tag{17}$$

Cooperating individuals divide the wealth equally with members of the same region, and defecting individuals retain all their wealth. Finally, the groups are made up of members from each region, $P(g | i) = \mathbb{I}(\texttt{region}(i) = g)$, the indexing function which is 1 when individuals belong to region g and 0 otherwise. In short, at each time t the environment influences individuals, and individuals influence the groups of their own time and the individuals of time $t + 1$. This model has 3 hyperparameters: the vector of strategies $\vec{s}$, the probability of the environment p, and the size of the groups N.

The evolutionary problem we are interested in is the selection of cooperative individuals given the environment within each group (level 1), $P(\texttt{coop}(i^T) | \vec{e}^1, \ldots, \vec{e}^{T-1}, g)$, the selection of groups given the environment (level 2), $P(g^T | \vec{e}^1, \ldots, \vec{e}^{T-1})$, and selection of cooperative individuals given the environment for all groups (multilevel), $P(\texttt{coop}(i^T) | \vec{e}^1, \ldots, \vec{e}^{T-1})$. The multilevel selection is obtained by integrating the product of level 1 and 2 selections,

$$\underbrace{P(\texttt{coop}(i^T) | \vec{e}^1, \ldots, \vec{e}^{T-1})}_{\text{Multilevel selection}} = \sum_{g=0}^{N} \underbrace{P(\texttt{coop}(i^T) | \vec{e}^1, \ldots, \vec{e}^{T-1}, g)}_{\text{Level 1 selection}} \cdot \underbrace{P(g^T | \vec{e}^1, \ldots, \vec{e}^{T-1})}_{\text{Level 2 selection}} \tag{18}$$
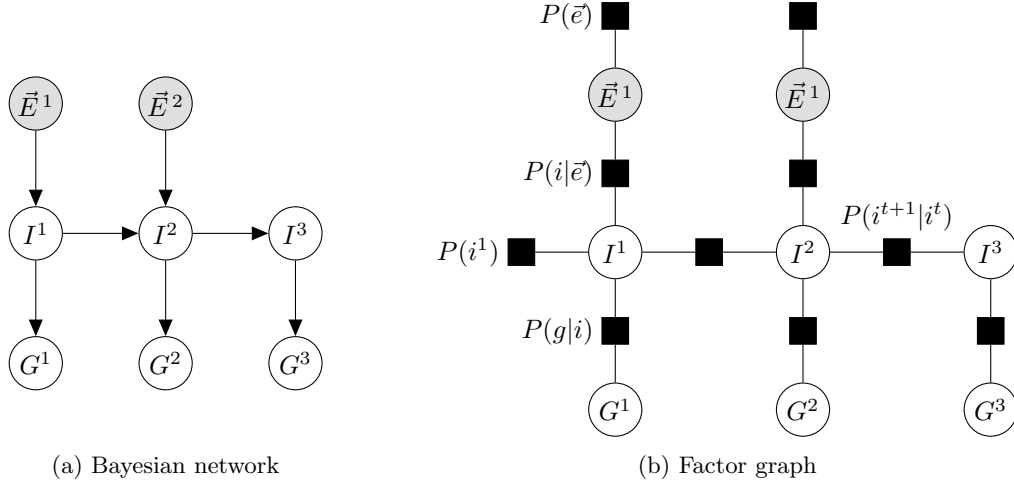
(a) Bayesian network   (b) Factor graph

Figure 9: Hierarchical model. Figure 9a: the probabilistic dependencies arising from the multilevel causal model. Figure 9b: the factor graph induced by the Bayesian network, which will be used to apply the sum-product algorithm. The gray variables are observed.

An alternative way to compute the multilevel selection marginal (Eq. 18) is by integrating the probability of all cooperating individuals given the environments

$$P(\texttt{coop}(i^T)|\vec{e}^1,\ldots,\vec{e}^{T-1}) = \sum_{j=1}^{M} P(I^T = j|\vec{e}^1,\ldots,\vec{e}^{T-1})\mathbb{I}(\texttt{coop}(j)) \tag{19}$$

where $\mathbb{I}(\cdot)$ is the indicator function. Then, the posteriors of individuals are (a detailed mathematical proof can be found in the appendix section "Posteriors of individuals in the extended causal model")

$$P(k|\vec{e}^1,\ldots,\vec{e}^T) = \begin{cases} P(k)\prod_{t=1}^{T}\sum_{j}^{\texttt{partners}(r)}\frac{1}{N}P(j|\vec{e}^t) & \texttt{coop}(k) \\ \left(P(k)\prod_{t=1}^{T}P(k|\vec{e}^t)\right) + \left(\sum_{t=1}^{T}P(c|\wedge_{q=1}^{t}\vec{e}^q)\prod_{q=t+1}^{T}P(k|\vec{e}^q)\right) & \neg\texttt{coop}(k) \end{cases} \tag{20}$$

where $r = \texttt{region}(k)$ is the region to which individual k belongs, $\texttt{partners}(r)$ is the set of cooperating individuals in region r, and c is a cooperative individual belonging to that specific region, $c \in \texttt{partners}(r)$.

3.2   The multiplicative nature of evolutionary and probability theories

Even if our causal model does not assume any kind of process to update resources, the result of the inference is proportional to the resources obtained through a multiplicative process. All the assumptions of our model are made explicit in the Bayesian network in Figure 9. Individuals are affected just by the environment and by the social behaviors of cooperation and defection of their context. However, our probabilistic causal model and the multiplicative process discussed in the introduction are equivalent. A detailed mathematical proof can be found in the appendix section "Isomorphism of the extended causal model". In general, the posterior of individuals is no more than the proportion of resources they manage (all steps are described in the long article).

$$P(k|\vec{e}^1,\ldots,\vec{e}^T) = \frac{\omega_k(T)}{\sum_j \omega_j(T)} \tag{21}$$

The proportionality between the posterior probability of individuals and the trajectories of resources studied in section "Introduction" allows us to work with both expressions interchangeably.

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The multiplicative updating of the probabilities of individuals, which arises naturally from applying the rules of probability to the causal model, is in line with the long-established idea in evolutionary theory that the growth of lineages follow multiplicative processes [8, 18]. This coincidence is an additional support to the hypothesis of isomorphism between evolutionary and probability theories, previously identified between their fundamental equations: the Bayes theorem and the replicator dynamic [12, 13].

3.3 Commons dilemma

In the last few decades evolutionary biology has begun to adopt the analogy of the "tragedy of the commons" [19]. This concept contains the idea that the commons has a payoff structure isomorphic to the N-player prisoner's dilemma [20]. In a two-player prisoner's dilemma, cooperating implies a cost c for the other person to receive a benefit b, with $b > c$, and defecting means refusing to cooperate and carries no cost.

$$
\begin{array}{cc}
 & \begin{array}{cc} C & D \end{array} \\
\begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b - c & -c \\ b & 0 \end{pmatrix}
\end{array}
\tag{22}
$$

Players gain more if they opt for mutual cooperation than for mutual defection, since $b - c > 0$. However, regardless of what the other player does, it is better not to cooperate: if my partner defects, it is better for me to defect than to cooperate, since $0 > -c$; if my partner cooperates, it is still better for me to defect than to cooperate, since $b > b - c$. This creates a dilemma: although mutual cooperation is a preferable outcome, no individual has the incentive to cooperate.

If our causal model had a payoff structure isomorphic to the prisoner's dilemma, then defectors would have a higher growth rate than cooperators. However, the first defector from an entirely cooperative group obtains a lower growth rate than before defecting. In the figure 10 we can observe the trajectories of the resources, equivalent to the proportional posterior (see previous section), of the individuals that are in a group of size 100. The resources of the first individual defector (blue
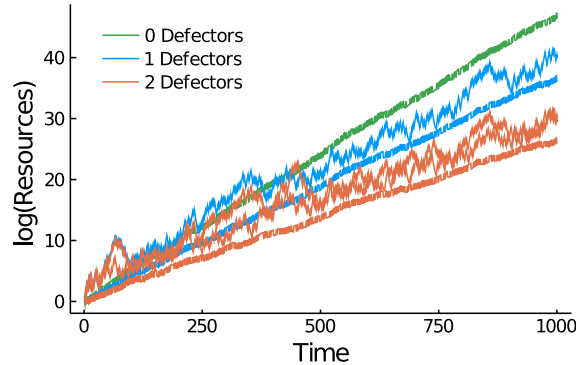

Figure 10: The colors represent groups of size 100 with 0, 1 and 2 defectors. The curves of the individual defectors are those at the top of each of the groups.

group with 1 defector), is below the resources of the individuals in the fully cooperative group (green group with 0 defectors). The reduction in resources occurs even for the second individual who changes from cooperative to a defective behavior.

Defecting, instead of increasing the growth rate of the defective individuals, reduces it. In other words, the commons does not have the structure of the prisoner's dilemma, as is usually claimed in the literature. Let us calculate the payoff matrix arising from the cooperative causal model. We want to estimate the temporal growth rate of the posteriors,

$$
\frac{P(k|\vec{e}^1, \dots, \vec{e}^T)}{P(k)} \approx g(k|\vec{s}, p, N)^T
\tag{23}
$$

where the approximation is an equality when time tends to infinity, $\lim_{T\to\infty}$. The growth rate depends on the hyperparameters of the model, $\vec{s}$, p and N. Here we will only consider models in which all individuals have the same strategy s. We will solve this problem by cases, depending on whether the behavior is cooperative, g_C, or defective, g_D, for different social contexts $g^n_{[\cdot]}(k|\cdot)$, where n represents the number of cooperators with which the individual k interacts (excluding k). A detailed mathematical proof can be found in the appendix section "Growth Rates".

In figure 11a we show the proprotional growth rate as a function of the number of defectors in a group of size 1000. In Figure 11b we rescale the proportional growth rate by a factor $R = 2.1$, and we see that it overlaps over the trajectories of resource presented in Figure 10. Note that the

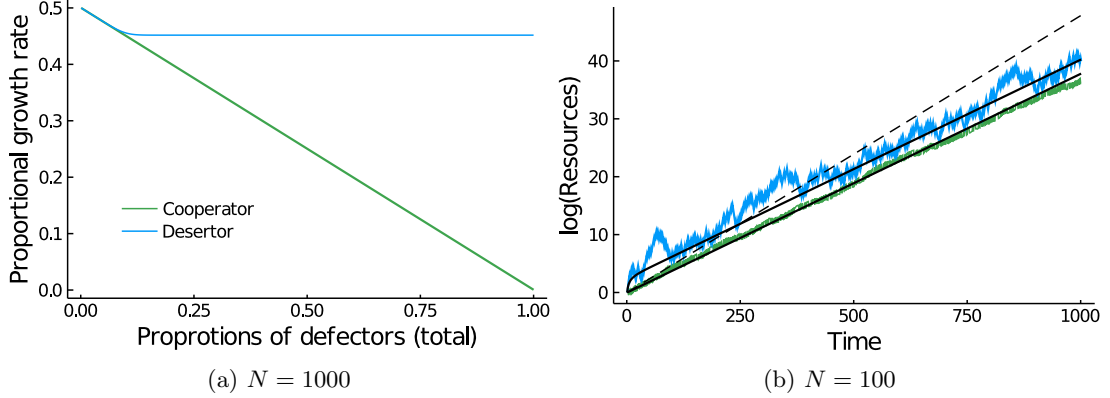(a) $N = 1000$ (b) $N = 100$

Figure 11: Figure 11a: proportional growth rate in mixed groups of size 1000. Figure 11b: trajectory of the resources of a defector (blue) and cooperator (green) in a group of size 100 with a single defector (see figure 10), the black curves are the estimates growth, and the dotted black curve are the resources of cooperators in regions without defectors.

growth rate of the individual defector is higher than that of the cooperators only in the first few time steps, which places the defectors in a better relative position. But regardless of the size of the group, mutual cooperation always offers the highest growth rate, and the first defection always produces a drop in all growth rate, reducing even the growth rate of the individual defector. The following matrices summarize the growth rates of cooperators and defectors (rows), for different numbers of defectors in the social context (columns), in groups of size 2 (left) and size 16 (right).

$$g^n_{[\cdot]}(k|s = 0.71,\, p = 0.5,\, N = 2)$$

$$\propto \begin{array}{c} \\ C \\ D \end{array} \begin{array}{cc} n=1 & n=0 \\ \left(\begin{array}{cc} 0.475 & 0.226 \\ 0.452 & 0.452 \end{array} \right) \end{array}$$

$$g^n_{[\cdot]}(k|s = 0.71,\, p = 0.5,\, N = 16)$$

$$\propto \begin{array}{c} \\ C \\ D \end{array} \begin{array}{cccc} n=15 & n=14 & n=13 & n=12 \\ \left(\begin{array}{cccc} 0.497 & 0.466 & 0.435 & 0.403 \\ 0.466 & 0.452 & 0.452 & 0.452 \end{array} \right) \end{array}$$

The first agent that unilaterally "decides" to defect will reduce its own growth rate. Similarly, when all (or many) of the group members are defectors, the first agent who unilaterally "decides" to cooperate will also reduce his own growth rate. This means that the payoff matrix is not isomorphic to a prisoner's dilemma. In fact, the payoff structure of the left-hand matrix is known as stag-hunt.

Conclution 1 (Commons are not prisoner's dilemmas)**.** Without penalties, defector strategies negatively affect their own long-term growth rate because their own behavior increases the fluctuations of the random variable on which they depend.

In all cases, the highest growth rate is obtained by mutual cooperation.

3.4 Selection of level 1, level 2 and multilevel

In the previous section we have seen that unilateral defection reduces the growth rate of the defectors themselves compared to what they could have through mutual cooperation. However, the growth rate of cooperators is reduced to a greater extent. This means that the defectors always have a better relative position than the cooperators in their own group. Therefore, evolution will favor defector behaviors through individual selection (level 1). In Figure 12 we can see the posterior of cooperating and deserting individuals in regions with 1 defector in groups of size 2 and 16. Defector behaviors can invade within groups of size 2, as the posterior of the defectors
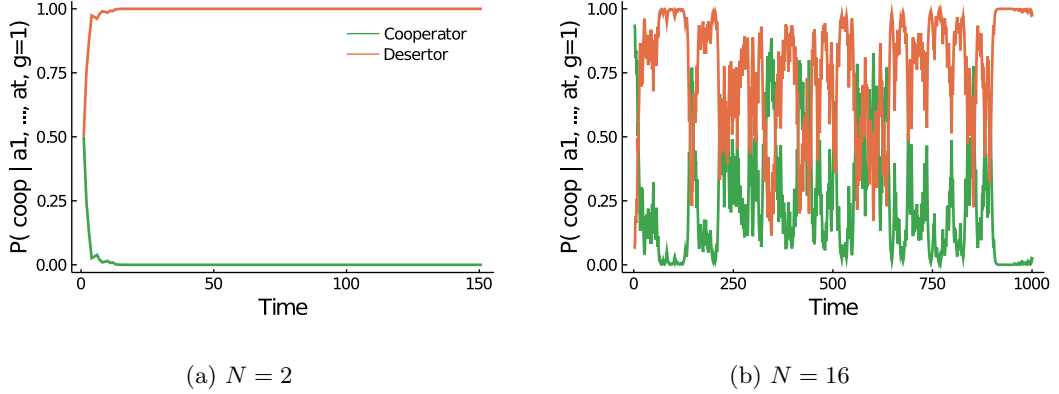

(a) $N = 2$ (b) $N = 16$

Figure 12: Posterior of cooperator/defector social behaviors within a region with 1 defector in groups of size 2 and 16.

quickly stabilizes at 1. However, defector behaviors cannot invade within groups of size 16, as the posterior of both behaviors never stabilizes at 0 and 1.

Although defectors may invade groups of size 2, regions that remain fully cooperative will have a great advantage over mixed regions because the growth rate of mutual cooperation is always the highest one. Therefore, evolution will favor fully cooperative groups through group selection (level 2). In figure 13 we see the posterior of the groups, of size 2 and 16. Note that the prior of the
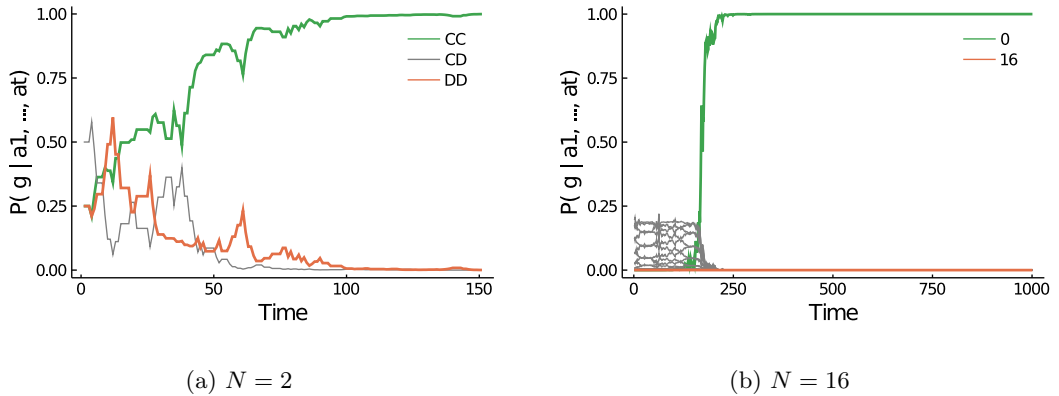

(a) $N = 2$ (b) $N = 16$

Figure 13: Group selection (level 2) of size 2 and of size 16. The gray lines represent the posterior of mixed groups.

entirely cooperative group is 0.25 in groups of size 2 and approximately $\mathcal{B}(0|N = 16, 0.5) \approx 0$ for groups of size 16. The choice of a prior that rejects homogeneous populations causes the advantage of the cooperating group to take time to stabilize. With a uniform prior, the advantage of the fully cooperative group would be seen immediately. In any case, since the prior of homogeneous

populations is never zero and the growth rate of the fully cooperative population is higher than the rest, there is always a time t at which the posterior of the fully cooperative group will be higher than the others. The larger N is, the closer the cooperators are to the arithmetic mean, but the more weight individuals from mixed regions receive. Given a maximum time, the optimal group size will always be finite, which is reasonable in evolutionary terms.

When there is level 2 selection in favor of fully cooperative groups, there is also multilevel selection in favor of cooperative individuals. In Figure 14 we see the posterior of the cooperative individuals, integrating all groups.
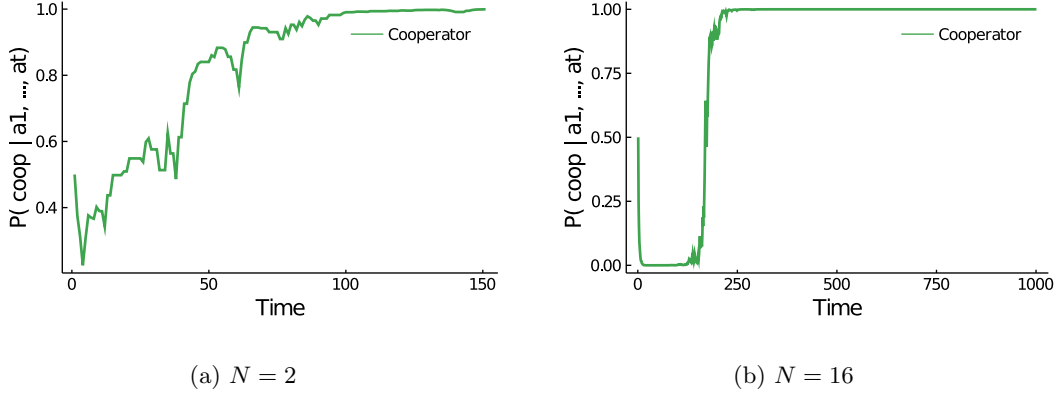

(a) $N = 2$ (b) $N = 16$

Figure 14: Multilevel selection of cooperative individuals when $N = 2$ and $N = 16$.

The probability of cooperative individuals starts at 0.5 due to the symmetry of the binomial prior between regions and the uniform prior between cooperative and defective behaviors. Because in most mixed regions the posterior of cooperative individuals drops abruptly, we see at the beginning a drop in the multilevel posterior. But since the advantage of the fully cooperative group is imposed after a certain time (delay produced by the binomial prior), we finally observe that cooperative behaviors can invade populations with defectors as the posterior multilevel stabilizes at 1.

Conclution 2 (The evolutionary advantage of cooperation)**.** Multilevel selection favors cooperative strategies even with groups of minimum size (two).

3.5 The advantage of specialization

To explain evolutionary transitions, it is necessary to demonstrate the evolutionary advantage of cooperation in the presence of defection, but also the advantage of specialization. Generalist strategies are those that achieve similar returns in each of the environmental states. The most extreme case is the strategy $s = 0.5$, which has the same individual growth rate $g(k|s = 0.5, p, N = 1) \propto 0.5$ irrespective of the type of environment p. By contrast, specialist strategies have high returns in one of the environmental states and high losses in the other. The extreme case is the strategy $s = 1.0$, unfeasible in stochastic environments because its individual growth rate is $g(k|s = 1.0, p, N = 1) = 0$ when $p \neq 0$.

We have seen, in section "Methodology", that the individual strategy best adapted to the environment $p = 0.71$ was $s^* = 0.71$. In general the optimal individual strategy is $s^* = p$. Now that we know that there is an evolutionary advantage in favor of cooperation, is there another strategy that is better adapted to the environment? If there were an advantage in favor of specialization we would expect to see that if the probability of the environment is biased toward one of the states, then the optimal strategy is biased even more, $s^* > p > 0.5$ or $s^* < p < 0.5$.

In figure 15 we compute the individual (solid lines) and cooperative (dashed line) growth rate of the strategies $s \in \{0.5, 0.71, 0.99\}$ at all possible p values of the environment. Note that the

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individual growth rates are proportional to the geometric mean, and that the cooperative growth rates are proportional to the arithmetic mean (groups of infinite size), and that both means are equal for the strategy $s = 0.5$. The arrow represents the Yaari-Peters conclusion discussed in the
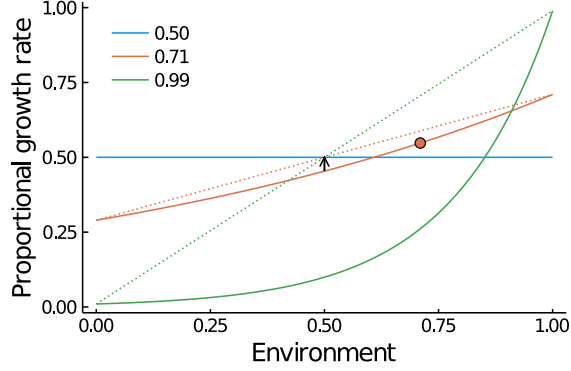

Figure 15: Individuals and cooperative growth rates (continuous and dotted lines) of three strategies ($s \in \{0.5, 0.71, 0.99\}$) in different environment p.

introduction: mutual cooperation can increase the individual growth rate, equal to the geometric mean, to a cooperative growth rate equal to its arithmetic mean. The red dot represents the conclusion we made in section "Methodology", that in an environment with $p = 0.71$ the best adapted individual strategy is $s^* = 0.71$.

With the figure 15 we can derive some new conclusions. Note that above the red dot is the cooperative growth rate of the specialist strategy $s = 0.99$. This suggests that a strategy that is individually poorly adapted to the environment, as is the case of the specialist strategy $g_D^0(k|s = 0.99, p = 0.71, N = 1) < g_D^0(k|s = 0.71, p = 0.71, N = 1)$, achieves in cooperative groups a growth rate that is higher than the growth rate that the individually well adapted strategy achieves through cooperative groups, $g_C^{N-1}(k|s = 0.99, p = 0.71, N = \infty) > g_C^{N-1}(k|s = 0.71, p = 0.71, N = \infty)$.

We have computed the cooperative growth rate for groups of infinite size. To be an interesting conclusion for evolutionary theory we need this result to emerge also in small groups. In Figure 16 we plot the growth rates of the specialist strategy $s = 0.99$ for cooperative groups of size 1 to 5.
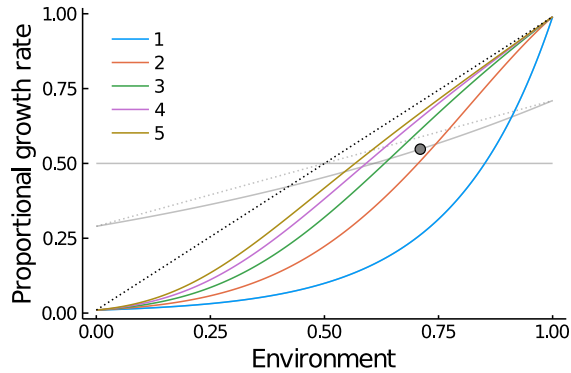

Figure 16: Growth rate of the specialist strategy ($s = 0.99$) as a function of the probability of environment p, for cooperative groups of size 1 to 5. The black dotted line represents the growth rate of an infinitely large cooperative group. The gray lines are visual references to the strategies $s \in \{0.5, 0.71\}$ discussed in the previous figure.

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Note that in an environment $p = 0.71$ the specialist strategy $s = 0.99$ achieves in cooperative groups of size 3 a growth rate that is above the growth rate of the strategy individually well adapted to the environment $s = 0.71$, outperforming even the growth rate that the individually well-adapted strategy obtains in cooperative groups of infinite size, $g_C^2(k|s = 0.99, p = 0.71, N = 3) > \lim_{N \to \infty} g_C^{N-1}(k|s = 0.71, p = 0.71, N)$! It is extraordinary that the same basic assumption that offers an evolutionary advantage in favor of cooperation also offers an evolutionary advantage in favor of specialization, even in small groups. The emergence of cooperation immediately produces an evolutionary advantage in favor of specialization.

The optimal level of specialization depends on the size of the groups. In Figure 17 we set the environment at $p = 0.71$ and analyze how the cooperative growth rate of all possible strategies varies in groups of sizes 1 to 5. When the group has size 1, the optimal strategy is $s^* = p$.
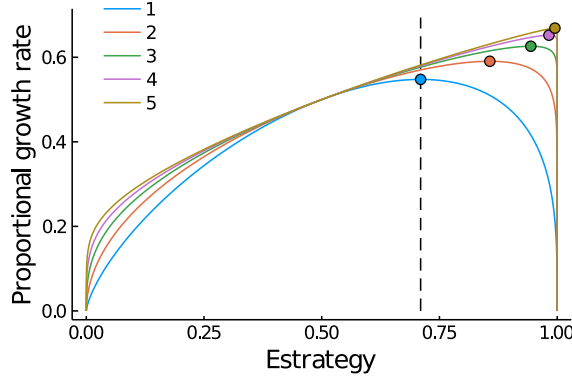

Figure 17: The proportional growth rate of all possible strategies for entirely cooperative groups of size 1 to 5, in an environment $p = 0.71$. The dots indicate the optimum strategy in each of the sizes.

But as soon as cooperation arises, an advantage in favor of the specialist strategies $s^* > p = 0.71$ appears. The larger the groups, the more specialist the optimal strategy becomes. At the extremes (cooperative groups of infinite size) the optimal strategy is reached at the maximum level of specialization, $s = 1$.

Conclution 3 (The advantage of specialization)**.** Cooperation offers an advantage in favor of specialist strategies in groups of minimum size (two). Strategies that individually are poorly adapted to the environment, cooperatively achieve better results than those obtained by cooperative groups of individually well-adapted strategies.

4 Irreversibility of evolutionary transitions

The reason why an advantage in favor of cooperation and specialization arises in our simple causal model is due to the multiplicative (non-ergodic) nature of probability theory and its isomorphism with evolutionary theory. If the population structure persists for a certain minimum time, the evolutionary advantage in favor of cooperation is immediately produced. With the formation of cooperative groups, an evolutionary advantage emerges in favor of specialist strategies. Specialist strategies are able to improve, within cooperative groups, the performance that individually well-adapted strategies can achieve both individually and cooperatively. But a characteristic of specialist strategies is that they are individually maladapted to the environment. This means that, once the individuals of the groups acquire a specialist strategy, they are obliged to remain within the group, since leaving it produces a considerable drop in their evolutionary viability. The evolutionary advantage of cooperation and specialization therefore produces the irreversibility of evolutionary transitions.

Conclution 4 (Irreversibility of evolutionary transitions)**.** The evolutionary advantage of specialization produces the irreversibility of evolutionary transitions, since individuals cannot leave groups without a reduction of their evolutionary viability.

5   Discussions

In this paper we specify a probabilistic causal model, in which individuals are affected just by the environment and by the social behaviors of cooperation and defection of their context. Under this minimal set of hypotheses, where we consider *unconditionally* cooperative individuals who generate a common good that can be exploited by defecting individuals without receiving some kind of punishment in return (e.g. end of cooperation), the evolution of cooperation literature predicts defection as the only evolutionarily stable strategy. It is assumed that common goods, if not accompanied by special conditions (such as communication allowing coordination, memory allowing rewards or punishments, etc.), lead to their overexploitation, because even if the optimum is obtained through mutual cooperation there would be an individual incentive to defect. This type of scenario is known in the social sciences as the "tragedy of the commons" [20], an analogy that evolutionary biology has begun to adopt in recent decades [19].

However, cooperation is consistently observed in the history of life. In the last third of the universe's history, a simple self-replicating organization of matter emerged on earth. The errors produced during replication diversified the life forms, and the growth rates of the different strategies favored those better adapted to the environment. The current complexity of life is the consequence of a series of evolutionary transitions in which entities capable of self-replication after the transition become part of higher level cooperative units. Therefore, the theoretical paradigm of the "tragedy of the commons" is obliged to identify in each case the special conditions that explain the tendency observed in nature in favor of cooperative aggregation (and specialization).

Without including any of these special conditions, the result of the probabilistic inference that emerges from the proposed causal model reveals an advantage in favor of cooperation and specialization over time. How can this counter-intuitive result emerge from such a simple model? While our model only specifies that environments affect individuals proportionally to certain values, the rules of probability theory update the posterior of individuals through the product rule. Because in multiplicative processes the impacts of losses are greater than those of gains, fluctuations produce a negative effect on growth rates, which can be reduced through mutual cooperation. As soon as cooperation emerges, an advantage in favor of specialist strategies appears, because it is no longer necessary for individuals to reduce fluctuations through generalist strategies that avoid bad outcomes in all possible states, and can devote themselves together with other individuals to take advantage of the most frequent environmental state.

Even if our causal model does not assume any kind of process to update resources, the result of the inference is proportional to the resources obtained through a multiplicative process. The multiplicative updating of the probabilities of individuals, which arises naturally from applying the rules of probability to the causal model, is in line with the long-established idea in evolutionary theory that the growth of lineages follow multiplicative processes [8, 18]. This coincidence is an additional support to the hypothesis of isomorphism between evolutionary and probability theories, previously identified between their fundamental equations: the Bayes theorem and the replicator dynamic [12, 13]. Based on this isomorphism, the co-author of the concept of evolutionary transitions (Szathmary [3, 4]) recently proposed to analyze the evolution of populations subject to multilevel selection by means of Bayesian hierarchical models [11].

To the best of our knowledge, our work would be the first to develop a Bayesian hierarchical model to solve an evolution problem under multilevel selection. We were able to identify in it a "multilevel posterior" (i.e. the probability of individuals integrating all groups) as the average of the "level 1 posteriors" (i.e. probability of individuals within groups) weighted by the "level 2 posteriors" (i.e. probability of groups). The reason why an advantage in favor of cooperation and specialization arises in our simple causal model is due to the multiplicative (non-ergodic) nature of probability theory and its isomorphism with evolutionary theory. That is, contrary to the belief

established since the mid-20th century in economics, we show that the dynamics of common goods cannot be represented by a prisoner's dilemma payoff matrix. Moreover, contrary to the belief that specialization is too complex a feature to produce a benefit in simple aggregations, we show that as soon as cooperation emerges, an advantage in favor of specialist strategies appears even in groups of size 2. Since the specialist strategies are individually poorly adapted to the environment, an irreversibility of the evolutionary transition is created.

It is extraordinary that such a simple system as the one analyzed has such fundamental conclusions to understand the complexity of life. Cooperation and specialization are the two main characteristics of the major evolutionary transitions, through which life acquired increasing complexity. Using Czégel-Zachar-Szathmáry's methodological approach [11] (multilevel selection as hierarchical Bayesian inference) we formally demonstrate the evolutionary advantage of cooperation and specialization suggested by Yaari-Peters [9, 10] (noisy multiplicative processes). And in turn, with the Yaari-Peters model we provided the concrete example that was missing from the methodological proposal of Czegel et al. Both proposals combined offer a new solution to the problem of major evolutionary transitions, which is simpler than the previous ones (noisy multiplicative processes), based on well-founded mathematical principles (the strict application of the rules of probability).

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6 Appendix

6.1 Sum-product algorithm

The *sum-product algorithm* takes advantage of the factoriztion of the joint probability distribution, induced by the causal model, to efficiently apply the rules of probability. It is a way of computing the rules of probability (the sum and product rule) by message passing between probability distributions and their variables. For this purpose, it is convenient to represent the graphical model with a *factor graph*, a bipartite graph with variable nodes (white circles) and function nodes (black squares). The edge between node variables and node functions represents the mathematical relationship "the variable v is an argument of the function f". The following factor graph of the graphical model 7.
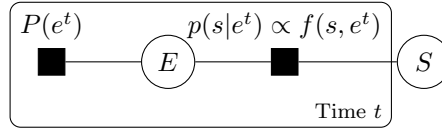

Figure 18: Graphical way of representing the factorization of joint distribution induced by the basic causal model (Fig. 7). The box represents repetition.

There are two types of messages: those sent by variable-type nodes to their function-type neighbors ($m_{V \to F}(v)$) and the ones that function-type nodes send to their variable-type neighbors ($m_{F \to V}(v)$). The former partially performs the product rule.

$$m_{V \to F}(v) = \prod_H^{\boldsymbol{H}} m_{H \to V}(v) \qquad \text{(product step)}$$

where $\boldsymbol{H} = n(V) \setminus \{F\}$ represents the set of neighbor nodes to V except F. In a brief, the messages sent by the variable-type node V are simply the product of the messages that V receives from the rest of their neighbors $H \in n(V)$ except F. The other messages sent by the function-type nodes encode a portion of the sum rule.

$$m_{F \to V}(v) = \sum_{u_1}^{U_1} \cdots \sum_{u_n}^{U_n} \left(F(u_1, \ldots, u_n, v) \prod_{U_i}^{\boldsymbol{U}} m_{U \to F}(u_i) \right) \qquad \text{(sum step)}$$

where $U_i \in \boldsymbol{U} = n(F) \setminus \{V\}$ is the set of all neighbors to F except V of size n, u_i is a specific value of the variable U_i, $u_i \in U_i$, and $F(u_1, \ldots, u_n, v)$ represents the function F, evaluated in all its arguments. In short, the messages sent by the function-type node F to a neighboring variable-type node V is simply the sum (or integration) over $\boldsymbol{U}$ of the product of itself and all the messages that receives from the rest of its neighbors $\boldsymbol{U}$ except V. Finally, the marginal probability distribution of a variable V is simply the product of the messages that V receives from all its neighbors.

$$P(V = v) = \prod_{H \in n(V)} m_{H \to V}(v) \qquad \text{(marginal probability)}$$

When we observe some variable u, we exclude it from the summations, which allows us to compute the marginal probability over two variables, $P(v, u)$. This algorithm encodes the minimum number of steps required to calculate any marginal probability distribution.

6.2 Posteriors of strategies in the basic causal model

As we will later use the sum-product algorithm to solve the extended causal model, we show its use in this basic causal model (figure 7) to gain some intuition. Using this procedure we will

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obtain the marginal distribution of the strategies and a vector of observations $p(s, \vec{e})$, and we will normalize it to obtain the posterior $p(s|\vec{e})$. To compute $p(s, e)$, we will consider $e = e^*$ observable. Then, the message from the environment factor $P(e)$ to the environment variable E is,

$$m_{P(E)\to E}(e^*) = P(e^*) = m_{E\to p(S|E)}(e^*) \tag{24}$$

which is the same message that the variable E sends to the strategy factor $p(S|E)$. Then, the message sent by the strategies factor $p(S|E)$ to the strategies variable S is,

$$m_{p(S|E)\to S}(s) \propto P(e^*)f(s, e^*) \tag{25}$$

Note that we do not integrate the values of the environment because e^* is observable and therefore constant. Then, the marginal of the strategies and a vector of environmental states $\vec{e}$ is,

$$p(s, \vec{e}) \propto \prod_e^{\vec{e}} P(e)f(s, e) \tag{26}$$

Normalizing it we obtain the posterior,

$$p(s|\vec{e}) = \frac{\prod_e^{\vec{e}} f(s, e)}{\int_s \prod_e^{\vec{e}} f(s, e)} \tag{27}$$

Then, the posterior belongs to the Beta distribution (note that the denominator of the equation 27 is the Beta function or the Euler integral).

$$P(s|\vec{e}) = \mathrm{Beta}(\mathtt{sum}(\vec{e}), \mathtt{length}(\vec{e}) - \mathtt{sum}(\vec{e})) = \frac{s^{\mathtt{sum}(\vec{e})} \cdot (1-s)^{\mathtt{length}(\vec{e})-\mathtt{sum}(\vec{e})}}{B(\mathtt{sum}(\vec{e}), \mathtt{length}(\vec{e}) - \mathtt{sum}(\vec{e}))} \tag{28}$$

with $B(\cdot, \cdot)$ the Beta function. The result of the posterior will indicate the evolutionary stability of the strategies.

6.3   Posteriors of individuals in the extended causal model

The probability of individuals, when the environmental states $\vec{e}^t$ are observed, is

$$P(i^T, \vec{e}^1, \ldots, \vec{e}^{T-1}) = m_{P(I^T|I^{T-1})\to I^T}(i^T) \tag{29}$$

This message is recursively defined.

$$m_{P(I^{t+1}|I^t)\to I^{t+1}}(i^{t+1}) = \sum_{i^t} P(i^{t+1}|i^t)\, P(\vec{e}^t)\, P(i^t|\vec{e}^t)\, m_{P(I^t|I^{t-1})\to I^t}(i^t) \tag{30}$$

In all cases, the marginal is equal to the posterior times the probability of the observed environment,

$$P(I^{T+1} = k, \vec{e}^1, \ldots, \vec{e}^T) = P(k|\vec{e}^1, \ldots, \vec{e}^T) \prod_{t=1}^{T} P(\vec{e}^t) \tag{31}$$

where (all steps are described in the next section)

$$P(k|\vec{e}^1, \ldots, \vec{e}^T) = \begin{cases} P(k)\prod_{t=1}^{T} P(k|\vec{e}^t) & r = 0 \\ P(k)\prod_{t=1}^{T} \sum_j^{\mathtt{partners}(r)} \frac{1}{N} P(j|\vec{e}^t) & r = N \\ \left(P(k)\prod_{t=1}^{T} P(k|\vec{e}^t)\right) + \left(\sum_{t=1}^{T} P(c|\wedge_{q=1}^{t} \vec{e}^q)\prod_{q=t+1}^{T} P(k|\vec{e}^q)\right) & 0 < r < N \end{cases} \tag{32}$$

where $r = \mathtt{region}(k)$ is the region to which individual k belongs, $\mathtt{partners}(r)$ is the set of cooperating individuals in region r, and c is a cooperative individual belonging to that specific region, $c \in \mathtt{partners}(r)$.

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6.4 Marginal distributions of the extenden causal model step by step

To compute the posteriors of the extended causal model it will be sufficient to compute the marginal probabilities, since both expressions are proportional. The marginal probabilities can be obtained by applying the sum-product algorithm in the model of figure 9, taking as observed the variables that in the posterior appear in the conditional (see section "Methodology"). The marginal probability of the individuals at time T, when the environment variables $\vec{e}^t$ and the group variable g are observed, is

$$P(i^T, \vec{e}^1, \ldots, \vec{e}^{T-1}, g) = m_{P(I^T|I^{T-1}) \to I^T}(i^T) \cdot m_{P(G^T|I^T) \to I^T}(i^T) \tag{33}$$

the product of the messages that the variable i^T receives from the social factor $P(I^T|I^{T-1})$ and from the group factor $P(G^T|I^T)$, in the model that has the set $\{\vec{e}^1, \ldots, \vec{e}^{T-1}, g\}$ as observed variables. The marginal probability of the groups at time T, when we observe all the environmental states $\vec{e}^t$, is

$$P(g^T, \vec{e}^1, \ldots, \vec{e}^{T-1}) = m_{P(G^T|I^T) \to G^T}(g^T) \tag{34}$$

the message that the variable G^T receives from the group factor $P(G^T|I^T)$, in the model that has $\{\vec{e}^1, \ldots, \vec{e}^{T-1}\}$ as observed variables. An alternative way to compute the multilevel selection marginal (Eq. 18) is by integrating the probability of all cooperating individuals given the environments

$$P(\texttt{coop}(i^T), \vec{e}^1, \ldots, \vec{e}^{T-1}) = \sum_{j=1}^{M} P(I^T = j, \vec{e}^1, \ldots, \vec{e}^{T-1}) \mathbb{I}(\texttt{coop}(j)) \tag{35}$$

where the probability of individuals, when the environmental states $\vec{e}^t$ are observed, is

$$P(i^T, \vec{e}^1, \ldots, \vec{e}^{T-1}) = m_{P(I^T|I^{T-1}) \to I^T}(i^T) \tag{36}$$

the message that the variable i^T receives from the social factor $P(I^T|I^{T-1})$ in the model that has $\{\vec{e}^1, \ldots, \vec{e}^{T-1}\}$ as observed variables. In summary, we need to compute only three messages.

Messages	$m_{P(G^T|I^T) \to I^T}(i^T)$	$m_{P(G^T|I^T) \to G^T}(g^T)$	$m_{P(I^T|I^{T-1}) \to I^T}(i^T)$
Observed	$\{g\}$	$\{\vec{e}^1, \ldots, \vec{e}^{T-1}\}$	$\{\vec{e}^1, \ldots, \vec{e}^{T-1}\}$

Table 1: The messages that comprise the marginals of the level 1, 2 and multilevel selection.

The first message, which is sent by the group factor to the individual variable when the group variable is observed, is

$$m_{P(G^T|I^T) \to I^T}(i^T) = P(g|i) = \mathbb{I}(\texttt{region}(i) = g) \tag{37}$$

the indicator function which is 1 for individuals in the region $r = g$ and 0 for the rest. The second message, which the group factor sends to the group variable, is

$$m_{P(G^T|I^T) \to G^T}(g^T) = \sum_i P(g^T|i) \, m_{P(I^T|I^{T-1}) \to I^T}(i) \tag{38}$$

which is composed of the third message, which the social factor sends to the individuals' variable. To compute this third and last message we must find the preceding messages that compose it. Among them are the messages that the environmental factor sends to the environmental variable,

$$m_{P(\vec{E}^t) \to \vec{E}^t}(\vec{e}^t) = P(\vec{e}^t) = m_{\vec{E}^t \to P(I^t|\vec{E}^t)}(\vec{e}^t) \tag{39}$$

which is the same message that the environment variable sends to the individuals factor. Then we can generate the message that the individuals factor sends to the individuals variable,

$$m_{P(I^t|\vec{E}^t) \to I^t}(i^t) = P(\vec{e}^t) \, P(i^t|\vec{e}^t) \tag{40}$$

that since the environmental variable is observed, the integration is not performed. And finally, the message that the individual variable sends to the social factor,

$$m_{I^t \to P(I^{t+1}|I^t)}(i^t) = m_{P(I^t|\vec{E}^t) \to I^t}(i^t)\, m_{P(I^t|I^{t-1}) \to I^t}(i^t) \tag{41}$$

We do not include in the product the message that the group factor sends to the individual variable, because as it is not observed, the message is automatically cancelled, $m_{P(g^t|i^t) \to i^t}(i^t) = \sum_g P(g|i^t) = 1$. Finally, the third target message (encoding multilevel selection) introduces the social factor over individual resources.

$$m_{P(I^{t+1}|I^t) \to I^{t+1}}(i^{t+1}) = \sum_{i^t} P(i^{t+1}|i^t)\, P(\vec{e}^t)\, P(i^t|\vec{e}^t)\, m_{P(I^t|I^{t-1}) \to I^t}(i^t) \tag{42}$$

Because this message is recursively defined, we will perform proofs by induction, by cases: first for the entirely defector regions, then for the entirely cooperator regions, and finally for the mixed regions.

6.4.1 Entirely defecting regions

We propose the following inductive hypothesis for the entirely defecting region $(\mathrm{HI}_d(T))$,

$$m_{P(I^{T+1}|I^T) \to I^{T+1}}(i^{T+1}) \stackrel{\mathrm{HI}_d}{=} P(i^{T+1}) \prod_{t=1}^{T} P(\vec{e}^t)\, P(i^{T+1}|\vec{e}^t) \tag{43}$$

with $\texttt{region}(k) = 0$.

Base case This hypothesis holds in the base case, $T = 1$, since $P(i^{t+1}|i^t) = \mathbb{I}(i^{t+1} = i^t)$,

$$\begin{aligned} m_{P(I^2|I^1) \to I^2}(i^2) &\stackrel{eq}{=} \sum_{i^1} P(i^2|i^1)\, P(\vec{e}^1)\, P(i^1|\vec{e}^1)\, P(i^1) \\ &= P(\vec{e}^1)\, P(i^2|\vec{e}^1) P(i^2) \end{aligned} \tag{44}$$

Note that a change of variable occurred because the only element of the summation that survives is $i^1 = i^2$. And since the inductive hypothesis holds for the time T, $\mathrm{HI}_d(T)$, it also holds for the time $T + 1$, because

$$\begin{aligned} m_{P(I^{T+1}|I^T) \to I^{T+1}}(i^{T+1}) &\stackrel{eq}{=} \sum_{i^T} P(i^{T+1}|i^T)\, P(\vec{e}^T)\, P(i^T|\vec{e}^T)\, m_{P(I^T|I^{T-1}) \to I^T}(i^T) \\ &\stackrel{case}{=} P(\vec{e}^T)\, P(i^{T+1}|\vec{e}^T)\, m_{P(I^T|I^{T-1}) \to I^T}(i^{T+1}) \\ &\stackrel{\mathrm{HI}_d}{=} P(\vec{e}^T)\, P(i^{T+1}|\vec{e}^T)\, P(i^{T+1}) \prod_{t=1}^{T-1} P(\vec{e}^t)\, P(i^{T+1}|\vec{e}^t) \\ &= P(i^{T+1}) \prod_{t=1}^{T} P(\vec{e}^t)\, P(i^{T+1}|\vec{e}^t) \end{aligned} \tag{45}$$

Then, the posterior of individuals in the entirely defecting region is,

$$P(i^{T+1}|\vec{e}^1, \dots, \vec{e}^T) \stackrel{case}{=} P(i^{T+1}) \prod_{t=1}^{T} P(i^{T+1}|\vec{e}^t) \propto P(i^{T+1}) \prod_{t=1}^{T} f(s_i, e_i^t) \tag{46}$$

with $i = i^{T+1}$.

6.4.2 Entirely cooperating regions

We propose the following inductive hypothesis for the fully cooperative group ($\mathrm{HI}_c(T)$),

$$m_{P(I^{T+1}|I^T)\to I^{T+1}}(i^{T+1}) = P(i^{T+1})\prod_{t=1}^{T} P(\vec{e}^t) \sum_{j}^{\mathtt{partners}(r)} \frac{1}{N} P(j|\vec{e}^t) \tag{47}$$

where $r = \mathtt{region}(i^{T+1})$, and $\mathtt{partners}(r)$ is the set of all cooperating members belonging to the region r. This hypothesis holds in the case $T = 1$.

$$
\begin{aligned}
m_{P(I^2|I^1)\to I^2}(i^2) &\stackrel{eq}{=\!=} \sum_{i^1} P(i^2|i^1)\, P(\vec{e}^1)\, P(i^1|\vec{e}^1)\, P(i^1) \\
&= P(\vec{e}^1) \sum_{j}^{\mathtt{partners}(r)} \frac{1}{N} P(j|\vec{e}^1)P(j) \\
&= P(i^2)P(\vec{e}^1) \sum_{j}^{\mathtt{partners}(r)} \frac{1}{N} P(j|\vec{e}^1)
\end{aligned}
\tag{48}
$$

because $P(i^{t+1}|i^t) = \frac{1}{N}\mathbb{I}(\mathtt{region}(i^{t+1}) = \mathtt{region}(i^t))$, and for all $j \in \mathtt{partners}(region(i^2))$ it holds $P(j) = P(i^2)$. And since the inductive hypothesis holds for time T, $\mathrm{HI}_c(T)$, it also holds for time $T + 1$, because

$$
\begin{aligned}
m_{P(I^{T+1}|I^T)\to I^{T+1}}(i^{T+1}) &\stackrel{eq}{=\!=} \sum_{i^T} P(i^{T+1}|i^T)\, P(\vec{e}^T)\, P(i^T|\vec{e}^T)\, m_{P(I^T|I^{T-1})\to I^T}(i^T) \\[4pt]
&\stackrel{\text{case}}{=} \sum_{j}^{\mathtt{partners}(r)} P(\vec{e}^T)\frac{1}{N} P(j|\vec{e}^T) m_{P(I^T|I^{T-1})\to I^T}(j) \\[4pt]
&\stackrel{*}{\underset{\text{case}}{=}} \left(\sum_{j}^{\mathtt{partners}(r)} P(\vec{e}^T)\frac{1}{N} P(j|\vec{e}^T) \right)\left(m_{P(I^T|I^{T-1})\to I^T}(i^{T+1}) \right) \\[4pt]
&\stackrel{\mathrm{HI}_c}{=} \left(\sum_{j}^{\mathtt{partners}(r)} P(\vec{e}^T)\frac{1}{N} P(j|\vec{e}^T) \right)\left(P(i^{T+1})\prod_{t=1}^{T-1} \sum_{j}^{\mathtt{partners}(r)} P(\vec{e}^t)\frac{1}{N}P(j|\vec{e}^t) \right) \\[4pt]
&= P(i^{T+1})\prod_{t=1}^{T} P(\vec{e}^t) \sum_{j}^{\mathtt{partners}(r)} \frac{1}{N} P(j|\vec{e}^t)
\end{aligned}
\tag{49}
$$

where $\stackrel{*}{\underset{\text{case}}{=}}$ holds because in fully cooperative groups the messages $m_{P(I^T|I^{T-1})\to I^T}(j)$ are the same for all group members j, which allows us to replace the index j by the variable i^{T+1}. Therefore, the marginal in the case of the entirely cooperative group is,

$$P(i^{T+1}|\vec{e}^1,\dots,\vec{e}^T) \stackrel{\text{case}}{=} P(i^{T+1})\prod_{t=1}^{T} \sum_{j}^{\mathtt{partners}(r)} \frac{1}{N}P(j|\vec{e}^t) \propto P(i^{T+1})\prod_{t=1}^{T} \sum_{j}^{\mathtt{partners}(r)} \frac{1}{N}f(s_j, e_j^t) \tag{50}$$

6.4.3 Mixed regions, cooperating individuals

The commons are generated by the set of cooperating individuals in the region r, $\mathtt{partners}(r)$. The size of the set depends on the number of cooperators. However, the common good continues to be divided equally among all members of the region.

$$P(i^{T+1}|\vec{e}^1,\dots,\vec{e}^T) = P(i^{T+1})\prod_{t=1}^{T} \frac{1}{N} \sum_{j}^{\mathtt{partners}(r)} P(j|\vec{e}^t) \tag{51}$$

where the proof is equivalent to the previous case.

6.4.4 Mixed regions, individual defectors

Before proposing an inductive hypothesis, let us see what happens with the first messages of the recursion, in order to gain intuition. By definition,

$$m_{P(I^2|I^1)\to I^2}(k) = \sum_{i^1} P(k|i^1)P(\vec{e}^1)P(i^1|\vec{e}^1)P(i^1) \tag{52}$$

In the case of mixed regions, the social factor is 1 when $k = i^1$ and is $1/N$ when $i^1 \in \texttt{partners}(r)$.

$$m_{P(I^2|I^1)\to I^2}(k) = P(\vec{e}^1)\Big(P(k)P(k|\vec{e}^1) + P(c)\underbrace{\overset{\texttt{partners}(r)}{\sum_{j}}\frac{1}{N}P(j|\vec{e}^1)}_{P(c|\vec{e}^1)}\Big) \tag{53}$$

where $P(c|\vec{e}^1)$ is the posteriors of the cooperating individuals. By definition, the next message is

$$m_{P(I^3|I^2)\to I^3}(k) = \sum_{i^2} P(k|i^2)P(\vec{e}^2)P(i^2|\vec{e}^2)m_{P(I^2|I^1)\to I^2}(i^2)$$

$$= P(\vec{e}^2)\Big(P(k|\vec{e}^2)\underbrace{m_{P(I^2|I^1)\to I^2}(k)}_{P(k)P(k|\vec{e}^1)P(\vec{e}^1)} + \overset{\texttt{partners}(r)}{\sum_{j}}\frac{1}{N}P(j|\vec{e}^2)\underbrace{m_{P(I^2|I^1)\to I^2}(j)}_{P(c|\vec{e}^1)P(\vec{e}^1)}\Big) \tag{54}$$

where all the messages received by the cooperating individuals j, $m_{P(I^2|I^1)\to I^2}(j)$, are equal.

$$m_{P(I^3|I^2)\to I^3}(k) = \Big(\prod_{t=1}^{2} P(\vec{e}^t)\Big)\Big(P(k|\vec{e}^2)P(k|\vec{e}^1)P(k) + P(c|\vec{e}^1)\overset{\texttt{partners}(r)}{\sum_{j}}\frac{1}{N}P(j|\vec{e}^2)\Big)$$

$$= \Big(\prod_{t=1}^{2} P(\vec{e}^t)\Big)\Big(\underbrace{P(k|\vec{e}^2)P(k|\vec{e}^1)P(k) + P(c|\vec{e}^1, \vec{e}^2)}_{P(k|\vec{e}^1, \vec{e}^2)}\Big) \tag{55}$$

Opening the recursion we find,

$$P(k|\vec{e}^1, \vec{e}^2) = P(k)P(k|\vec{e}^1)P(k|\vec{e}^2) + P(k|\vec{e}^2)P(c|\vec{e}^1) + P(c|\vec{e}^1, \vec{e}^2) \tag{56}$$

Then, the inductive hypothesis $\text{HI}_M(T)$ for an individual defector k from a mixed r region is,

$$P(k|\vec{e}^1, \ldots, \vec{e}^T) \overset{\text{HI}_M(T)}{=} \Big(P(k)\prod_{t=1}^{T} P(k|\vec{e}^t)\Big) + \Big(\sum_{t=1}^{T} P(c|\wedge_{q=1}^{t}\vec{e}^q)\prod_{q=t+1}^{T} P(k|\vec{e}^q)\Big)$$

$$m_{P(I^{T+1}|I^T)\to I^{T+1}}(k) = P(k|\vec{e}^1, \ldots, \vec{e}^T)\prod_{t=1}^{T} P(\vec{e}^t) \tag{57}$$

where the posterior of the individual defector in a mixed region r is the sum of the posterior of an individual defector in an entirely defector region, and an exponential moving average of the posterior of the cooperating individuals.

Base case. The base case is already proven by extension.

Inductive step. Given $\text{HI}_{M_D}(T)$, $\text{HI}_{M_C}(T)$ I want to prove $\text{HI}_{M_D}(T+1)$.

$$m_{P(I^{T+1}|I^T)\to I^{T+1}}(k) = \sum_{i^T} P(k|i^T)P(\vec{e}^T)P(i^T|\vec{e}^T)m_{P(I^T|I^{T-1})\to I^T}(i^T)$$

$$= P(\vec{e}^T)\Big(P(k|\vec{e}^T)m_{P(I^T|I^{T-1})\to I^T}(k) + \overset{\texttt{partners}(r)}{\underset{j}{\sum}}\frac{1}{N}P(j|\vec{e}^T)m_{P(I^T|I^{T-1})\to I^T}(j)\Big)$$

$$\overset{\text{HI}}{=} \Big(\prod_{t=1}^T P(\vec{e}^t)\Big)\Big(P(k|\vec{e}^T)P(k|\vec{e}^1,\ldots,\vec{e}^{T-1}) + P(c|\vec{e}^1,\ldots,\vec{e}^T)\Big)$$

$$= \Big(\prod_{t=1}^T P(\vec{e}^t)\Big)\Big(\Big(P(k)\prod_{t=1}^T P(k|\vec{e}^t)\Big) + \Big(\sum_{t=1}^T P(c|\wedge_{q=1}^t \vec{e}^q)\prod_{q=t+1}^T P(k|\vec{e}^q)\Big)\Big)$$

$$(58)$$

Therefore, the inductive hypothesis is true.

6.5 Isomorphism of the extended causal model

Our probabilistic causal model and the multiplicative process discussed in the introduction are equivalent. The posterior of individuals from the entirely defecting region is,

$$P(i^{T+1}|\vec{e}^1,\ldots,\vec{e}^T) \overset{r=0}{\equiv} P(i^{T+1})\prod_{t=1}^T P(i^{T+1}|\vec{e}^t)$$

$$\propto P(i^{T+1})\prod_{t=1}^T s_k^{e_k}(1-s_k)^{1-e_k} \propto P(i^{T+1})\prod_{t=1}^T R f(s_i, e_i^t)$$

$$(59)$$

where $r = \texttt{region}(i^{T+1}) = 0$ denotes the region without cooperators, f is the fitness function that we define in the equation 12. The first proportional is valid because of the normalization constant of the probability distribution $P(i^t|\vec{e}^t)$. And the second proportional simply includes the factor R, so that the fitness function matches the one proposed by Lewontin-Cohen, when $R = 2.2$, or the one proposed by Peters, when $R = 2.1$. When the prior $P(i^{T+1})$ represents the initial resources $\omega(0)$, then the posterior of the individual defectors in entirely defecting groups is proportional to the growth of the individual resources studied in section "Introduction".

The same is true for the posteriors of cooperating individuals. First, the message sent by the individual variables to the social factor is proportional to the second node of the cooperative protocol (figure 4), in which the previous resources $\omega_i(t)$ are updated by the product of the fitness function.

$$m_{I^t\to P(I^{t+1}|I^t)}(i^t) = m_{P(I^t|\vec{E}^t)\to I^t}(i^t)\, m_{P(I^t|I^{t-1})\to I^t}(i^t)$$

$$= P(i^t|\vec{e}^t)\, P(i^t, \vec{e}^t,\ldots,\vec{e}^t)$$

$$\propto R f(s_i, e_i^t)\omega(t-1)$$

$$(60)$$

Again, the proportionality holds by construction of the probability distribution $P(i^t|\vec{e}^t)$. And the message that the social factor sends to the individual variable of the following time is proprotional to the individual resources after pooling and sharing,

$$m_{P(I^{t+1}|I^t)\to I^{t+1}}(i^{t+1}) = \sum_{i^t} P(i^{t+1}|i^t)\, P(\vec{e}^t)\, P(i^t|\vec{e}^t)\, m_{P(I^t|I^{t-1})\to I^t}(i^t)$$

$$= P(I^{t+1}, \vec{e}^1,\ldots,\vec{e}^T) \propto \sum_{i^t} P(i^{t+1}|i^t)\, f_{s_i}(e_i^t)\omega_i(t) = \omega_i(t+1)$$

$$(61)$$

where $P(i^{t+1}|i^t) = \frac{1}{N}$ when individuals belong to the same region $\texttt{region}(i^{t+1}) = \texttt{region}(i^t)$. This message generalizes the last node of the cooperative protocol (figure 4).

In the introduction we have not analyzed the resource trajectory of defectors in cooperative groups, but in general, the posterior of individuals is no more than the proportion of resources they manage.

6.6 Growth Rates

The growth rate depends on the hyperparameters of the model, $\vec{s}$, p and N. Here we will only consider models in which all individuals have the same strategy s. We will solve this problem by cases, depending on whether the behavior is cooperative, g_C, or defective, g_D, for different social contexts $g^n_{[\cdot]}(k|\cdot)$, where n represents the number of cooperators with which the individual k interacts (excluding k). The growth rate of mutual defection is,

$$\lim_{T\to\infty} g^0_D(k|s,p,N)^T = \prod_{t=1}^T P(k|\vec{e}^{T+1}) \propto \prod_{t=1}^T s^{e^t_k}(1-s)^{1-e^t_k}$$

$$\lim_{T\to\infty} g^0_D(k|s,p,N) \propto \Big(\prod_{t=1}^T s^{e^t_k}(1-s)^{1-e^t_k}\Big)^{1/T} = s^p(1-s)^{1-p} \tag{62}$$

which is independent of the size N. The proportional is valid because of the normalization constant of the probability distribution $P(i^t|\vec{e}^t)$. The growth rate of a strategy $s = 0.71 \approx 1.5/2.1$ in an environment with $p = 0.5$ is $0.71^{1/2} \cdot 0.29^{1/2} \approx 0.452$.

The growth rate of the cooperators can also be computed using the geometic average,

$$\lim_{T\to\infty} g^n_C(k|s,p,N)^T = \prod_{t=1}^T \sum_j^{\texttt{partners}(k)} \frac{1}{N} P(j|\vec{e}^t) \propto \prod_{t=1}^T \sum_j^{\texttt{partners}(k)} \frac{1}{N} s^{e^t_j}(1-s)^{1-e^t_j}$$

$$\lim_{T\to\infty} g^n_C(k|s,p,N) \propto \Big(\prod_{t=1}^T \sum_j^{\texttt{partners}(k)} \frac{1}{N} s^{e^t_j}(1-s)^{1-e^t_j}\Big)^{1/T} = \prod_{x=0}^{n+1} \Big(\frac{x}{N}s + \frac{n+1-x}{N}(1-s)\Big)^{\mathcal{B}(x|n+1,p)} \tag{63}$$

where x represents the number of successes within the cooperating group, and $\mathcal{B}(x|n+1,p)$ is the binomial probability of obtaining x successes in a sample of size $n+1$. Then, the cooperative growth rate in a group of size 2 are $g^2_C(k|s=0.71,p=0.5,N=2) \propto 0.71^{1/4} \cdot 0.5^{1/2} \cdot 0.29^{1/4} \approx 0.475$ and $g^1_C(k|s=0.71,p=0.5,N=2) \propto (\frac{0.71}{2})^{1/4} \cdot (\frac{0.29}{2})^{1/2} \approx 0.226$. When the group is very large, $N \to \infty$,

$$\lim_{N\to\infty} g^n_C(k|s,p,N) \propto \Big(ps + (1-p)(1-s)\Big)\frac{n+1}{N} \tag{64}$$

the growth rate is just the arithmetic mean, weighed by the proportion of cooperators.

The growth rate of the defectos in goups with at least one cooperator is,

$$\lim_{T\to\infty} g^n_D(k|s,p,N)^T = \Big(\prod_{t=1}^T P(k|\vec{e}^t)\Big) + \Big(\sum_{t=1}^T \prod_{q=1}^t \sum_j^{\texttt{partners}(k)} \frac{1}{N} P(j|\vec{e}^q) \prod_{q=t+1}^T P(k|\vec{e}^q)\Big)$$

$$\approx g^0_D(k|s,p,N)^T + \sum_{t=1}^T g^{n-1}_C(k|s,p,N)^t g^0_D(k|s,p,N)^{T-t}$$

$$\propto (s^p(1-s)^{1-p})^T + \sum_{t=1}^T \Big(\prod_{x=0}^n (\frac{x}{N}s + \frac{n-x}{N}(1-s))^{\mathcal{B}(x|n,p)}\Big)^t (s^p(1-s)^{1-p})^{T-t} \tag{65}$$

the sum of individual growth plus a moving average of the growth of cooperators weighted by individual growth, which we approximate using the growth rates g^0_D and g^n_C. This growth rate is not constant, but quickly stabilizes at the higher growth rate, $g^n_D(k|s,p,N) \approx \texttt{max}(g^0_D(k|s,p,N), g^n_C(k|s,p,N))$.