Supplementary material for "A simple rule for the evolution of contingent cooperation in large groups"

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Philosophical Transactions of the Royal Society B doi 10.1098/RSTB.2015.0099

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1 Introduction

In this supplementary material, we review the Islands with Local Regulation (ILR) population structure that we introduced in [3], and then extend the results of that paper in several ways. We will not repeat the motivation for the population structure, which is explained in the introduction of [3] and further elaborated in the conclusion section of that paper. But for the reader's benefit, we include in the next two sections the basic definitions and background ideas needed to make this supplement mathematically self-contained. These two sections follow closely the corresponding ones in [3]. In the remaining sections of this supplement we then present new results on the evolution of an inherited behavior in an ILR setting. The most important extension of the results from [3] are those in Section 4, where we analyze the regime in which migration and group size regulation (quatified by group rigidity, as defined in Section 2) are comparable forces. In Section 5 we make explicit a remark in the conclusion section of [3] on the effect of having both, local and global regulation of the population size. For this purpose we analyze a population structure that we call "Islands with Local and Global Regulation" (ILGR), which includes ILR as a special case. In that section, we will also discuss what are the minimal conditions for a weak selection analysis to be valid. In Section 6 we explain how our conclusions about ILGR can be refrased in terms of regression coefficients, and how this can be used to test the theory against computer simulations. In Section 7 we apply the results of the previous sections to iterated games with cooperation persisting contingent on the presence of a threshold number of cooperators in the group. We complement the analysis of these games provided in the paper, which is based there on an approximation, by producing exact solutions in two important cases. We them use these exact solutions to discuss when the approximations provided in the paper are good.

2 Islands with local regulation

First we introduce the population structure in the absence of selection. This population structure is similar to Wright's island model, but group size is not fixed and instead is allowed to vary around a typical value n_0. The population is split into g groups. Generations are non-overlaping and reproduction is asexual. In the beginning of a new generation cycle, groups contain only adult individuals. The size of a group is the number n of these individuals. In the beginning of a cycle, adults produce offspring that remain in the group until the end of the cycle when they reach adulthood, if they survive. Each adult produces a random, statistically independent, number of adult offspring, with a distribution that depends on the number of adult individuals in its group. When group size is n, the mean of this individual adult offspring distribution is $h(s)$, where $s = n/n_0$ is the scaled group size. This implies that the scaled expected number of adult offspring produced by the group is $nh(s)/n_0 = sh(s)$. We assume that $h(1) = 1$, $h(s)$ has a continuous derivative $h'(s) < 0$, and $sh(s) < 1$, when $s < 1$ (this last condition implies $h'(1) \geq -1$.) Thus $h(s)$ captures the idea that increasing group size decreases fitness. At the end of the cycle the adults present in the beginning die, while each adult born in that cycle either migrates to a randomly chosen group with probability m, or otherwise stays in its group of birth.

We assume that g is large (idealized by taking $g \to \infty$). This implies that migration is long range and that averages across groups or individuals are well approximated by expected values for a randomly chosen focal group or individual. We also suppose, unless when stated otherwise, that n_0 is large. This implies that fluctuations in size across groups can be neglected. In the absence of migration, the scaled group size behaves then as a discrete time dynamical system, with s being mapped to $sh(s)$ in each iteration. The assumptions about $h(s)$ imply that if initially $s < 1$, then s increases towards $s_0 = 1$. If initially $s > 1$, then s decreases towards $s_0 = 1$, or decreases towards a value smaller than 1 and then increases towards $s_0 = 1$. The speed at which this happens depends on the derivative $\frac{dsh(s)}{ds}$, at $s = 1$. Standard computations [2] show that the relaxation time is of order $1/\lambda$, where $\lambda = -h'(1)$ will be called "the rigidity parameter", and will play a major role in this paper. The assumptions on $h(s)$ imply that $0 < \lambda \leq 1$. A small value of λ indicates a very elastic group environment, and a large value a very rigid environment. (The assumptions that we are making on $h(s)$ can be somewhat relaxed, but attraction to the equilibrium at $s = 1$ could occur then through damped oscilations, rather than monotonically. We are focusing on the simpler monotonic picture for simplicity. See [2] for a detailed analysis of the dynamical system that maps s to $sh(s)$, and their Table 2, for a list of forms that $h(s)$ has taken in the literature. Note also that a very large value of λ would make the fixed point $s = 1$ unstable, therefore one cannot hope to produce a limit of infinite rigidity, i.e., fixed group size, by letting $\lambda \to \infty$.)

Groups are also pulled towards a common size by migration. Since migration is assumed to occur at a fixed rate, larger groups will produce more migrants than smaller ones, tending to equalize group size in a time of order $1/m$.

The combined effects of rigidity and migration, will produce an equilibrium, in which each group has size close to n_0. The number of migrants produced by a focal group in a cycle will then be close to a binomial with n_0 attempts and probability m of success. The number of migrants that the same group receives in a cycle is well approximated by a Poisson distribution with mean $n_0 m$, because there are $g n_0 m$ migrants, each one migrates to the focal group with probability $1/g$, and g is large. The net flux of migrants into the focal group is hence a random variable with mean 0, and variance of order $O(n_0 m)$. Therefore, this net flux produces a change in s of the order of $\sqrt{n_0 m}/n_0 = \sqrt{m/n_0} << 1$.

To see the similar role that λ and m have in equilibrating group sizes, we compute next the linearized form of the evolution of the size of one focal group. Suppose that at an arbitrary time, a group has scaled size s that may differ but only slightly from 1, in the sense that $|s-1| << 1$. Our goal is to compute the expected size s' of the group, one generation later. Since s is close to 1, so should also be s' and we want to compute the difference $s'-1$ to first order in $s-1$. Including migration after reproduction out of the group and into the group, we have $s' = sh(s)(1-m) + m$. Since $d(sh(s))/ds = 1-\lambda$, at $s=1$, we obtain, $s' = (1 + (1-\lambda)(s-1) + O(s-1)^2)(1-m) + m$, which yields up to an error of order $(s-1)^2$, the linearized evolution of the disturbances from equilibrium:

$$s' - 1 \;=\; (s-1)(1-\lambda)(1-m). \tag{1}$$

Note that λ and m play exactly the same role here.

Selection is introduced by assuming that each individual is of type A or N (typically representing cooperators and non-cooperators), and that the type is inherited by the offspring without mutation. The expected number of adult offspring of an individual of type $*$ (representing A or N), in a group with k_A individuals of type A and k_N individuals of type N will be supposed to be $w^*_{\vec{k}} = (1 + \delta v^*_{\vec{k}})h(s)$, where $\vec{k} = (k_A, k_N)$, $s = n/n_0$, with $n = k_A + k_N$, the parameter $\delta \geq 0$ measures the strength of selection, and the quantities $v^*_{\vec{k}}$ are in principle arbitrary but assumed to be bounded in absolute value by some $v_{\max}$. (In order for δ to properly account for the strength of selection, we suppose, with no loss of generality, that, until stated otherwise, the order of magnitude of $v_{\max}$ is that of 1. This assumption will be lifted in Section 5, and for this reason will not be needed in Section 6 and in the paper). We assume that when $k_A = 0$, we have $v^N_{\vec{k}} = 0$, so that in case all individuals are of type N, the model behaves as the neutral one. When $\delta = 0$, we also recover the neutral model, and the types A and N are then neutral markers. Selection operates on a time scale of order $1/\delta$. When $\delta > 0$ is small enough that this time scale is longer than the other relevant ones, namely $1/\lambda$ and $1/m$, selection is weak. In this case it is natural to refer to the quantities $v^*_{\vec{k}}$ as "marginal fitness functions". (One could argue that this name should be given to $v^*_{\vec{k}} h(n/n_0)$, but when selection is weak, we will see that in the relevant situations, $h(n/n_0) = 1 + O(\delta)$, so that the difference is negligeable.) We will denote by $\bar{v}_{\vec{k}} = \frac{k_A v^A_{\vec{k}} + k_N v^N_{\vec{k}}}{k_A + k_N}$ the average marginal fitness function in a group with composition $\vec{k}$. In case the interaction among group members is well represented by a linear public goods game, we have $v^A_{\vec{k}} = -C + B(k_A - 1)/(n-1)$, $v^N_{\vec{k}} = Bk_A/(n-1)$, where $0 < C < B$ are the usual cost and benefit parameters. When n is large, it is natural to assume that $v^*_{\vec{k}} = \widetilde{v}^*_x + O(1/n)$, with $x = k_A/n$, $n = k_A + k_B$, for some piecewise continuous function $\widetilde{v}^*_x$, $0 \leq x \leq 1$. For instance, for the linear public goods game we have $\widetilde{v}^A_x = -C + Bx$, $\widetilde{v}^N_x = Bx$. In an abuse of notation we will drop the tilde from $\widetilde{v}^*_x$ and will also write $\bar{v}_x = xv^A_x + (1-x)v^N_x$. The fitness function now reads

$$w^*(s,x) \ = \ h(s)\,(1 + \delta v^*_x). \tag{2}$$

3 Weak selection and quasi-equilibria

We will always suppose that selection is weak. For the moment we will assume that selection is weak in a "worst scenario sense", by assuming $\delta << m$ and $\delta << \lambda$. This is a worst scenario sense in that it makes $\delta v^*_x << m, \lambda$, in all circumstances. This will simplify the analysis, but in Section 5 we will explain that actually weak selection requires a less stringent assumption for our purposes.

Our assumption above implies that for each frequency p of types A, groups will reach a quasi-equilibrium in a time much shorter than $1/\delta$ and this lasts for a period of time of order $1/\delta$, before changes in p become relevant.

We can think of the quasi-equilibrium with frequency p of types A as a small perturbation from what we would observe if we had $\delta = 0$. With $\delta = 0$, we would have the neutral equilibrium described in the previous section. The fraction of type A individuals in the population would be p, which would vary by drift only in a time scale of order g^2, assumed much larger than all the relevant time scales, including $1/\delta$. Selection with a small $\delta > 0$, perturbs this picture, and leads to changes in the values of p and s in a time scale of order $1/\delta$. The direction in which p varies will be our main concern below. But before we can address this question, we note that the effects of weak selection on the value of s will be small, in the sense that at any time and for any value of p we will have $s = s_p = 1 + O(\delta/\lambda)$. This fact is a consequence of the fact that fitnesses are always between the two values given by $(1 \pm \delta v_{\mathrm{max}})h(s)$. Therefore they are larger than 1, when s is below s_{min} that solves $(1 - \delta v_{\mathrm{max}})h(s_{\mathrm{min}}) = 1$. And they are smaller than 1, when s is above s_{max} that solves $(1 + \delta v_{\mathrm{max}})h(s_{\mathrm{max}}) = 1$. Solving each one of these two equations, with the notation s_{m} for s_{min}, or s_{max}, gives $h(s_{\mathrm{m}}) = 1 + O(\delta)$. Since $h(s)$ is continuously differentiable, with $h(1) = 1$, $h'(1) = -\lambda$, we have $h(s) = 1 - \lambda(s-1) + o(s-1)$ and hence $s_{\mathrm{m}} = 1 + O(\delta/\lambda)$. To complete the argument, observe now that s_p must be constrained to be inside the interval $[s_{\mathrm{min}}, s_{\mathrm{max}}]$, since it would be pushed back up if becoming smaller than s_{min} and back down if becoming larger than s_{max}.

The quasi-equilibrium with a given value of p can now be described as follows, thanks to a well known result by S. Wright [5] on the distribution of alleles in the infinite island model. Groups have size close to n_0, and the distribution of the fraction x of types A over these groups is therefore well approximated by that of an infinite islands model with this group size, namely a beta distribution with parameters lp and lq, where $l = 2m_e n_e$, the effective migration rate (for non-overlaping generations) is $m_e = m(1-m/2)/(1-m)^2$ (which is close to m when $m << 1$), and the effective population size is $n_e = n_0/\sigma^2$, where σ^2 is the variance in the number of adult offspring that each individual produces in a life cycle (see [1], pp. 105,6, but be aware that his N relates to our n_0 as $N = 2n_0$). For instance, when the adult offpring distribution is Poisson, we have $n_e = n_0$. The parameter l is related to the relatedness R between individuals in the same group through the expression $R = \frac{1}{1+l}$, that allows one to obtain estimates of l from empirical estimates of R. For this purpose we should equate R with $F_{\text{st}} = \frac{\text{Var}(x)}{pq}$, so that $l = \frac{1}{F_{\text{st}}} - 1$. This is so because a beta distribution with parameters lp and lq has mean p and variance $\frac{pq}{1+l}$, implying that the empirical F_{st} should be $\frac{1}{1+l}$.

Since we will focus on a situation in which $s = n/n_0$ is typically close to 1, the main way in which the function $h(s)$ is relevant is through the value of the rigidity parameter $\lambda = -h'(1)$. Note that the larger λ, the stronger is the effect of intra-group competition in decreasing fitness.

4 ILR when m and λ are comparable

In [3] we analyzed cases in which either $\lambda << m$ ("Hamilton regime"), or $m << \lambda$ (called "Taylor regime" there, and now called "crowded regime"). Here we provide a more elaborate analysis, which does not depend on the relation between λ and m. In this way we address the issue left open in [3], of the case in which m and λ are comparable, and also recover the results of [3].

Our goal is to compute the change in p over one generation, Δp, when the population is in one of the quasi-equilibria. For this we will use the well known formula

$$\Delta p \;=\; pq\,\frac{W^A - W^N}{\bar{W}}, \tag{3}$$

where W^* is the average number of adult offspring of individuals of type $*$, and $\bar{W}$ is the average number of adult offspring of all the individuals in the population.

To compute W^*, one can select a focal individual at random from the population, and compute its expected number of adult offspring, conditioned on its type being $*$. We will denote by $\mathbb{E}^*_p$ the expectation conditioned on the focal being of type $*$. Referring to (2), our task is, therefore, to compute $W^* = \mathbb{E}^*_p(h(s)(1+\delta v^*(x)))$. Since s only differs from 1 by amounts of order δ and $h(1) = 1$, we have, up to an error of order δ^2, $h(s)(1+\delta v^*_x) = h(s) + \delta v^*_x$ and hence

$$W^* \;=\; \mathbb{E}^*_p(h(s)) \;+\; \delta\,\mathbb{E}^*_p(v^*_x). \tag{4}$$

First we address the second term. The expectation $\mathbb{E}^*_p(v^*_x)$ can be made more explicit, by using the beta distribution described in the previous section. We will use the notation $\text{beta}(x|\alpha,\beta) = \frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)} x^{\alpha-1}(1-x)^{\beta-1}$, to denote the probability density of a beta distribution with parameters α and β. The only special care that needs to be taken is that conditioning on the type of the focal modifies the allele distribution in its group. For instance, the information that the focal is type A indicates that there are more types A in the group than a randomly selected group would have (sampling bias). This can be easily taken care of, using Bayes' formula. Since given that a group has a fraction x of types A yields probability x that an individual taken at random from this group will be type A, we obtain an extra factor x in the density, when conditioning on the focal being type A. Normalizing the distribution, gives a beta with parameters $lp+1$ and lq. Analogously, conditioning on the focal being type N, yields a beta with parameters lp and $lq+1$. We can now write

$$\mathbb{E}_p^A(v_x^A) \;=\; \int_0^1 \mathrm{beta}(x|lp+1, lq)\, v_x^A\, dx, \qquad \mathbb{E}_p^N(v_x^N) \;=\; \int_0^1 \mathrm{beta}(x|lp, lq+1)\, v_x^N\, dx. \tag{5}$$

When one can neglect the first term in (4), one obtain from (3) and (5),

$$\Delta p \;=\; \delta pq \left(\int_0^1 \mathrm{beta}(x|lp+1, lq)\, v_x^A\, dx - \int_0^1 \mathrm{beta}(x|lp, lq+1)\, v_x^N\, dx \right) \;+\; o(\delta). \tag{6}$$

In [3] we showed that this is the case when $\lambda << m$, and referred to this regime as Hamilton regime.

In the case of the linear public goods game, $v_x^A = -c + bx$, $v_x^N = bx$, we can use the fact that the mean of a beta distribution with parameters α and β is $\alpha/(\alpha+\beta)$, to compute the beta integrals and see that, regardless of the value of p, $\Delta p = \delta pq(-c+bR) + o(\delta)$, where $R = \frac{1}{1+l}$ is Wright's expression for the relatedness in the infinite island model, for haploids. In particular the condition for altruism to increase in frequency becomes then Hamilton's $c < bR$.

We call the second term in (4) the Hamilton term. By contrast the first term in (4) will be called the extra-Hamilton term, and will be our concern below.

The meaning of the extra-Hamilton term $\mathbb{E}_p^*(h(s))$ is not hard to understand. Looking back in time, the lineage of the focal individual of type $*$ was in its group for a random time with a geometric distribution with probability of success m. While in the group, that lineage and its descendants affected the fitness of the group members and hence the present value of s. These fitness effects are of order δ, so that the cummulative effect on s should be of order δ. This means that $s - s_p = O(\delta)$, where s_p is the quasi-equilibrium value. And since s_p is within a difference of order δ from 1, where $h'(1) = -\lambda$, we have

$$\begin{aligned}
\mathbb{E}_p^*(h(s)) \;&=\; h(s_p) + \mathbb{E}_p^*[h'(s_p)(s-s_p)] + \mathbb{E}_p^*[O((s-s_p)^2)] \\
&=\; h(s_p) + \mathbb{E}_p^*[(h'(1)+O(\delta))(s-s_p)] + \mathbb{E}_p^*[O((s-s_p)^2)] \\
&=\; h(s_p) - \lambda \mathbb{E}_p^*(s-s_p) + O((\delta)^2).
\end{aligned} \tag{7}$$

This means that an effect of order δ on $s - s_p$ renders the extra-Hamilton term $\mathbb{E}_p^A(h(s)) - \mathbb{E}_p^N(h(s))$ also of order δ, and hence comparable to the Hamilton term $\delta(\mathbb{E}_p^A(v_x^A) - \mathbb{E}_p^N(v_x^N))$.

To compute now the effect of $*$ on $s - s_p$, given by $\mathbb{E}_p^*(s - s_p)$, and complete the computation in (7), we will look back in time (calling the present time 0), and ask for each previous time $-t$, $t = 1, 2, ...$ whether the lineage of the focal was still in the group or not, and if it was, what effect this has on the present expected size of the group. The probability that the lineage of the focal was in the group at time $-t$ is simply $(1-m)^t$. If it was not in the group at that time, it produced no effect. If it was in the group then, this means that we had an ancestor of the focal in the group then. In other words, we are given the information that our group at time $-t$ had a focal individual (the ancestor of our time 0 focal) of type $*$. And conditioning on this information implies that the distribution of x at time $-t$ should be well approximated by $\text{beta}(x|lp+1, q)$, in case $*$ is A, and by $\text{beta}(x|lp, lq+1)$ in case $*$ is N. In particular the conditional expected value of $\bar{v}_x$ at time $-t$ would then be, respectively,

$$e^A \;=\; \int_0^1 \text{beta}(x|lp+1, lq)\, \bar{v}_x\, dx, \qquad e^N \;=\; \int_0^1 \text{beta}(x|lp, lq+1)\, \bar{v}_x\, dx.$$

The average fitness of members of a group is $h(s) + \delta\bar{v}_x + O(\delta^2)$. Therefore, from time $-t$ to time $-t+1$, the expected increment in s, due to the effect on $\bar{v}_x$ of the possible presence of the lineage of the focal there would be, up to an error of order δ^2,

$$(1-m)^t \left(\delta\, \mathbb{E}_p^*(\bar{v}_x \text{ at time } -t \,|\, E)\right) (1-m) \;=\; \delta\, e^*\, (1-m)^{t+1}, \tag{8}$$

where E is the event that the lineage of the focal is in the group at time $-t$, the factor $(1-m)^t$ is the probability of E and the other $(1-m)$ factor is due to migration out of the group between time $-t$ and $-t+1$. Now, from time $-t+1$ to time 0, the disturbance to the equilibrium value of s, computed in (8) is partially dissipated, due to the fact that through λ and m effects, the dynamical evolution in the group pushes its size towards the equilibrium value s_p. As we are always within distance of order δ of that equilibrium, which itself is within distance of order δ from 1, we can use for the computation of this dissipative effect a linearized form of the evolution in the absence of selection, given by (1). The quantity in (8) should therefore be multiplied by $[(1-\lambda)(1-m)]^{t-1}$, to give the contribution from time $-t$ to the expectation $\mathbb{E}_p^*(s-s_p)$, at the present time 0. Therefore, summing over t, we have

$$\mathbb{E}_p^*(s-s_p) \;=\; \delta\, e^* \sum_{t=1}^{\infty} (1-m)^{2t}(1-\lambda)^{t-1} \;=\; \delta\, e^* \frac{(1-m)^2}{1 - (1-\lambda)(1-m)^2}.$$

Referring back to (7), we obtain the extra-Hamilton term as

$$\mathbb{E}_p^A(h(s)) - \mathbb{E}_p^N(h(s)) \;=\; \delta\, (e^A - e^N)\, Q, \tag{9}$$

where

$$Q \;=\; \frac{-\lambda(1-m)^2}{1 - (1-\lambda)(1-m)^2} \;=\; -\frac{1}{1 + 2m_e/\lambda}, \tag{10}$$

with

$$m_e \;=\; m\, \frac{1 - m/2}{(1-m)^2}. \tag{11}$$

The effective (for non-overlaping generations) migration rate m_e is the same that appears in the expression of the relatedness

$$R = \frac{1}{1 + 2m_e n_e}. \tag{12}$$

When m is small, $m_e \approx m$. The similarity between (10) and (12) is intriguing, but we do not have a complete explanation for why these expressions look so much alike. What is important to keep in mind is that given the parameters of the neutral population, we obtain n_e, m, and λ and hence R and Q. And that those two are the only numerical features from that neutral population structure that will appear in the condition for the spread of types A. One should keep also in mind that Q varies in the interval $[-1, 0]$, with the bottom being reached when $m << \lambda$ (crowded regime) and the top being reached when $\lambda << m$ (Hamilton regime).

Combining the Hamilton and the extra-Hamilton terms in (4), as computed respectively in (5) and in (9), we obtain for the change over one generation in the frequency p of types A:

$$\Delta p = pq \frac{W^A - W^N}{\bar{W}} = \delta pq F(p) + o(\delta), \tag{13}$$

where $q = 1 - p$ and

$$F(p) = F_{\text{Hamilton}}(p) + F_{\text{extra-Hamilton}}(p), \tag{14}$$

$$F_{\text{Hamilton}}(p) = \int_0^1 \text{beta}(x|lp + 1, lq)\, v_x^A \, dx - \int_0^1 \text{beta}(x|lp, lq + 1)\, v_x^N \, dx,$$

$$F_{\text{extra-Hamilton}}(p) = Q \left[\int_0^1 \text{beta}(x|lp + 1, lq)\, \bar{v}_x \, dx - \int_0^1 \text{beta}(x|lp, lq + 1)\, \bar{v}_x \, dx \right].$$

The condition for the spread of types A is $F(p) > 0$, which in the limit $p \to 0$ (in which $\text{beta}(x|lp, lq + 1)$ concentrates on $x = 0$, as its mean and standard deviation vanish) gives raise to the invasion condition

$$\int_0^1 \text{beta}(x|1, l)\, v_x^A \, dx + Q \int_0^1 \text{beta}(x|1, l)\, \bar{v}_x \, dx > 0. \tag{15}$$

For an alternative, equivalent and more compact way of stating the results above, we define

$$\hat{v}_x^* = v_x^* + Q\bar{v}_x. \tag{16}$$

With this definition, we can write

$$F(p) = \int_0^1 \text{beta}(x|lp + 1, lq)\, \hat{v}_x^A \, dx - \int_0^1 \text{beta}(x|lp, lq + 1)\, \hat{v}_x^N \, dx. \tag{17}$$

And the condition (15) takes the form

$$\int_0^1 \text{beta}(x|1,l)\, \hat{v}_x^A \, dx \ > \ 0. \tag{18}$$

From the results above, one can readily recover the results in [3] in the two extreme cases of Q. When $\lambda << m$ (Hamilton regime), Q vanishes and hence so does also $F_{\text{extra-Hamilton}}(p)$. In contrast, when $m << \lambda$ (crowded regime), $Q \approx -1$, from which it is easy to show that if cooperation is costly, meaning $v_x^A \le v_x^N$ for all x, with strict inequality for some interval of values of x, then $\Delta p < 0$ and types A are eliminated by selection. (To see it, observe that $\bar{v}_x$ is between v_x^A and v_x^N, which implies that, with $Q = -1$, $\hat{v}_x^A$ is never positive and must be negative in some interval, while $\hat{v}_x^N$ is never negative and must be positive in some interval. From (17) we obtain $F(p) < 0$, for all p, and reference to (13) completes the argument.)

In the case of a linear public goods game, $v_x^A = -c+bx$, $v_x^N = bx$, $\bar{v}_x = xv_x^A+(1-x)v_x^N = (b-c)x$. These yield $\hat{v}_x^A = -c + (b + Q(b-c))x$, $\hat{v}_x^N = (b + Q(b-c))x$. Therefore (13) and (17) give (using the fact that the mean of a beta distribution with parameters α and β is $\alpha/(\alpha+\beta)$ to compute the beta integrals)

$$\Delta p = \delta pq(-c + (b + Q(b-c))R) + o(\delta), \tag{19}$$

where $R = 1/(1+l) = 1/(1+2m_e n_e) = 1/(1+2m_e(n_0/\sigma^2))$, when n_0 is large and m is small and where σ^2 is the variance of the offspring distribution. In particular, regardless of the value of p, the condition $F(p) > 0$ for altruism to increase in frequency becomes

$$-c + bR + Q(b-c)R \ > \ 0. \tag{20}$$

When $Q = 0$, this reduces to the standard Hamilton condition $c < bR$, while in the opposite extreme, when $Q = -1$, it reduces to the condition $-c(1-R) > 0$, and altruism cannot spread.

One can easily remember the effect of Q on the linear public goods games as simply changing the benefit b into the effective benefit $b + Q(b-c)$, while not affecting the cost c.

5 Islands with local and global regulation. Range of weak selection

Selection can be in part local and in part global. To modify the ILR population structure into ILGR (Islands with Local and Global Regulation), we define N as the total population size and $S = N/(gn_0)$, as the scaled total population size. (Recall that there are g groups, and that their equilibrium size in the absence of selection is n_0, so that the equilibrium total population size is then gn_0.) The ILRG population structure is introduced by assuming that the fitness of an individual of type $*$ in a group of scaled size s and fraction of types A given by x, when the total scaled population size is S, is given by

$$w^*(x,s,S) \ = \ H(s,S) \ + \ \delta h(s) v_x^*, \tag{21}$$

where the function $H(s, S)$ takes the value 1 at $(s, S) = (1, 1)$, is strictly decreasing in s and S, and and is continuously differentiable, with $\partial H(s, S)/\partial s = -\lambda$, $\partial H(s, S)/\partial S = -\lambda_g$ at $(s, S) = (1, 1)$. We will suppose that the parameters λ and λ_g are both positives and their sum is at most 1. An example to keep in mind is the logistic $H(s, S) = 1 + r_0 a(1 - s) + r_0(1 - a)(1 - S)$, where $0 \leq a \leq 1$ is a parameter that splits the regulation into a local part (fraction a) and a global part (fraction $(1 - a)$). In this example $\lambda = ar_0$ and $\lambda_g = (1 - a)r_0$. The function $h(s)$ is now only supposed to be differentiable and to have $h(1) = 1$.

In the absence of selection ($\delta = 0$), there is a stable equilibrium in which all groups have size close to n_0. (As before, we assume that g and n_0 are large, so that fluctuations around this equilibrium group size will be neglected in the analysis.) And the distribution of the fraction x of types A over the groups will again be well approximated by a beta distribution with parameters lp and lq.

If now δ is positive but sufficiently small, and the population is initially close to the ($\delta = 0$)-equilibrium described above (i.e., is in quasi-equilibrium), then the same arguments and computations done in the case of ILR produce the following result. The fraction p of types A in the population evolves according to (13), in which λ appears as before in the expression (10) of Q, but λ_g is absent. This difference in λ and λ_g effects is intuitive. In the computation of $F(p)$ and in particular of the extra-Hamilton term, we are looking at the effect that knowledge of the type of the focal has on its group's x and s. This knowledge can be seen as a "distubance of that group", but not of the other groups, and hence amounts to a negligeable disturbance of S. For this reason only λ and m reflect on the effect of this "disturbance", not λ_g.

But λ_g has an important effect on the evolution of the average scaled size of the groups. When the frequency of types A is p, the population is close to a quasi-equilibrium in which average scaled group size s_p is such that the average fitness is one. Since groups will all have approximatelly this average size, this means that also $S = s_p$, and we must have $H(s_p, s_p) + \delta h(s_p) I\!E_p(\bar{v}_x) = 1$, where $I\!E_p$ is the expectation with respect to beta$(x|lp, lq)$. If δ is sufficiently small, an approximate solution is obtained from $1 - \lambda(s_p - 1) - \lambda_g(s_p - 1) + \delta I\!E_p(\bar{v}_x) = 1$, which yields

$$s_p \;=\; 1 + \frac{\delta I\!E_p(\bar{v}_x)}{\lambda + \lambda_g} \;=\; 1 + \frac{\delta \int_0^1 \text{beta}(x|lp, lq)\, \bar{v}_x \, dx}{\lambda + \lambda_g}. \tag{22}$$

This result is also very intuitive. Global and local regulation are equally important in keeping the average group size from changing.

Note that in Section 2 we assumed a condition that was sufficient to make the equilibrium with $s = 1$ a universal attractor (apart from the population being extinct), so that even if started far from it, regulation and migration would drive the population to that equilibrium when $\delta = 0$ and to quasi-equilibrium when $\delta > 0$ is small. In the ILGR case, this condition is that $sH(s, s) < 1$, when $s < 1$. We either add such an assumption, or assume that initially the population is close to quasi-equilibrium.

We turn now to the question of how small δ must be for selection to be regarded as weak. In doing this we will no longer assume that all the values $|v_x^*|$ are necessarily smaller than 1, as v_x^* will appear explicitly in the conditions for weak selection, multiplying δ. The computation leading to (22) illustrates the fact that for selection to be weak, when the frequency of types A in the population is p, we do not need the full power of the "worst case scenario" condition introduced in Section 3, which relies on δv_x^* to be appropriately small uniformly in x. In the computation above we only needed

$$\delta\, |I\!\!E_p(\bar{v}_x)| \ << \ \lambda + \lambda_g, \quad \text{or equivalently} \quad \delta \left| \int_0^1 \text{beta}(x|lp, lq)\, \bar{v}_x \, dx \right| << \ \lambda + \lambda_g, \qquad (23)$$

and corrections to (22) will be of order $(\delta I\!\!E_p(\bar{v}_x))^2$.

In addition to (23), the only other condition for weak selection is the requirement that group sizes and the distribution of x equilibrate, with the given value of p much faster than p evolves. Since group size equilibrates in a time scale at least as fast as $1/m$ and the distribution of x equilibrates in a time scale of order $1/m$, this additional condition for selection to be weak when the frequency of types A is equal to p is that the evolution of p occurs on a time scale that is much longer than $1/m$. In the reasoning that follows we will use the time evolution equation (13) obtained under the assumption of weak selection. This means that we are verifying under what conditions the assumption of weak selection is self-consistent. From (13), the change in p over one generation is $\delta pqF(p)$. When p and q are far from 0, the term pq is of order 1 and the time scale for p to change is then of order $1/(\delta|F(p)|)$. When p is close to 0, the time scale for relevant changes in p is the time scale in which p changes by an amount comparable to the current value of p. But in this case $q \approx 1$, and (13) becomes in leading order $\Delta p/p = \delta F(p)$. The relevant time scale for significant changes in p is again $1/(\delta|F(p)|)$. The case in which $p \approx 1$ is analogous. The additional condition for weak selection, when the fraction of types A is p is therefore simply given by

$$\delta\, |F(p)| \ << \ m. \qquad (24)$$

We can summarize now our conclusions about ILGR (including the special case of ILR) and weak selection. Conditions (23) and (24) are sufficient for the evolution to be well described as weak selection, when the frequency of types A is p. In this case p evolves according to (13), in which Q is given by (10). And as p(t) evolves by (13), scaled group size equilibrates at $s_{p(t)}$ given by (22). The value of Q and hence of Δp depends on how the strength of local regulation, λ, compares to the strength of migration, m, but does not depend on the strength of global regulation, λ_g. Global regulation plays nevertheless a role identical to that of local regulation in attenuating group size change, as p changes.

In case $p << 1$ (invasion case), there is a further simplification in the conditions for selection to be weak. In this case the beta integral in (23) is 0, as that beta has mean and variance converging to 0 as $p \to 0$, and $\bar{v}_0 = v_0^N = 0$. Therefore (23) is always satisfied, and therefore weak selection requires only (24).

For the iterated games that are our main concern in the paper, the values of v_x^* may vary by factors comparable to the number of iterations of the game, as x varies from 0 to 1. Therefore, when we analyze invasion by cooperators, it is important that we only have the relatively mild condition (24) as reqirement to apply the weak selection results.

6 The theory in terms of regression coefficients. Comparison with simulations

In this section we explain that the partition (14) of $F(p)$ can be written in terms of regression coefficients. In addition to its conceptual value, this remark provides a way to measuring Q in simulations or (at least in principle) real data. We will also explain that if the observed value of Q is close to the theoretical one and the observed distribution of types in groups is also close to the theoretical beta distribution, this is sufficient to trust the predictions of the theory.

It is well know that (3) can be rewritten in terms of covariances or regression coefficients. For this purpose, we will consider the random experiment in which a focal individual is chosen at random from the population. This random experiment is equivalent to choosing a group at random, with probabilities proportional to group size, and then choosing the focal individual at random from this group. We use the notation I_A for the random variable that takes the value 1 if the focal is of type A and 0 if it is of type N. And for arbitrary random variable f we will use the notation $\beta_{f,*} = \mathrm{Cov}(f, I_A)/\mathrm{Var}(I_A) = \mathrm{Cov}(f, I_A)/(pq)$ for the regression coefficient of f on I_A. Simple algebraic manipulations (see, e.g., Section 3 in the supplementary material of [4]), show that (assuming quasi-equilibrium with fraction p of types A)

$$\beta_{f,*} \;=\; \mathbb{E}_p^A(f) \;-\; \mathbb{E}_p^N(f). \tag{25}$$

In particular, (3) can be rewritten as

$$\Delta p \;=\; pq\,\frac{\beta_{w,*}}{\bar{W}}, \tag{26}$$

where w is the absolute fitness of the focal individual. In quasi-equilibrium $\bar{W} = 1 + O(\delta)$, so that we can ignore it in the weak selection case.

Using (21), the partition into a Hamilton and an extra-Hamilton term in Section 4 can now be seen as a partition of the regression coefficient in (26) as

$$\beta_{w,*} \;=\; \beta_{H(s,S),*} \;+\; \beta_{\delta h(s) v_x^*,*}. \tag{27}$$

Under weak selection in quasi-equilibrium, $s = 1 + O(\delta)$ and $h(s) = 1 + O(\delta)$, so that (26) and (27) together become

$$\Delta p \;=\; pq\delta \left(\beta_{v_x^*,*} \;+\; \frac{1}{\delta}\,\beta_{H(s,S),*} \right) \;+\; O(\delta^2). \tag{28}$$

The two terms inside the parenteses in (28) are respectively the Hamilton and extra-Hamilton terms. The analysis of the extra-Hamilton term in Section 4, is equivalent to the statement that

$$\beta_{H(s,S),*} \;=\; \delta\, Q\, \beta_{\bar{v}_x,*} \;+\; o(\delta), \tag{29}$$

with Q given by (10), and where $\bar{v}_x$ is the average payoff in the focal's group. In other words, if we define the empirical value of Q as

$$Q\text{emp} \;=\; \frac{1}{\delta}\,\frac{\beta_{H(s,S),*}}{\beta_{\bar{v}_x,*}}, \tag{30}$$

then our analysis in Section 4 led to the claim that

$$Q\text{emp} \;=\; Q, \tag{31}$$

with Q given by (10). While this theoretical claim depended on the assumption that n_0 is very large, we observed in our simulations good agreement in (31) with fairly small n_0 (see Table 1 in the paper).

Now, suppose that (31) is closely verified in the data. This allows us to replace (28) with the approximation

$$\Delta p \;\approx\; pq\delta\,\left(\beta_{v_x^*,*} \;+\; Q\;\beta_{\bar{v},*}\right) \;=\; pq\delta\,\beta_{\hat{v}_x^*,*}, \tag{32}$$

with Q given by (10) and $\hat{v}_x^* = v_x^* + Q\bar{v}_x$. And this means (thanks to (25) with $f = \hat{v}_x^*$) that if the distribution of x in the groups is given by the beta(lp,lq) distribution, with $l = 1/Fst - 1$, then (17) holds in good approximation.

In summary, to test the theory in simulations, it is sufficient to test that in good approximation (31) holds and the distribution of the fraction of types A in the groups is close to the theoretical beta(lp,lq). Results along these lines are presented in Table 1 in the paper. In our simulations, we chose $h(s) = 1$, and it is interesting to observe that in this special case the term $O(\delta^2)$ in (28) is actually 0. And we chose the logistic $H(s,S) = 1 + r_0 - \lambda s - \lambda_g S$ (actually this expression becomes negative when s or S are very large, and $H(s,S)$ is then assumed to be 0, but when n_0 is large s or S are rarely that large). In this case we can use the independence between S and the type of the focal (valid as a good approximation when g is large), to conclude that $\beta_{S,*} = 0$, and hence $\beta_{H(s,S),*} = -\lambda\beta s, *$. In this case (30) becomes

$$Q\text{emp} \;=\; -\frac{\lambda}{\delta}\,\frac{\beta_{s,*}}{\beta_{\bar{v}_x,*}}. \tag{33}$$

7 Some iterated games

We apply now the invasion condition (18) to some iterated games, as discussed in the paper. For this purpose we assume an underlying game with payoffs to types A and N being given, respectively, by v_x and v'_x. If the fraction x of types A in the group is smaller than a threshold θ the game is played only once, but if $x \geq \theta$, then the game is played T times. The complete game has then payoffs $v_x^A = v_x$ and $v_x^N = v'_x$, if $x < \theta$ and $v_x^A = Tv_x$ and $v_x^N = Tv'_x$, if $x \geq \theta$.

The invasion condition can then be written as

$$F(0) \;=\; \int_0^\theta \mathrm{beta}(x|1,l)\, \hat{v}_x \, dx \;+\; T \int_\theta^1 \mathrm{beta}(x|1,l)\, \hat{v}_x \, dx \;>\; 0, \tag{34}$$

where $\hat{v}_x = v_x + Q\bar{v}_x = v_x + Q(xv_x + (1-x)v'_x)$.

Because the beta distribution density in this integral has the simple form $\mathrm{beta}(x|1,l) = l(1-x)^{l-1}$, one can perform the integration explicitly in various cases of interest. We present two of these below.

First we consider the case $v_x = v_0$ for $x \in [0,\theta)$, $v_x = v_\theta$ for $x \in [\theta, 1]$, $v'_x = 0$ for $x \in [0,\theta)$, $v'_x = v'_\theta$ for $x \in [\theta, 1]$. In this case we obtain

$$\begin{aligned} F(0) \;=\; & v_0 \left\{1 + QR - [1 + \theta Q + (1-\theta)QR]\,(1-\theta)^l\right\} \\ & + T\,[\hat{v}_\theta + (1-\theta)(v_\theta - v'_\theta)QR]\,(1-\theta)^l, \end{aligned} \tag{35}$$

where $\hat{v}_\theta = v_\theta + Q(\theta v_\theta + (1-\theta)v'_\theta)$, and we used the fact that $\hat{v}_0 = v_0$.

This exact expression helps us better understand under which conditions the much simpler (8) and (12) in the paper are good approximations. (For the payoffs we are studying, these displays in the paper are exact when $Q = 0$, as can be readily checked from (35), but we are interested in arbitrary Q.) Inspecting (35), we see that $QR << 1$ is needed. But this is not enough, as the term $v_0 Q\theta(1-\theta)^l$ in the first line, needs also to be negligeable as compared to the term $T\hat{v}_\theta(1-\theta)^l$ in the second line. This can be assured if $T >> |v_0/\hat{v}_\theta|$.

We are interested in the critical value of T, for which $F(0) = 0$. If we compute it using display (12) in the paper, we obtain the value $T = |v_0/\hat{v}_\theta|\widetilde{T}$, where $\widetilde{T} = (1-\theta)^{-l} - 1$. The last condition in the previous paragraph tells us that we should not trust this approximation, and must instead use the full (35), unless $\widetilde{T} >> 1$. On the other hand, if $\widetilde{T} >> 1$, it follows that $(1-\theta)^{1/R} >> 1$ and hence $R << 1$. This implies that the condition $QR << 1$ in the previous paragraph is also satisfied. In conclusion: we can trust display (12) in the paper as a reasonable approximation if it provides a critical value $T >> |v_0/\hat{v}_\theta|$, but not otherwise.

We turn now to the iterated linear public goods game $v_x = -c + bx$, $v'_x = bx$, $0 < c < b$, as the underlying game. In this case $\hat{v}_x = -c + b_Q x$, where $b_Q = b + Q(b-c)$, and (34) yields

$$\begin{aligned} F(0) \;&=\; -c \;+\; b_Q R \;+\; (T-1)\,[-c + b_Q\theta + (1-\theta)b_Q R]\,(1-\theta)^l \\ &=\; v_0 \;+ b_Q R \;+\; (T-1)\,[\hat{v}_\theta + (1-\theta)b_Q R]\,(1-\theta)^l. \end{aligned} \tag{36}$$

For display (8) in the paper to be a good approximation, we need $b_Q R << c$. This reduces (36) to

$$F(0) = v_0 + (T-1)\hat{v}_\theta(1-\theta)^l, \tag{37}$$

which is not quite the left-hand-side of display (8) in the paper, but is also very simple. Moreover, since $Q \in [-1, 0]$, we have $b_Q \geq c$ and hence the assumption $b_Q R << c$ implies

$R << 1$. Therefore also $(1-\theta)^l << 1$ and $\widetilde{T} = (1-\theta)^{-l} - 1 \approx (1-\theta)^{-l} >> 1$. And hence, the condition for invasion $F(0) > 0$, is well approximated in this case by

$$T \; > \; \frac{-v_0}{\hat{v}_\theta} \widetilde{T} \; + \; 1. \tag{38}$$

Unless $|v_0/\hat{v}_\theta| << 1$, the right-hand-side is $>> 1$, and this condition on T is basically the same as that which appears in display (12) of the paper.

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