

# The Selection of Altruistic Behaviour

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**Summary:** Altruistic behaviour is disadvantageous for the individual while is advantageous for its group. If the target of the selection is the individual, one would expect the selection process to lead to populations formed by wholly homogeneous groups, made up of either altruistic or egoistic individuals, where the winning choice depends on the balance between group advantage and individual disadvantage. We show in a simple model that populations formed by *inhomogeneous* groups can be stabilized in some circumstances. We argue that this condition is realized when there is a relative advantage conferred by the presence of a few altruists to all the members of the group.

## I. Introduction

Natural selection is an egoistic process: individual organisms compete for representation of their genes in the next generation, and only those genomes better able to survive and reproduce are likely to be maintained in the evolutionary process. In this framework it is difficult to explain how “altruistic” genes (that is genes which determine a behavior disadvantageous to the carrier, but beneficial for other individuals) can be selected. Nevertheless, we can find in nature some examples of altruistic behavior, like social organization in insect societies [5, 6], parental care [8, 10] and warning calls in birds [9]. So far, there is no evidence of a genetical basis for altruistic behavior. However, it is an interesting problem in itself to understand how interactions between individuals may be reflected on the action of individual natural selection. The presence of altruists increases

the chances of the group which it belongs to. The general problem is not only to understand what is the level of selection action, but also how the different levels may interact under the selective pressure.

Classically, two main mechanisms have been proposed to explain the origin and evolution of altruism: kin selection [4], [5, 6], [8, 10], and group selection [11], [3]. In both mechanisms it is necessary to assume that individual fitness depends not only on individual genotype, but also on the genetical composition of the population. In kin selection the individual probability of survival is proportional to the relatedness that the individual shares with the altruist. The selection mechanism thus is limited only to related individuals, and the selection unit is the individual. In group selection, the interaction takes place between individuals belonging to the same group, and groups are defined by external constraints (for example spatial boundaries), disregarding any relatedness between individuals. In most cases, one ends up with a situation in which either egoistic or altruistic behavior is selected. Nevertheless, it is clear from observation that most often altruistic behavior is exhibited only by some individuals in the group.

A recent report concerns territorial defense by prides of lions. Female lions living in Serengeti National Park and Ngorongoro Crater (Tanzania) live in groups that hunt together and defend a common territory against other groups. Heinsohn and Packer report in [7] that some lionesses act more aggressively and swiftly in defense, while others tend to lag behind. No consistent relations were observed between physical size and defense-readiness. Furthermore, when engaging in aid of a pride-mate mounting a defense, no-consistent relation was found between the readiness of the helper, and the kin relation between the helper and the first defender. Territorial defense in groups of female lions therefore seems to be a case of altruistic behavior where kin relation does not play a role.

The fact that altruistic behavior can be selected both disregarding relatedness between individuals of the same group and maintaining the individual as the selection unit was already evidenced in [1]. In the following we prove this result with an exactly solvable model in which the total number of individuals is assumed to be very large, while the size of the groups is kept finite. Moreover, we show that the advantage of the presence of altruistically behaving individuals is already felt when their number is small. In this case the stable situation can be one in which *inhomogeneous* groups, formed of both egoistic and altruistic individuals, coexist with both fully egoistic and fully altruistic ones.

In section 2 we describe the phenomenology and we fix the ingredients which are relevant in the evolution dynamics. The precise mathematical model and its exactly solvable approximation are described in section 3. In section 4 we derive the phase diagram of the stable state and we discuss the condition for the existence of the non-trivial phase with inhomogeneous groups. A final discussion can be found in section 5.

## II. The Model

We consider a population made up of  $M$  individuals, divided in  $N$  groups (demes) of  $L = M/N$  individuals on average. We assume non-overlapping generations, heredity acting according to the usual Mendelian mechanism, and the presence of a behavioral locus with two alleles: A (recessive) and E (dominant). An individual of genotype AA is altruist, while AE and EE are not. However, as a first approximation, we disregard the individual genetical structure, considering only the two classes of individuals: altruist (A) and egoist (E). Demes have a variable number  $j$  of altruistic individuals A. If, for a given deme,  $j$  is greater than a threshold  $j^*$  the deme is called *altruistic*, otherwise *egoistic*. We shall call any deme with exactly  $j$  altruistic individuals a  $j$ -deme.

To each individual  $\alpha$  in a generation we associate its fitness value  $f(\alpha)$ , which is proportional to the survival probability of its genome in the population over one step. The fitness  $f(\alpha)$  of the individual  $\alpha$  depends on two factors:

1. *on its genotype*: if the individual is altruist (genotype A), its fitness is *reduced* by a factor  $(1 - r)$  with respect to the other members of its deme;
2. *on its deme composition*: if the individual (whatever its genotype) belongs to an altruistic deme its fitness is *enhanced* by a factor  $1/(1 - c)$ , with respect to individuals with the same genotype belonging to an egoistic one.

The parameter  $r$  is called *intrademic selection rate* and  $c$  is called *interdemic selection rate*.

The form of the fitness is summarized in Table 1.

**Table 1:** Fitness table. Rows: *individual* genotypes; columns: genetical *group* composition. The number of “altruistic” individuals in a deme is denoted by  $j$ . The fitness of an individual belonging to a deme in which  $j$  exceeds the threshold  $j^*$  is enhanced by a factor  $1/(1 - c)$  with respect to those not belonging to such a deme. The fitness of an “altruistic” individual is reduced by a factor  $(1 - r)$  with respect to “egoistic” individuals belonging to the same deme.

	$j < j^*$	$j \geq j^*$
A	$1 - r$	$(1 - r)/(1 - c)$
E	1	$1/(1 - c)$

In the next section we shall define, in a mathematically precise way, the stochastic dynamics that defines our model. For the time being, in order to ease the exposition, we anticipate that it involves the following two steps:

1. *Selection and reproduction*: Taking into account the internal genetical structure, one can consider both asexual and sexual reproduction mechanisms. In the following, we will consider only the asexual case, but the reproduction mechanism does not affect the essential results. The average number of the offspring of an individual  $\alpha$  is given by

$$\overline{v(\alpha)} = \frac{M f(\alpha)}{\sum_{\beta=1}^M f(\beta)}, \quad (1)$$

where  $f(\alpha)$  is the fitness of the individual  $\alpha$ , as defined in Table 1, and the sum runs over the whole population. At the end of this step, the offspring of the individuals of one deme in one generation form one deme.

2. *Deme splitting*: The mean size of the demes is equal to  $L = M/N$ . However, after the reproduction step, some demes can disappear and the mean size of the surviving demes would correspondingly increase. In particular, some demes may have become much greater than  $L$ . We assume that too large demes split in such a way as to keep the mean size  $L$  constant. This rule is motivated by the analogy with social animals, which do not typically live in too large groups. In fact, a group of lions or wolves has a typical size which cannot be exceeded in ordinary conditions; the same happens for social insects, like ants or termites, which have the well known mechanism of swarming to keep the group size below a threshold. Splitting is somehow the analogue of reproduction at the group level. It is also a necessary ingredient for purely modeling reasons: if there is no maximal size of demes, sooner or later one of the demes would take over the whole population, and interdemic selection would cease to operate.

Notice that an A individual has always less chances than an E individual belonging to the same deme, but all the individuals in an altruistic deme may have a greater survival probability than individuals belonging to egoistic demes, independently of their genotypes.

Let us stress that the effect of mutation is not taken into account. This is not a simplification but it is a consequence of the fact that the probability of a mutation from a an altruistic genome to an egoistic one or viceversa is absolutely negligible with respect to the inverse of the typical times involved in this population dynamics. Mutations is sometimes introduced in this kind of evolution problems only as a technical artifice in order to avoid model pathologies.

### III. The Master Equation

We assume that the total number of individuals  $M$  tends to infinity along with deme number  $N$ , keeping the typical deme size  $L$  finite. For the sake of simplicity of computation we assume that the number  $L$  is the same for all demes and remains constant from generation to generation.

We denote by  $n_j(t)$  the number of  $j$ -demes at generation  $t$ , and by  $\rho_j(t) = n_j(t)/N$  the corresponding fraction. The fractions  $\rho_j(t)$  are normalized:

$$\sum_j \rho_j(t) = 1, \quad \forall t. \quad (2)$$

Equation (1) yields the average number of offspring of a single individual after the reproduction step. Assuming that reproduction events are independent from one another, the number of offspring of a single individual is Poisson distributed with expected value equal to  $\overline{v(\alpha)}$  [Eq. (1)]. As a consequence, the number of offspring of a whole deme  $\delta$  after the reproduction step is also Poisson distributed, with average  $Q(\delta)$  given by the sum of  $\overline{v(\alpha)}$  over its members:

$$Q(\delta) = \sum_{\alpha \in \delta} \overline{v(\alpha)}. \quad (3)$$

It follows from Eq. (1) that the size of the offspring of the  $j$ -deme  $\delta$  depends only on the number  $j$  of its altruists and is given, on average, by  $Q(\delta) = V_j L$ , where

$$V_j = \frac{T_j}{\sum_{k=0}^L T_k \rho_k(t)}. \quad (4)$$

In this equation we have introduced the function

$$T_j = \frac{1 - rj/L}{1 - c\Theta(j - j^*)}, \quad (5)$$

where  $\Theta(x)$  is the unit step function. We stress that this is the *average* new size of the deme, disregarding its new genetic composition. Indeed, the genetic composition of a new deme which originates from a  $j$ -deme is also random. We recall that the number of altruists in the old deme is  $j$  while the corresponding number of egoists is  $L - j$ ; on the other hand, the relative probability of survival in the same deme is  $1 - r$ . The probability that a given offspring of a  $j$ -deme is altruist is therefore

$$p_j = \frac{(1 - r)j}{L - rj}. \quad (6)$$

Since reproduction events are independent, the number of altruists is binomially distributed with success probability  $p = p_j$ . This means that the aver-

age fraction of altruists in the reproduced deme is equal to  $p_j$ , while its variance is approximately given by

$$\sigma_j^{\text{rep}} = p_j(1 - p_j) \frac{1}{V_j L}. \quad (7)$$

This expression holds in the approximation in which the average size of the offspring deme is substituted for its actual size: in the reproduction process, demes grow up and shrink, so that their actual size is not constant.

We now consider the effects of deme splitting. First we notice that it produces new demes with smaller size but with the same composition in average and, assuming independence, we have again a binomial redistribution of individuals in the splitted demes. As a consequence, the average fraction of altruists is still given by  $p_j$ , but the variance is increased by an amount, approximately given by

$$\sigma_j^{\text{split}} = p_j(1 - p_j) \frac{1}{L}. \quad (8)$$

We then notice that the distribution of the sizes depends on the assumed splitting mechanism, with the only constraint that the average size is brought back to  $L$ . For the sake of simplicity we assume that all demes after breaking have again size  $L$ .

If  $L$  is large enough, we can approximate the binomial distribution of altruist numbers in the new demes by a gaussian. This approximation is meaningful whenever a gaussian is a good approximation of a binomial and surely does not modify the qualitative behavior of the model. Define

$$G_{ij} = \exp \left( - \frac{(i - p_j L)^2}{2\sigma_j L^2} \right), \quad j \neq 0, L \quad (9)$$

where

$$\sigma_j = \sigma_j^{\text{split}} + \sigma_j^{\text{rep}}. \quad (10)$$

The transition probability matrix (i.e., the probability of having  $i$  altruist in a deme at time  $t + 1$  from a  $j$ -deme at time  $t$ , after the reproduction and splitting steps) is given by

$$A_{ij} = \frac{G_{ij}}{\sum_i G_{ij}}, \quad j \neq 0, L \quad (11)$$

Since, in the absence of mutations, all demes originating from a homogeneous deme (be it altruistic or egoistic) are also homogeneous and of the same type, we have

$$A_{LL} = A_{00} = 1; \quad (12)$$

$$A_{iL} = 0, \quad i \neq L; \quad (13)$$

$$A_{i0} = 0, \quad i \neq 0. \quad (14)$$

It should be remarked that only large demes split and therefore  $\sigma_j = \sigma_j^{\text{rep}}$  for small demes. Nevertheless the error we introduce extending (10) to all demes is negligible, because for small demes  $V_i < 1$ , so that  $\sigma_j^{\text{split}} < \sigma_j^{\text{rep}}$ .

The number of demes changes because of splitting: however, since the number of demes,  $N$ , goes to infinity, the fraction of demes originating from  $j$ -demes is equal to its average because of the law of large numbers. This number is given by

$$V_i \rho_j = \frac{T_i \rho_j(t)}{\sum_{k=0}^L T_i \rho_j(t)}, \quad (15)$$

We are thus led to the equation

$$\rho_j(t+1) = \frac{1}{Z(t)} \sum_i A_{ij} T_j \rho_j(t), \quad (16)$$

which closely resembles Eigen's quasispecies equation [2]. The normalization factor  $Z_t$  is given by

$$Z(t) = \sum_j T_j \rho_j(t) \quad (17)$$

The main difference between eq. (16) and the quasispecies equation lies in the fact that the matrix of transition probabilities ( $A_{ij}$ ) also depends on the vector  $[\rho_j(t)]$  via the variances ( $\sigma_j$ ). This implies that the equation (16) is nonlinear, but nevertheless, it is easy to solve it numerically. When  $t$  is large the distribution reaches a stationary state and (16) becomes an ordinary equation for the time independent  $\rho_j$ . In principle, one can now find out the analytical solution, and, indeed, this is feasible for small  $L$ . On the contrary, when  $L$  increases, this task becomes practically impossible and the numerical solution remains the only open option.

#### IV. Results

In the long run, the population reaches a steady distribution, which may be of one among three types. The first two types correspond to a population composed only by altruistic or egoistic individuals. It is trivial to remark that the demes for these two phases have an homogeneous composition. The third type correspond to a situation where, together with homogeneous demes of both kinds, one has inhomogeneous demes, formed by both egoistic and altruistic individuals.

Let us first imagine that the population is initially composed only by homogeneous demes of either kind: completely altruistic and completely egoistic. In this case no mixed demes can be generated, since homogeneous demes only reproduce themselves. The advantage for the completely altruistic

deme is  $1/(1 - c)$  while its disadvantage is  $1 - r$ . It is easy to understand that, in this case, the population will end up being made of only completely altruistic demes if  $c > r$  and only egoistic ones if  $c < r$ . In other words:

$$\rho_{eq}(j) = \begin{cases} 1, & \text{for } j = 0; \\ 0, & \text{for } j > 0; \end{cases} \quad \text{for } c < r; \quad (18a)$$

$$\rho_{eq}(j) = \begin{cases} 0, & \text{for } j < L; \\ 1, & \text{for } j = L; \end{cases} \quad \text{for } c > r. \quad (18b)$$

If we mark with dots the region in which only altruistic individuals are present and with short vertical lines the region where only egoistic ones are present in the  $(r, c)$  plane, we obtain the “phase diagram” of Fig. 1. We call “phases” the different regimes of the equilibrium population: egoistic, altruistic, or mixed.

Suppose now that also inhomogeneous demes are initially present. In this case demes with  $j \geq j^*$  share with completely altruistic ones the “altruistic advantage” and, since they have  $L - j$  egoistic individuals, they partially share the “egoistic advantage” with the completely egoistic demes. From this point of view, the fittest demes would be those with  $j = j^*$ . Nevertheless, reproduction and splitting changes their composition, so that they most of the times do not reproduce. Briefly, mixed demes can generate homogeneous demes but not viceversa. Due to these competing effects, it is

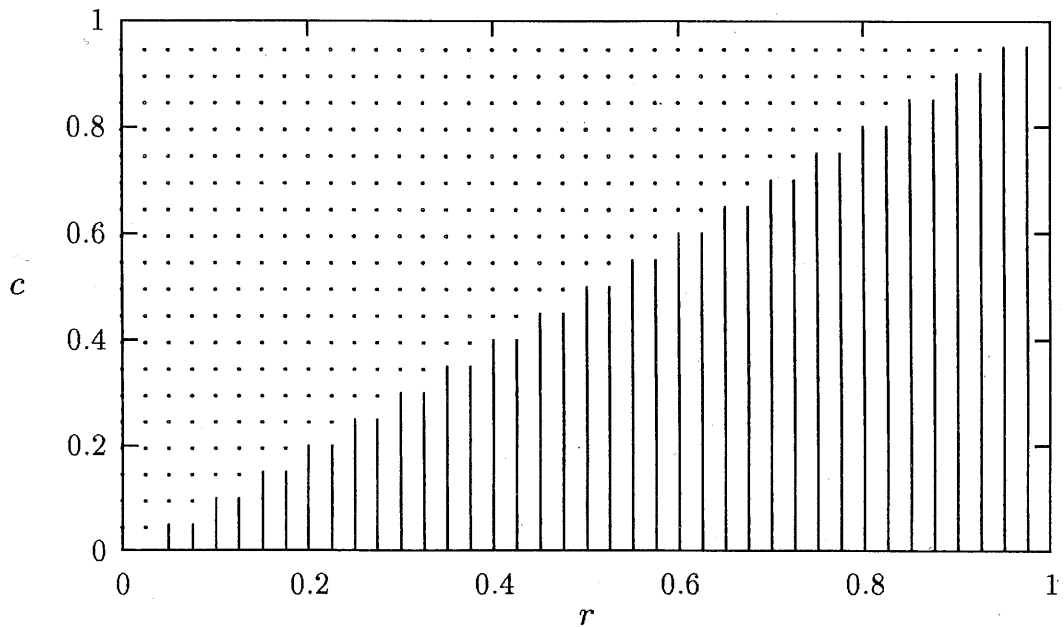


Fig. 1: Phase diagram in the  $(r, c)$  space for  $L$  (deme size) equal to 20 and  $j^*$  (threshold) equal to 4. One observes the stability of a wholly altruistic population (dots) for  $c > r$  and a fully egoistic one (vertical lines) for  $c < r$ .



not *a priori* clear if the dynamics may lead to mixed populations. If it is so, we expect that this will happen provided that  $j^*$  is so small that the mixed demes can take advantage of both altruistic and egoistic behavior in the best way. This is shown by the equilibrium solution of the master equation. Compare, in fact, Fig. 1 with Fig. 2, in which  $L = 20$  again, but  $j^* = 1$  instead of 4. One sees the co-existence, at equilibrium, of both altruistic and egoistic individuals. Figs. 3 and 4 correspond to an intermediate situation with  $j^* = 2$ . It is clear that the region where mixed populations are stable becomes progressively smaller from  $j^* = 1$  to  $j^* = 2$  and disappears for  $j^* = 4$ .

Let us stress that the equilibrium distribution  $\rho_{\text{eq}}(j)$  is non-trivial when the equilibrium population is inhomogeneous (see, for example, Fig. 4).

In fact, together with mixed demes, also homogeneous demes are present since they arise as offsprings of mixed demes at any generation. The edges of the stability region of the mixed phase depend both on  $L$  and on  $j^*$ . Figures 1–4 correspond to  $L = 20$ , but for larger  $L$  the qualitative behavior it is the same if we increase  $j^*$  the domain of mixed phase becomes smaller and, above a critical value ( $j_{\text{cr}}^*$ ), it disappears. The value of  $j_{\text{cr}}^*$  depends on  $L$ . Plotting  $j_{\text{cr}}^*$  vs.  $L$ , we obtain the graph represented in Fig. 5, from which one clearly sees that

$$\lim_{L \rightarrow \infty} j_{\text{cr}}^* / L = 0, \quad (19)$$

while  $j_{\text{cr}}^* / L = \text{const.}$ , for  $L < 60$ .

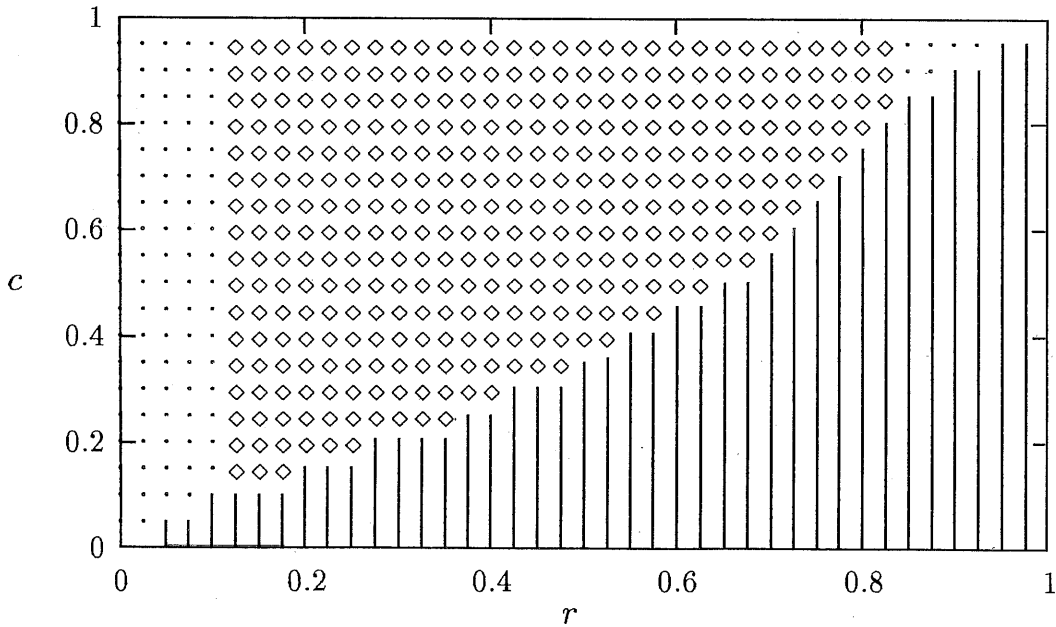


Fig. 2: Phase diagram in the  $(r, c)$  space for  $L = 20$  and  $j^* = 1$ . One observes the appearance of a region of stability of an *inhomogeneous* (mixed altruistic-egoistic) population (diamonds). The coexistence of altruists and egoists is made possible by the value of the threshold  $j^*$ , which is smaller than in Fig. 1.

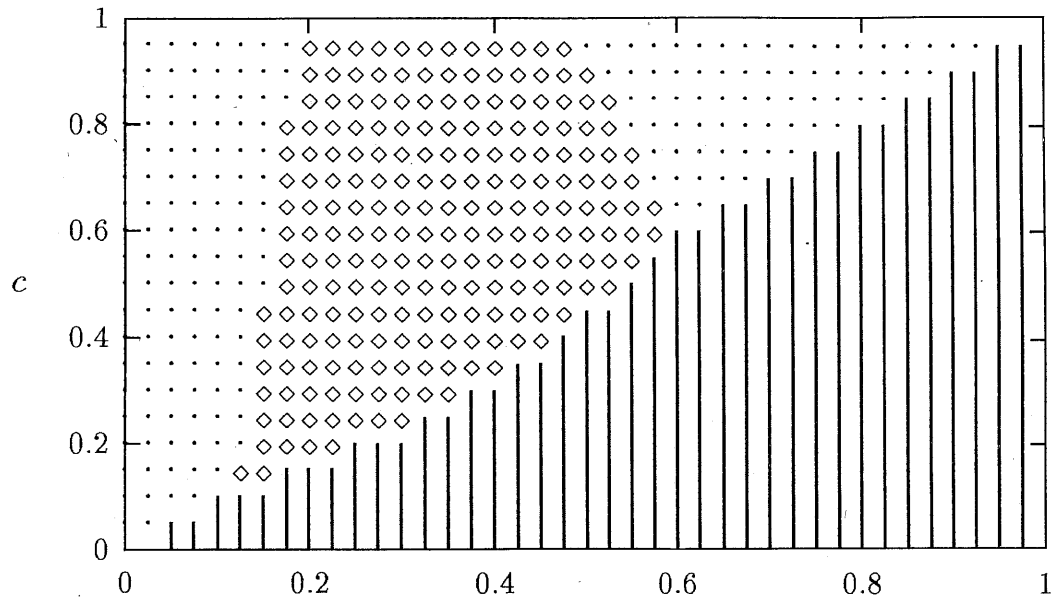


Fig. 3: Phase diagram in the  $(r, c)$  space for  $L = 20$  and  $j^* = 2$ . The region of stability of the inhomogeneous population (diamonds) has shrunk.

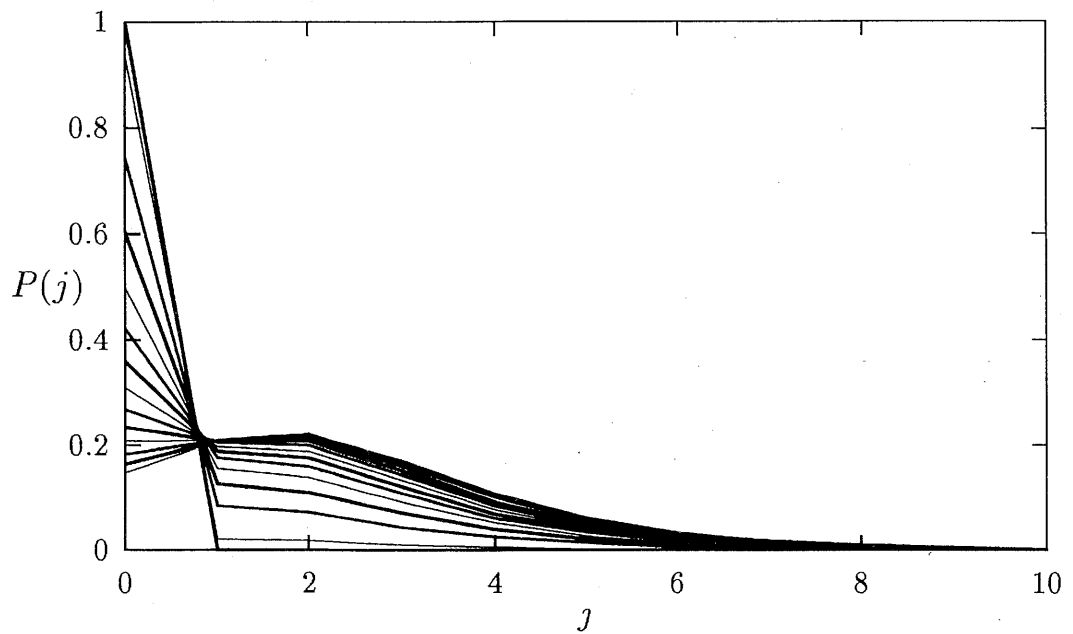


Fig. 4: Distribution of the number  $j$  of altruistic individuals in each deme for  $L = 20$ ,  $j^* = 2$ ,  $r = 0.4$ ,  $c = 0.0, 0.05, 0.1 \dots, 0.95$ . One sees that most demes are inhomogeneous ( $j \neq 0, L$ ) and none is formed only by altruistic individuals.

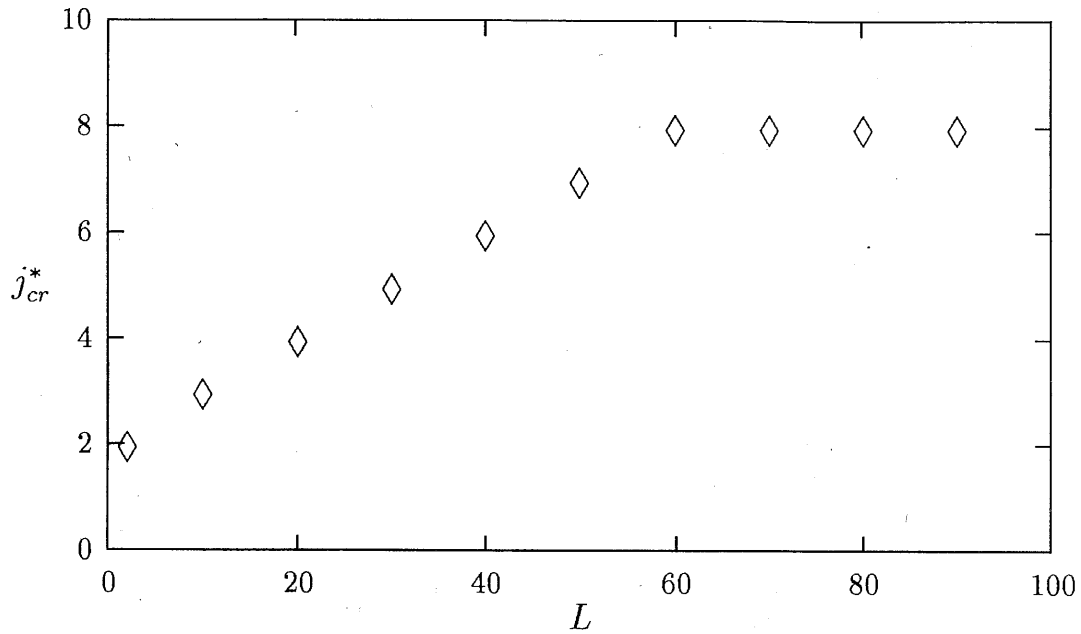


Fig. 5: The critical value  $j_{cr}^*$  of the threshold  $j^*$ , for which the population becomes homogeneous (altruistic or egoistic), as a function of deme size  $L$ . For  $L < 60$ , one has  $j_{cr}^* \propto L$ , while  $j_{cr}^*$  attains a constant value for  $L > 60$ .

This behavior suggests that for large demes the mixed phase can exist only if the altruistic advantage is granted by a small number of altruistic individuals.

## V. Discussion

The most important feature of our model is that *selection acts at individual level*, although the individual survival probability takes into account also of the “interaction” among individuals. This very simple interaction is modeled by the dependence of the fitness function (see Tab. 1) on the genetic composition of group: the individual survival probability is sensitive to the presence of other altruists in the group. We do not have to specify what makes a deme, although one of the consequences of our hypothesis is that individuals belonging to the same deme are more likely to be genetically related than individuals belonging to different demes. So, without invoking either a kin selection or a group selection mechanism for the maintenance of altruists in the population, we have seen that, when the group advantage balances the individual (altruistic) disadvantage, mixed groups may co-exist at equilibrium. However, this kind of equilibrium is fragile, since it also depends on the percentage of altruists in a deme (for small enough demes, i.e.,  $L < 60$ ). For larger demes the *coexistence* of

altruistic and egoistic individuals is stabilized only if the threshold is very low. Since inhomogeneity is maintained by fluctuations in the deme composition at splitting, and since for large demes these fluctuations are negligible, this results corresponds to the expectations.

Let us remark that the stabilization of inhomogeneous populations is reached in the absence of the (rather improbable) mutations of the "altruistic" into the "egoistic" gene (and viceversa): the key role is played by the fluctuations in the composition of daughter demes from inhomogeneous ones. These fluctuations are even more important when, as in Ref. [1], the size of the daughter demes is allowed to vary.

Summarizing, we have shown in a numerically solvable model that if the advantage of the altruistic behavior of a few individuals falls (above a given threshold) on the whole of a sufficiently large deme, a stable situation arises in which inhomogeneous demes (consisting of both altruistic and egoistic individuals) coexist with homeogenous ones. For large average deme size, the average number of altruistic individuals approaches the threshold.

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