

# Inclusive fitness in a homogeneous environment

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## SUMMARY

A general formulation of inclusive fitness is proposed which specifically accounts for competitive effects between relatives. As an example, for an asexual population in a homogeneous inelastic environment, such as is found in a stepping-stone model of dispersal, the inclusive fitness of a breeding female, under weak selection, is independent of her direct effect on the fitness of other individuals in the population. More precisely, suppose a female acts in a way that changes not only her own fitness but the fitness of several other females in the population who may be relatives (i.e. she changes the number of their offspring). I call these changes the direct effects of the action. There will also be indirect effects on the fitness of these and other females which come from the competitive impact of the extra offspring in the next generation. The principal result is that these indirect effects exactly cancel all the direct effects except the direct effect of the actor on herself.

## 1. INTRODUCTION

The inclusive fitness approach to the modelling of behaviour requires us to add up the effects of an action on the fitness of all individuals in the population, each effect weighted by the relatedness of the actor to the individual. If the resulting sum is positive, then the action is selectively favoured. A difficulty with this formulation is that the offspring of close relatives are often in competition with those of the actor, so that an increase in the fitness of a relative may not benefit the actor as much as might be supposed. This difficulty is inherent: the tendency of offspring to move quite slowly from their native habitat (called population viscosity by Hamilton (1964)) makes it likely that an actor will interact with close relatives, and at the same time tends to bring the offspring of these relatives into conflict with those of the actor.

An inclusive fitness analysis which takes account of such competitive interactions must recognize two types of 'closeness': genetic closeness, or relatedness, which measures the extent to which a neighbour's genes are identical to those of the actor, and competitive closeness, which measures the extent to which a neighbour's genes will compete in the next generation with genes that are identical to those of the actor. These two measures act in opposition: altruism is encouraged by high genetic closeness but discouraged by high competitive closeness, and a general inclusive fitness formulation must take account of both measures. Inclusive fitness models which are set in a well-defined population structure, for example, a patch structure with limited dispersal between patches, tend automatically to do this, because fitness is measured by a count of breeding offspring, but general verbal models of altruism tend to consider only relatedness.

For example, suppose we have a 'site' at each lattice

point in the plane, each site occupied by a single haploid plant. Every generation, each plant disperses asexual seeds to neighbouring sites, and the seeds at each site compete for next-generation occupancy. Because of the limited nature of the dispersal, individuals are related, on average, to their neighbours, and standard fitness theory predicts that they should compete for resources somewhat less fiercely with one another than if they were unrelated. Furthermore, the smaller the average radius of dispersal, the higher the average relatedness between neighbours, and the more altruistic should be their local interactions. The results of this paper show that this is not always the case. Because of the limited nature of the dispersal, the offspring from each site must compete with offspring from neighbouring sites, and this will offset the inclusive fitness advantage of altruistic behaviour. In the simplest case of a homogeneous inelastic environment, I show (equation (5)) that neighbouring plants should compete with one another as strongly as if they were unrelated. That is, individuals should interact with their neighbours as if the population were panmictic. Using the terminology of the above discussion, genetic and competitive closeness, in this model, are exactly balanced.

The significance of competitive interactions in the formulation of inclusive fitness has been recognized for a long time, but their importance has perhaps been underestimated. Hamilton (1964) mentions that for populations which are subdivided into 'standard-sized batches', each of which is allotted a 'standard-sized pool of reproductive potential', the progress of an altruistic gene will be slowed. He credits the original observation of this phenomenon to a paper of Haldane (1924) on sib competition. Hamilton (1971) again asserts that 'the most "system-like" version of an "isolation-by-distance" model, which is supposed to

preclude long-range migration and elastic expansion from vigorous areas, is rather hostile to altruism.' Grafen (1983) observed that, in a group-structured population, altruistic acts can be selectively favoured only to the extent that an altruistic group is able to export some fraction of the benefits it generates; specifically, some of the extra offspring produced must compete with individuals of relatively low relatedness.

The key concept here is what Hamilton refers to as 'elastic expansion', by which is meant the capacity of the environment to expand to accommodate (and give reproductive potential to) extra offspring produced by the altruistic behaviour. In a homogeneous 'structured population' it turns out to be irrelevant whether or not the population has 'long-range migration', because the positive effects of such migration (the likelihood that the benefits conferred on the recipient will not stay to compete with the actor's offspring) are exactly offset by the negative effects (the lower relatedness between actor and recipient). Equation (4) below shows that what counts is not that extra offspring are sent any great distance, or that they compete with individuals of relatively low relatedness, but that they can be accommodated by the environment in such a way that the offspring they would normally compete with do not feel the full effects of their presence. This environmental elasticity is the only force which can mitigate the damping effect of local competition on the selective advantage of altruism toward relatives.

## 2. THE GENERAL MODEL

To construct a general inclusive fitness model, I consider an infinite population occupying  $n$ -dimensional space ( $n = 1, 2$  or  $3$ ) with a breeding site at each lattice point (integer coordinates) indexed by  $i$ . (For  $n > 1$ ,  $i$  will stand for a pair or a triple of coordinates.) I suppose that generations are discrete and non-overlapping and that selection is weak, and I begin by assuming that reproduction is asexual. Think of a population of annual plants which grow at the lattice points of the plane, with a certain geometric pattern of dispersal of asexual seeds.

The variables of the model are as follows:

$n_{ij}$  = the average number of offspring competing for site  $j$  who come from  $i$ .

$n_j = \sum_i n_{ij}$ , the average total number of offspring competing for site  $j$ .

$p_{ij} = n_{ij}/n_j$ , the average proportion of offspring competing for site  $j$  who come from  $i$ . Note that  $\sum_i p_{ij} = 1$ .

$q_i$ , the probability that site  $i$  is occupied in any generation. Having  $q_i < 1$  allows the possibility of elasticity in the environment.

$w_j = \sum_k p_{jk} q_k$ , the fitness of site  $j$ , that is, the average contribution to next-generation breeders by site  $j$ .

$c_{ij} = \sum_k (p_{ik} q_k / w_i) p_{jk}$ , the competitive effect of  $i$  on  $j$ .

This measures the extent to which a random successful  $i$ -offspring has displaced a  $j$ -offspring. The term in brackets is the probability that a random successful  $i$ -offspring breeds on site  $k$ , and the second term is the probability that site  $k$  might have been won by a  $j$ -offspring.

$e_i$ , the elasticity of site  $i$ , defined as the derivative of  $\ln q_i$  with respect to  $\ln n_i$ . If  $n_i$  is increased by a small multiplicative factor  $\nu$ , this results in an increase in  $q_i$  by the factor  $e_i \nu$ .

$r_{ij}$ , the relatedness between breeders on sites  $i$  and  $j$ .

At equilibrium, the relatedness coefficients are determined as the solutions to the recursion equations

$$r_{ij} = \sum_{k,m} r_{km} p_{ki} p_{mj} \quad (i \neq j) \quad (1)$$

with, of course,  $r_{ii} = 1$ .

Now I consider an actor breeding on site 0, who acts to change the fecundity of the breeder on site  $i$ , for every  $i$ , by a small multiplicative factor  $\delta_i$ . This will cause a change in several of the variables. The new values, to first order in the  $\delta_i$ , are as follows:

$$n'_{ij} = n_{ij}(1 + \delta_i),$$

$$n'_j = \sum_i n'_{ij} = n_j(1 + \sum_i \delta_i p_{ij}),$$

$$p'_{ij} = n'_{ij}/n'_j = p_{ij}(1 + \delta_i - \sum_k \delta_k p_{kj}),$$

$$q'_j = q_j(1 + e_j \sum_i \delta_i p_{ij}),$$

and

$$w'_j = \sum_k p'_{jk} q'_k.$$

The change in site  $j$  fitness is calculated to be

$$\Delta w_j = w'_j - w_j = \delta_j w_j - \sum_i \delta_i w_i c_{ij} + \sum_{i,k} \delta_i p_{ik} p_{jk} q_k e_k. \quad (2)$$

This expression consists of three terms. The first term is the direct effect due to the  $\delta_j$  donation, the second term is the sum over  $i$  of the indirect competitive effect of the extra offspring given to site  $i$ , and the third term is the reduction of this competitive effect due to the elasticity of the environment at each site  $k$ . The change in inclusive fitness of the actor is

$$\begin{aligned} \Delta W_1 &= \sum_j \Delta w_j r_{0j} \\ &= \sum_j \delta_j w_j r_{0j} - \sum_{i,j} \delta_i w_i c_{ij} r_{0j} + \sum_{i,j,k} \delta_i p_{ik} p_{jk} q_k e_k r_{0j}. \end{aligned} \quad (3)$$

The first term is the standard inclusive fitness, and, as above, the next two terms represent the competitive effects and the mitigating effects of environmental elasticity on this competition.

## 3. THE ASSUMPTION OF ENVIRONMENTAL HOMOGENEITY

If we allow the sites to differ in quality, there is not much that can be done to simplify equation (3), but if we assume, as we do now, that the sites are uniform, we can use the relatedness recursions (1) to get a striking simplification. In this case, the variables  $q_i = q$  and  $e_i = e$  are independent of  $i$ , and the variables  $p_{ij}$ ,  $c_{ij}$  and  $r_{ij}$  depend only on  $j-i$ . For these variables, it is convenient to use only one subscript, and write  $p_{j-i}$  instead of  $p_{ij}$ . Thus, for any  $i$ ,  $p_j$  is the proportion of offspring competing for site  $i+j$  who come from  $i$ ,  $c_j$  is the competitive effect of  $i$  on  $i+j$ , and  $r_j$  is the relatedness between breeders on sites  $i$  and  $i+j$ . It

follows that  $w_j = q \sum_k p_{k-j} = q$  is independent of  $j$ . If, after some algebraic manipulations, equation (1) is put into (3), we get

$$\Delta W_1/q = \delta_0[r_0 - (1-e) \sum_i c_i r_i] + e \sum_{i \neq 0} \delta_i r_i. \quad (4)$$

The principal conclusion is that in an inelastic environment ( $e = 0$ ),

$$\Delta W_1/q = \delta_0(r_0 - \sum_i c_i r_i), \quad (5)$$

and inclusive fitness depends only on  $\delta_0$ . The first term in the parentheses of (5) represents the direct effect of the actor on her own fitness, and the second term represents the reduction in her fitness due to the competitive effects of her own extra offspring on the offspring of related neighbours. Direct fitness donations to other breeding females have no effect on her inclusive fitness no matter how closely related these other females are.

#### 4. DISCUSSION

Equation (5) parallels the result obtained by Wilson *et al.* (1992) and Taylor (1992) in a homogeneous, inelastic patch-structured population with multiple breeders per patch and within-patch interactions. In their models, the competitive effects exactly nullify all fitness donations to neighbours, and the inclusive fitness of the actor depends only on her direct effect on her own fitness. In both cases, it is the equilibrium recurrence relation (1) among the relatedness coefficients which annihilates the  $\delta_i$  terms for  $i \neq 0$ . This may well be a general result, at least when reproduction is asexual. In homogeneous, inelastic, structured populations, the local allelic distributions equilibrate at a point at which the two types of closeness described above, genetic and competitive, balance in such a way that inclusive fitness reduces essentially to direct fitness.

It is not clear just how important is environmental elasticity in the evolution of altruistic traits. Certainly environments are expected to be variable in quality both in space and time, and occasions of high quality will favour local population expansion. In such instances, the environment is elastic, and by equation (4), altruistic interactions are more highly favoured. But such elasticity cannot persist indefinitely in any particular location, and the continuing spread of the altruistic allele must require that it find its way to other newly elastic patches.

It should be noted that the above results concern interactions between breeding females. At other points in the life cycle, the balance between genetic and competitive closeness might be quite different. For example, a simple population cycle might consist of a breeding phase and a dispersal phase. After the breeding phase, the population consists of 'family units' in which genetic closeness is relatively high but, depending on the nature of the dispersal, competitive closeness may be low. At such a point, the conditions for altruism are most favourable and, indeed, altruistic interactions between parent and child and between

sibs are important examples of this. But the competitive closeness must still be reckoned with. For example, if sons disperse more widely than daughters, then they are likely to be less competitively close, and altruism will be more favoured between brothers than between sisters.

In sexual populations, the above results continue to hold provided there are no dispersal differences between the sexes. For example, in a diploid hermaphroditic population with random fusion of male and female gametes (pollen and ovules) on each site after dispersal, equation (5) continues to hold if the pollen and ovule dispersal patterns are the same; otherwise, the inclusive fitness shows some dependence on the direct fitness contributions  $\delta_i$  to neighbouring individuals.

Indeed, suppose we have different migration probabilities:  $p_j = u_j$  for pollen and  $p_j = v_j$  for ovules. Then the competitive effects will also be gamete specific, and we let  $c_j$  denote the average of the competitive effects through pollen and ovules. With this notation, the sexual version of equation (5) (inelastic environment) is

$$\Delta W_1/q = \delta_0(r_0 - \sum_i c_i r_i) - \sum_{i \neq 0} \delta_i \sum_{k,j} [(v_{k-i} - u_{k-i})(v_{k-j} - u_{k-j})/4] r_j, \quad (6)$$

and it is clear that this reduces to (5) if the two gametes have the same dispersal pattern ( $v_j = u_j$ ).

The mathematical reason for the extra term in (6) is as follows. In a sexual population, the inclusive fitness change is obtained by averaging two versions of equation (3), one with the competitive effect through pollen (a  $uu$  product) and the other with the competitive effect through ovules (a  $vv$  product). However, the sexual version of the recursion equation for the relatednesses  $r_i$  is obtained by averaging four versions of equation (1), with  $uu$ ,  $uw$ ,  $vu$ , and  $vv$  products, accounting for the four different ways of choosing a random allele from each of two individuals. When the sexual version of (1) is substituted into (3), the  $\delta_i$  terms no longer completely drop out.

Equation (6) also applies in a diploid sexual population with sex-specific dispersal of male and female offspring, if the action is determined by the average genotype of the mated pair. This is essentially an assumption of additive gene action within a mated pair.

The coefficient of  $\delta_0$  in (6) is positive, but for  $i \neq 0$ , the coefficient of  $\delta_i$  might have either sign. As an example, I report the results of a one-dimensional stepping-stone model (see next paragraph) in which ovules remain on their native site and pollen disperses one site right or left each with probability  $d$ , and stays at home with probability  $u$ . Then the coefficient of  $\delta_i$  in (6) is positive for  $i = 0$ , but is negative for  $i \geq 2$  and  $i \leq -2$ . For  $i = \pm 1$ , it is positive for  $u$  near zero but negative for  $d$  near zero. In this example, even if there is no cost of a positive  $\delta_i$ , it may be profitable to help your neighbour, but help given to others, even at no direct cost, actually reduces your fitness.

The inelastic ( $e = 0$ ) lattice-point model, with every site occupied ( $q = 0$ ) and migration only to adjacent sites or to infinity is commonly known as the ‘stepping-stone model’. An early version of this model was introduced by Wright in 1943 to study his ‘isolation by distance’; Kimura formulated the model in 1953 and gave it its name, and Kimura & Weiss provided the first mathematical treatment in 1964–1965. Malecot worked with a similar model in 1959, and the mathematical treatment was extended by Maruyama in 1969–1970. These references and an analysis of the one-dimensional case (essentially the solution of the recurrence relation (1) in case migration is symmetric and only to neighbouring sites) can be found in Crow & Kimura (1970).

As equation (1) stands, its solution is  $r_i = 1$  for all  $i$ ; in this way, the population behaves like a closed finite population. This technical difficulty can be remedied by introducing a small mutation rate, or, what is formally equivalent, by including a site at ‘infinity’ and a non-zero probability  $p_\infty$  that any site will be colonized by an immigrant from infinity. Of course,  $p_\infty$  is also the expected number of offspring of each breeding female who breed at infinity. This approach is convenient because all the above equations remain valid, with  $\infty$  included in the index set, and  $\delta_\infty$  and  $r_\infty$  both set equal to zero.

## 5. CONCLUSION

Suppose we have an infinite asexual population of breeding individuals uniformly distributed in a homogeneous environment, with a given dispersal pattern of offspring which results in some pattern of relatedness between individuals which depends on the distance between sites, and some competition between offspring of relatives. Consider an action of one of these individuals which has a small direct effect on the fecundity of certain individuals in the population. Equation (5) shows that if the environment has no capacity for local expansion (inelastic), then selection pays attention to the direct effect of the actor on her own fitness, but not to her direct effects on any other

individual, no matter how closely related that individual is. An implication of this is that the conditions for the evolution of altruistic behaviour are the same as they would be in a panmictic population.

If these assumptions are not met, the conditions for the evolution of altruism may be relaxed. If the environment is non-homogeneous, and certain rich patches show a capacity for local expansion, then during this phase (which cannot persist indefinitely) altruistic behaviour may be selected for in this locality. Or if the population is sexual, and dispersal patterns are sex specific, selection may also act on fitness donations made to neighbours, but the direction of this selection is not clear, and further work should be done on this question.

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