

# Evolution of altruism in stepping-stone populations with overlapping generations

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Keywords: altruism, competition, inclusive fitness, prisoner's dilemma,  
overlapping generations, stepping-stone population.

Right Running Head: Evolution of altruism

Left Running Head: Irwin & Taylor

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December 18, 2000

## Abstract

We study the evolution of altruism in one- and two-dimensional stepping-stone populations with discrete overlapping generations. We find that increasing survival probability facilitates the evolution of altruism, in agreement with recent results for a patch structured population. We allow the altruistic behaviour to affect either fecundity or survival probability. In the first case, altruism is favoured compared to a randomly interacting population, but in the second case, altruism is less likely likely to evolve. We consider the iterated prisoner's dilemma as a description of an altruistic interaction and compare our results with recent simulations on lattice populations.

## INTRODUCTION

The evolution of altruism in spatially structured populations has a long history, repeatedly examined in the literature. Cooperative behaviours have been documented in an enormous variety of biological systems (e.g. Dugatkin 1997) and are thought to have been essential to the major transitions in evolution — from the incorporation of organelles into cells and the development of multicellularity to the creation of social communities (Maynard Smith & Szathmary 1995). At the centre of the discussion is the tension between cooperation and competition. A key question is whether limited dispersal, creating what Hamilton (1964) called a viscous population, promotes or inhibits altruistic behaviour compared with a randomly mixing population. We consider a model in which altruists assist all the individuals in their interaction group and dispersal is limited so that nearby individuals tend to be close relatives. Most of the benefit of altruism goes to relatives and therefore benefits the altruism gene. The benefit also leads to increased competition among relatives and thus inhibits the evolution of altruism. We use Hamilton's (1964) powerful inclusive fitness method to analyse this problem. This method determines the evolutionary fate of a behaviour by adding up the effects of the altruistic act on the fitness of all individuals in the population, weighted by the relatedness of the individual to the actor.

A surprisingly simple result is obtained for some simple population structures with discrete non-overlapping generations. The benefits of altruism exactly balance the changes in competitive effect and the inclusive fitness effect of the actor is simply the net direct effect of its behaviour on its own fitness (Wilson et al. 1992, Taylor 1992a,b). Thus altruistic

behaviour is selected exactly when it would be favoured in a randomly mixing population. Remarkably, this holds independently of the dispersal rate in these populations. The same result has also been found in finite deme-structured populations (Rousset & Billiard 2000, Taylor et al. 2001). Simulation studies of altruism in lattice populations have shown significant departures from this exact balance, often favouring the evolution of altruism. These simulations and the models of Wilson et al. (1992) and Taylor (1992a,b) differ in a variety of important ways. Instead of non-overlapping generations and constant population densities, these calculations allow generations to overlap (Nowak et al. 1994; Nakamaru et al. 1997, 1998) or allow variable population densities by permitting some sites to remain vacant (Mitteldorf & Wilson, 2000). It's not clear from these studies if the spatial structure of the population is the key ingredient which facilitates altruism or if other features (e.g. precise details of the altruistic interaction, population density, generational overlap, etc.) are responsible. Mitteldorf & Wilson (2000) argue that their variable population density can favour altruism; our investigations here are more restricted (but see also Kelly 1994).

Recently it was shown that overlapping generations promotes the evolution of altruism in a patch-structured population (Taylor & Irwin 2000). Furthermore, in this population structure there is a difference between altruistic acts which affect fecundity and those which affect survival. With the former, altruism is more strongly favoured and with the latter less strongly favoured than in a randomly mixing population. This difference persists throughout the entire range of survival probabilities. Here we present a model of altruism in one- and two-dimensional stepping-stone populations which extends the patch model of Taylor & Irwin (2000), and we obtain both of their results: overlapping generations promote altruism in stepping-stone populations, with a similar difference between altruistic gifts of fecundity and survival. Finally, we use the iterated prisoner's dilemma as an alternative model of altruistic interactions and compare our results with recent simulations.

## THE MODEL

We consider populations in a one-dimensional lattice with two nearest-neighbour sites and a two-dimensional lattice with four nearest-neighbours. The lattice is infinite with one asexually reproducing haploid individual per site. Prior to reproduction, nearest-neighbours interact with the possibility of altruistic behaviour. Each individual produces a large number

of offspring which disperse to one of the neighbouring sites with total probability  $d$ . Dispersers incur a cost and only a proportion  $1 - k$  arrive at a new site. The effect of  $d$  and  $k$  are combined into a single variable  $p_{j-i}$  the probability an offspring competing on site  $j$  was born on site  $i$ ,

$$p_{j-i} = \begin{cases} \frac{1-d}{1-kd}, & i = j \\ \frac{d(1-k)}{N(1-kd)}, & i, j \text{ are nearest-neighbours; } N \text{ is the number of nearest-neighbors} \\ 0, & \text{otherwise.} \end{cases} \quad (1)$$

Thus  $p_0$  is the probability an offspring is native. After reproduction, each adult survives and breeds again in the next generation with probability  $s$ . On a site in which the resident adult dies, the offspring, both native and immigrant, compete on an equal basis for the vacant spot. Offspring which do not win a site die and the cycle begins again. Our notation is summarized in Table 1.

An altruistic act costs the actor and benefits its neighbours, affecting either fecundity or survival. We denote by  $\delta_i$  the direct effect of an altruist at any site  $j$  on the breeding individual at site  $j + i$ . For example in our fecundity model,  $\delta_i$  is the multiplicative change in the number of offspring. In our stepping-stone population  $\delta_0$  is the effect on the actor,  $\delta_1$  the effect on each nearest-neighbour, and all other  $\delta_i$  are zero. These effects  $\delta_i$  are not changes in fitness but they alter the fitness of individuals by an amount which depends on dispersal and survival rate. For both fecundity and survival effects, an individual's fitness is its expected number of offspring which breed in the next generation plus its probability of surviving to breed again.

An inclusive fitness calculation adds up the fitness effects of a focal mutant weighted by the relatedness between the affected individual and the actor. We denote the relatedness between adults at sites  $i$  and  $j$  by  $r_{ij}$ . Our lattice is homogeneous so we often abbreviate this as  $r_{j-i}$  noting only the displacement between sites. Relatednesses for several pairs of nearby sites are computed using the lattice structure and stepping-stone dispersal pattern with no selection and this calculation is described in Appendix A. We assume that the costs and benefits are small (weak selection), so our inclusive fitness results are exact to first order in  $\delta_i$  and will give reasonable approximations for small  $\delta_i$  (Taylor 1996). We assume dispersal at the ES dispersal rate which depends on survival rate (Appendix B).

In the following sections we find conditions on the  $\delta_i$  which favour altruistic acts, considering first those which affect fecundity, then survival. Within each section we write a general expression for the inclusive fitness effect and find conditions in terms of the altruistic effects ( $\delta_i$ ) which select altruism in one- and two-dimensional stepping-stone populations. Finally, we adapt our general results to two examples of altruistic interactions: a simple cost-benefit altruism and the iterated prisoner's dilemma.

### *Fecundity effects*

We now analyse the effect of an altruistic mutant at site 0. The altruistic behaviour alters the fecundity of the mutant and individuals on neighbouring sites. Since there is some dispersal from sites  $\pm 1$  to sites  $\pm 2$ , there will be an effect on the number of competing juveniles at sites  $\pm 2$ . Since some offspring born on sites  $\pm 3$  will disperse to sites  $\pm 2$ , these offspring will experience a different amount of competition. Thus the inclusive fitness effect includes fitness changes of individuals up to three steps away.

The inclusive fitness effect  $\Delta w_{IF}$  is (see Appendix C)

$$\Delta w_{IF} = (1 - s) \left( \sum_i \delta_i r_i - \sum_{ijk} \delta_k p_{j-i} p_{j-k} r_i \right). \quad (2)$$

If  $s = 0$ , the relatedness recursion (A1) allows us to simplify (2), obtaining

$$\Delta w_{IF} = \delta_0 \left( r_0 - \sum_{ik} r_i p_k p_{k-i} \right). \quad (3)$$

(Taylor 1992b). With non-overlapping generations the inclusive fitness effect is independent of the effect of the mutant on other breeders ( $\delta_i, i \neq 0$ ). This is a general result for any dispersal pattern or range of altruistic interactions on a lattice of arbitrary dimension.

*One dimension.* In a one-dimensional stepping-stone population the inclusive fitness effect (2) simplifies to

$$\Delta w_{IF} = r_0 \Delta w_0 + 2r_1 \Delta w_1 + 2r_2 \Delta w_2 + 2r_3 \Delta w_3 \quad (4)$$

where the net fitness effects on breeders at a distance  $i$ ,  $\Delta w_i$ , are

$$\begin{aligned}\Delta w_0 &= (1-s)(\delta_0(1-p_0^2-2p_1^2)-\delta_1(4p_0p_1)) \\ \Delta w_1 &= (1-s)(-2\delta_0p_0p_1+\delta_1(1-p_0^2-3p_1^2)) \\ \Delta w_2 &= -(1-s)(\delta_0p_1^2+2\delta_1p_0p_1) \\ \Delta w_3 &= -(1-s)\delta_1p_1^2.\end{aligned}$$

In the limit as  $s \rightarrow 1$ , the fitness effects approach 0 as expected.

The altruistic behaviour is favoured if  $\Delta w_{IF} > 0$ , which can be written as

$$2\delta_1 \left[ \frac{r_1 - r_3 - p_0(4r_0 - 7r_1 + 4r_2 - r_3)}{2(r_0 - 2r_2 + p_0(3r_0 - 4r_1 + r_2))} \right] + \delta_0 > 0. \quad (5)$$

The quantity in square brackets is an altruism threshold: the cost-benefit ratio  $-\delta_0/(N\delta_1)$  must be smaller than this, assuming  $\delta_1 > 0$ , for altruism to be favoured. Survival probability does not appear explicitly in this threshold, but is felt through the relatedness  $r_i$ .

*Two dimensions.* In two dimensions, the inclusive fitness effect involves terms from the six kinds of sites identified in Figure 1,

$$\begin{aligned}\Delta w_{IF} &= r_{0,0}\Delta w_{0,0} + 4r_{0,1}\Delta w_{0,1} + 4r_{1,1}\Delta w_{1,1} + 4r_{0,2}\Delta w_{0,2} \\ &\quad + 8r_{1,2}\Delta w_{1,2} + 4r_{0,3}\Delta w_{0,3}\end{aligned} \quad (6)$$

where the net fitness effects on breeders at a distance  $i$ ,  $\Delta w_i$ , are

$$\begin{aligned}\Delta w_{0,0} &= (1-s)(\delta_0(1-p_0^2-4p_1^2)-\delta_1(8p_0p_1)) \\ \Delta w_{0,1} &= (1-s)(\delta_0(-2p_0p_1)+\delta_1(1-p_0^2-9p_1^2)) \\ \Delta w_{1,1} &= -2(1-s)(\delta_0(p_1^2)+\delta_1(2p_0p_1)) \\ \Delta w_{0,2} &= -(1-s)(\delta_0(p_1^2)+\delta_1(2p_0p_1)) \\ \Delta w_{1,2} &= -3(1-s)\delta_1p_1^2 \\ \Delta w_{0,3} &= -(1-s)\delta_1p_1^2.\end{aligned}$$

The altruistic behaviour is favoured if  $\Delta w_{IF} > 0$  which can be written as

$$4\delta_1 \left[ \frac{7r_{0,1} - 6r_{1,2} - r_{0,3} - p_0(8r_{0,0} - 25r_{0,1} + 16r_{1,1} + 8r_{0,2} - 6r_{1,2} - r_{0,3})}{4(3r_{0,0} - 2r_{1,1} - r_{0,2} + p_0(5r_{0,0} - 8r_{0,1} + 2r_{1,1} + r_{0,2}))} \right] + \delta_0 > 0. \quad (7)$$

### *Survival effects*

Now we want the altruistic behaviour to have an effect on survival probability, not on fecundity. Assuming a non-zero survival probability ( $s > 0$ ), the inclusive fitness effect of the mutant is (Appendix C)

$$\Delta w_{IF} = s \left( \sum_i r_i \delta_i - \sum_{ij} r_i \delta_j p_{j-i} \right). \quad (8)$$

*One dimension.* The inclusive fitness effect (8) in one dimension is

$$\Delta w_{IF} = \Delta w_0 + 2r_1 \Delta w_1 + 2r_2 \Delta w_2 \quad (9)$$

where the changes in fitness of the mutant and four nearest-neighbours are

$$\begin{aligned} \Delta w_0 &= s(\delta_0(1 - p_0) - 2\delta_1 p_1) \\ \Delta w_1 &= s(-\delta_0 p_1 + \delta_1(1 - p_0)) \\ \Delta w_2 &= -s\delta_1 p_1. \end{aligned}$$

The altruistic act is favoured if

$$2\delta_1 \left[ \frac{r_0 - 2r_1 + r_2}{2(r_1 - r_0)} \right] + \delta_0 > 0. \quad (10)$$

*Two dimensions.* The fitnesses of individuals on fewer sites are affected with survival effects in two dimensions compared to fecundity effects. Individuals two steps from the mutant are affected because of the change in survival of individuals one step away. The inclusive fitness effect is

$$\Delta w_{IF} = \Delta w_{0,0} + 4r_{0,1} \Delta w_{0,1} + 4r_{1,1} \Delta w_{1,1} + 4r_{0,2} \Delta w_{0,2} \quad (11)$$

where the fitness changes (C9) are

$$\begin{aligned} \Delta w_{0,0} &= s(\delta_0 - 4\delta_1 p_1 - \delta_0 p_0) \\ \Delta w_{0,1} &= s(\delta_1 - \delta_0 p_1 - \delta_1 p_0) \\ \Delta w_{1,1} &= -2s\delta_1 p_1 \\ \Delta w_{0,2} &= -s\delta_1 p_1. \end{aligned}$$

The altruistic act is favoured if

$$4\delta_1 \left[ \frac{r_{0,0} - 4r_{0,1} + 2r_{1,1} + r_{0,2}}{4(r_{0,1} - r_{0,0})} \right] + \delta_0 > 0. \quad (12)$$

*Computational results.* Figure 2 shows the altruism threshold  $-\delta_0/(N\delta_1)$  as a function of survival  $s$  for one- ( $N = 2$ ) and two-dimensional ( $N = 4$ ) stepping-stone populations with both fecundity and survival effects. The horizontal line at 0 is the threshold for a randomly interacting population; altruism is selected if the cost to the actor is in fact a direct benefit ( $\delta_0 > 0$ ). With fecundity effects, the threshold increases with  $s$  from 0 allowing altruism to be favoured for increasingly large costs. With survival effects, the threshold also increases with increasing survival but from an initial negative relatedness threshold, requiring a large negative cost to overcome the benefit given to neighbours. In the limit as  $s \rightarrow 1$  the threshold approaches 0. Adding a cost to dispersal (thin lines) pushes the threshold closer to that of a random-mixing population.

### *Shared benefit altruism*

We now briefly consider an altruistic act which costs the altruist  $c$  and provides a total benefit  $b$  which is shared equally throughout the  $N + 1$  sites in the neighbourhood. In one dimension,  $N = 2$ , so the altruist and its neighbours receive a benefit of  $b/3$  each. Substituting  $\delta_0 = -c + \frac{b}{3}$  and  $\delta_1 = \frac{b}{3}$  into the fecundity threshold (5) and solving for  $\frac{b}{3}/c$ , we obtain

$$\frac{b/3}{c} > \frac{\hat{d}(d(1-k)(1-\sqrt{1-\hat{d}}) - \hat{d}(1-kd))}{(3\hat{d} - 4(1-\sqrt{1-\hat{d}}))(d(1-k) - \hat{d}(1-kd)) - d\hat{d}(1-k)\sqrt{1-\hat{d}}} \quad (13)$$

and for no-cost dispersal ( $k = 0$ ) using the ES dispersal rate (B2) this reduces to

$$\frac{b/3}{c} > \frac{s+3}{5s+3}. \quad (14)$$

For survival effects, solving  $\Delta w_{IF} > 0$  from (9) obtains

$$\frac{b/3}{c} > \frac{\hat{d}}{3\hat{d} - 4(1-\sqrt{1-\hat{d}})}, \quad (15)$$

and for  $k = 0$ , the threshold (15) has an even simpler form obtained using the dispersal rate (B2),

$$\frac{b/3}{c} > \frac{s+3}{3s+1}. \quad (16)$$

In two dimensions, there is no explicit formula for the evolutionarily stable dispersal rate  $d^*$ ; we find  $d^*$  by solving (B3) numerically. Altruism is favoured if  $\Delta w_{IF} > 0$ . Since there are 5 recipients, each obtains a benefit  $b/5$  while the altruist incurs the full cost  $c$ . Setting  $\delta_0 = -c + b/5$  and  $\delta_1 = b/5$ , using the relatednesses (A5) and solving for  $b/5/c$  yields a threshold benefit-cost ratio for altruism to be favoured. The threshold is found numerically using equations obtained with the assistance of a computer algebra system.

Figure 3 shows the benefit-cost threshold  $\frac{b}{N+1}/c$  as a function of survival  $s$  for one- and two-dimensional stepping-stone populations with both fecundity and survival effects. The qualitative features have the same interpretation as our general results reported in Figure 2. The horizontal line at 1 corresponds to the threshold benefit-cost ratio for a randomly interacting population where the altruistic benefit is shared among  $N+1$  recipients. With fecundity effects, the threshold decreases as  $s$  increases from 1 at  $s = 0$ . With survival effects, the threshold also decreases with increasing survival but from an initial threshold much greater than for a random-mixing population, reaching 1 at  $s = 1$ .

### *Iterated prisoner's dilemma*

Our second example of altruistic behaviour is the iterated prisoner's dilemma game (Trivers 1971; Axelrod & Hamilton 1981). A pair of individuals play a series of prisoner's dilemma games, each game followed by another with a constant probability  $w$ . We consider two pure strategies: tit for tat (TFT) and all defect (AD). If a player adopts TFT, it first cooperates, and then repeats its partner's previous choice on subsequent interactions. AD players defect on each turn. The payoff matrix is shown in Table 2. We are especially interested in the possibility of altruists invading a selfish population so we use mixed strategies characterized by the (initially small) probability of cooperative behaviour. A related approach varies costs and benefits as a function of a common 'investment' parameter (Killingback et al 1999). We also note that although the iterated prisoner's dilemma is often used to describe complex organisms capable of long term memory, the TFT and AD strategies

are very simple, requiring very little sophisticated machinery.

Our inclusive fitness argument above can be adapted to this problem. The population-wide strategy is to use TFT with probability  $p$  and AD with probability  $1 - p$  while a mutant uses a deviant strategy  $p' = p + \delta$  (Appendix D). An actor's score ( $\delta_0$ ) is the average payoff it receives from interactions with all of its neighbours (not including itself). If the population-wide probability of playing TFT  $p$  is greater than a threshold (D5), then individuals with greater  $p'$  are selected. In randomly mixing populations (and populations with fecundity effects and non-overlapping generations), the threshold (D5) takes a simpler form, independent of the size of the interaction neighbourhood,

$$p > \frac{1 - w}{3w - 1} \text{ and } w > \frac{1}{3} \quad (17)$$

assuming the numerical values for the payoffs from Table 2.

Threshold values of  $p$  are shown as a function of  $s$  and  $w$  in Figures 4 and 5 respectively. Fecundity thresholds (solid lines) are below the random-mixing threshold (dotted line) and survival effects (dashed lines) are above the random-mixing threshold. Results for one (A) and two (B) dimensions are shown as well as zero-cost dispersal (thick lines) and dispersal with a small cost ( $k = 0.2$ , thin lines). Populations with  $p$  above the corresponding line favour increasing  $p$ , that is larger probabilities of playing TFT. Increasing dispersal cost  $k$  moves the thresholds closer to the random-mixing threshold (17), inhibiting altruism with fecundity effects and favouring it with survival effects. The pattern is the same as the previous altruism example: increasing  $s$  enlarges the area in parameter space where altruism is favoured. A fecundity benefit favours altruism more in a stepping-stone structured population than in an unstructured population, but survival benefits make it more difficult for altruism to evolve.

## DISCUSSION

The population model used in the paper is a stepping-stone structure with overlapping generations, and our primary interest is the effect of the survival rate of breeders on the selective advantage of altruism. We have three main results. First, there is a distinction between benefits of fecundity and survival. Under the former, altruism is more strongly favoured and under the latter altruism is less strongly favoured than in a random-mixing population. Second, there is an effect of overlapping generations. For both types of benefit,

an increased survival probability promotes altruism. Third, although the stepping-stone model describes a much richer population structure than a simple island population, our results here show the same qualitative results found in an island population (Taylor & Irwin 2000). This indicates that the precise details of a population's spatial structure may not be very important.

We use an inclusive fitness model to measure the effects of altruism, and in order for this to predict the course of genetic evolution, we need to assume that selection is 'weak,' that is, that altruistic behaviour has a small selective effect, which means that the costs and benefits are small (Taylor 1996). There are several reasons for this assumption, but an important one is that our calculation of relatedness (Appendix A) is valid only when the allele causing the altruistic behaviour is neutral. The selective advantage of altruism that we calculate is then actually the rate at which the fitness of this allele increases as the effect of the allele is increased above zero.

When breeder survival  $s$  is zero and there is no overlap between generations we find that, independent of the dispersal rate of offspring, the altruism threshold occurs where the direct effect  $\delta_0$  of the altruist on itself is positive (3). This is also expected in a random-mixing population, but the point is that it is also obtained when dispersal of offspring is only partial in both one- and two-dimensional stepping-stone populations. However, if breeder survival is positive, so that there is overlap between generations, a decrease in the dispersal rate does have an effect on the threshold level of altruism. But here there is a striking difference between gifts of fecundity and gifts of survival — relative to a random-mixing population, altruism is promoted under a fecundity benefit, but discouraged under a survival benefit. This is illustrated in Figures 2 and 3. The difference between these two cases is easily understood. A survival benefit can be regarded as a special class of extra offspring that have the appropriate probability of winning a site, but that do not disperse, so they must remain on their home site. This increases the local competition among offspring and reduces the advantage of altruism.

The altruism threshold decreases as breeder survival  $s$  increases, favouring higher levels of altruistic behaviour. The analysis of this effect is complicated because the threshold depends on both  $s$  and the dispersal rate  $d$ , and the ES value of  $d$  itself increases with  $s$  (Irwin & Taylor 2000). This latter relationship, the increase of dispersal rate with  $s$ , is an example of

the phenomenon we are discussing — increased altruism with higher  $s$ .

Increasing the cost of dispersal has different effects on the altruism threshold for fecundity and survival effects (Figures 2 and 3). First, with fecundity effects, increasing dispersal cost reduces the ES dispersal rate and inhibits altruism. This is because the increased cost reduces the proportion of immigrant offspring on a patch and thus increases competition among native offspring, resulting in a reduced benefit from the altruistic act. In contrast, a survival benefit increases competition on neighbouring sites. This affects the recipient's fitness only through its offspring which disperse to these sites. If dispersal cost is higher, a smaller fraction of offspring disperse, so the cost has less effect on the recipient.

Several recent studies of social behaviour in lattice-structured populations are worth comparing to our results. Nowak et al. (1994) simulated the prisoner's dilemma game on a lattice with fecundity effects and found that cooperators do better in models with overlapping instead of non-overlapping generations. Nakamaru et al. (1997, 98) studied the iterated prisoner's dilemma on the lattice with both survival and fecundity effects. They simulated populations of TFT and AD strategists in one- and two-dimensional stepping-stone populations. There are several differences between their model and ours: they assume complete dispersal ( $d = 1$ , an empty site can only be colonized by a neighbour, and not the offspring of the dead individual) and they use continuously overlapping generations — only one individual on the lattice dies per time-step. Despite these differences they obtained similar results, except while we found altruism benefitting a neighbour's fecundity to be favoured, in their model the same effect could work in either direction. Nakamaru et al. (1997, 98) attribute their results to population structure, but in our example of non-overlapping generations the results are identical in both structured and randomly mixing populations. In their model with sufficiently long games ( $w$  near 1), TFT is able to invade a population of AD individuals. In one dimension their result was especially striking: their threshold could be shown as a vertical line at  $w = 3/5$  on our Figure 5A. With fecundity effects and no-cost of dispersal, we find that TFT is the ESS if  $s > 3/7$  but that both TFT and AD are ESSs for smaller  $s$  (Fig. 3A). With survival effects we find no situation where a rare TFT can invade an AD population. One of their derivations of the vertical threshold was a 'pair-edge' analysis of the velocity of the interface between clusters of TFT and AD (Ellner et al. 1998, Nakamaru et al. 1998). A critical assumption in this calculation is that adjacent sites on the interface

can't die (and potentially be replaced with the other strategy) in the same generation. This is approximately true in our model only at high survival rates.

*Acknowledgements.* We thank Josh Mitteldorf for many helpful comments. PDT is supported by the National Science and Engineering Research Council of Canada.

APPENDIX A. RELATEDNESS COEFFICIENTS.

A recursion for the relatedness between an adult at site  $i$  and at site  $j$  in the next generation (denoted by a ') in terms of relatedness in the current generation is

$$r'_{ij} = \begin{cases} \sum_{k,m} r_{km} \tilde{p}_{ki} \tilde{p}_{mj}, & i \neq j \\ 1, & i = j \end{cases} \quad (\text{A1})$$

where the sums range over all sites and the probability an offspring competing on site  $j$  was born on site  $i$  is

$$\tilde{p}_{ij} = \begin{cases} 1 - d - \mu, & i = j \\ \frac{d}{N}, & i, j \text{ are nearest-neighbours; } N \text{ is the number of nearest-neighbors} \\ \mu, & i \text{ or } j = \infty \\ 0, & \text{otherwise.} \end{cases} \quad (\text{A2})$$

In the absence of any long-range dispersal or mutation these equilibrium relatednesses are all 1 (in one and two dimensions only), so we introduce as a technical device an additional dispersal  $\mu$  from the birth site to sites with unrelated individuals at infinity. Equations (A1) and (A2) do not include effects of overlapping generations or costly dispersal. These can be incorporated with a change of variables, replacing  $d$  and  $\mu$  in (A2) with  $\hat{d}$  and  $\hat{\mu}$ ,

$$\begin{aligned} \hat{d} &= d(1-s) \left( \frac{1-k}{1-k(d+\mu)} \right) \\ \hat{\mu} &= \mu(1-s) \left( \frac{1-k}{1-k(d+\mu)} \right) \end{aligned} \quad (\text{A3})$$

(Irwin & Taylor 2000). With these substitutions  $\tilde{p}_{ij}$  becomes  $\hat{p}_{ij}$  and its interpretation changes to the probability site  $j$  is won by an offspring or adult survivor from site  $i$ .

The solution of recursion (A1) in one dimension is described by Kimura & Weiss (1964) and for overlapping generations by Irwin & Taylor (2000). The coefficients  $r_j$  which we need are (dropping terms  $O(\mu)$ )

$$\begin{aligned} r_0 &= 1 \\ r_1 &= 1 - \Phi \\ r_2 &= 1 - 4 \frac{\sqrt{1-\hat{d}} - (1-\hat{d})}{\hat{d}} \Phi \\ r_3 &= 1 - \frac{16(1-\hat{d}) \left( 1 - \frac{\hat{d}}{2} - \sqrt{1-\hat{d}} \right) + \hat{d}^2}{\hat{d}^2} \Phi, \end{aligned} \quad (\text{A4})$$

where

$$\Phi = \sqrt{\frac{2\hat{\mu}}{\hat{d}(1-\hat{d})}}.$$

In two dimensions, the equilibrium relatedness between adults separated by the vector  $(j, k)$  is

$$r_{j,k} = c (A_{j,k}(z_1) + (-1)^{j+k} A_{j,k}(z_2)) \quad (\text{A5})$$

where

$$A_{j,k}(z) = \frac{1}{(2\pi)^2 \hat{d}} \int_0^{2\pi} \int_0^{2\pi} \frac{\cos(j\theta_1) \cos(k\theta_2)}{z - \cos\theta_1 - \cos\theta_2} d\theta_1 d\theta_2$$

and

$$\begin{aligned} z_1 &= 2 \left( 1 + \frac{\hat{\mu}}{\hat{d}} \right) \\ z_2 &= 2 \left( \frac{2 - \hat{\mu}}{\hat{d}} - 1 \right) \end{aligned} \quad (\text{A6})$$

and the constant  $c$  is determined by  $r_{0,0} = 1$  (Weiss & Kimura, 1965; Irwin & Taylor, 2000). Malécot (1975) uses a similar method to obtain results for both finite and infinite stepping-stone populations.

We evaluate the  $A_{j,k}(z)$  in two ways. If  $j = k$  then we can simplify the integrals using special functions eventually obtaining forms involving the complete elliptic integrals  $K(\cdot)$  and  $E(\cdot)$  (Abramowitz & Stegun 1964),

$$A_{0,0}(z) = \frac{2}{\pi z} K\left(\frac{2}{z}\right) \quad (\text{A7})$$

$$A_{1,1}(z) = \frac{1}{\pi} \left( z - \frac{2}{z} \right) K\left(\frac{2}{z}\right) - \frac{z}{\pi} E\left(\frac{2}{z}\right). \quad (\text{A8})$$

Off-diagonal elements are evaluated with algebraic manipulations and trigonometric identities, obtaining

$$\begin{aligned} A_{0,1}(z) &= -\frac{1}{2} + \frac{z}{2} A_{0,0} \\ A_{0,2}(z) &= 2z A_{0,1} - 2A_{1,1} - A_{0,0}. \end{aligned} \quad (\text{A9})$$

If the mutant affects the fecundity of the nearest-neighbours, two more relatedness coefficients are needed:

$$\begin{aligned} A_{1,2}(z) &= z A_{1,1} - A_{0,1} \\ A_{0,3}(z) &= 2z(A_{0,0} + A_{0,2}) - 2A_{1,2} - 5A_{0,1} - 2. \end{aligned} \quad (\text{A10})$$

## APPENDIX B. DISPERSAL.

Evolutionarily stable dispersal rates can be calculated with an inclusive fitness argument analogous to the calculation in this paper. In fact, dispersal can be thought of as an altruistic act because dispersers incur a cost of dispersal and benefit offspring which remain behind by reducing competition among relatives. The results we need are below and derivations can be found in Irwin & Taylor (2000).

The ES dispersal rate in one dimension is

$$d^* = \frac{1}{2k} \frac{2 \left( 1 - \sqrt{1 - k(1-k)(1-s)} \right) - k(1-s)}{1 - \sqrt{1 - k(1-k)(1-s)} - k(1-s)} \quad (\text{B1})$$

and with no cost ( $k = 0$ ),

$$d^* = \frac{3+s}{4}. \quad (\text{B2})$$

In two dimensions, the ES dispersal rate  $d^*$  is a solution of

$$2(2d^*sk - s - 1)K \left( \frac{(1-s)(1-k)d^*}{d^*(1-s+k+sk) - 2} \right) + \pi(2 - d^*(1-s+k+sk)) = 0 \quad (\text{B3})$$

where  $K(\cdot)$  is the complete elliptic integral of the first kind (Abramowitz & Stegun 1964).

## APPENDIX C. DERIVATION OF INCLUSIVE FITNESS EFFECTS.

*Fecundity effects.* The fitness of the adult on site  $i$  is the sum of 1 times the probability the adult survives and the probability its offspring out-compete other offspring on each site,  $\sum_j p_{ij}$ , times the probability the resident adult dies,

$$w_i = s + (1-s) \sum_j p_{ij}. \quad (\text{C1})$$

The number of individuals from site  $i$  which compete on site  $j$  once the mutant has been introduced  $n'_{ij}$  is the original number  $n_{ij}$  increased by a small relative change,

$$n'_{ij} = n_{ij}(1 + \delta_i). \quad (\text{C2})$$

The average number of individuals competing for site  $j$  is  $n_j = \sum_i n_{ij}$  and with the mutant this is

$$n'_j = \sum_i n'_{ij} = n_j \left( 1 + \sum_i \delta_i p_{ij} \right). \quad (\text{C3})$$

The new probability of an individual from site  $i$  obtaining a vacant breeding spot on site  $j$  is  $p'_{ij}$ , written to first order in  $\delta$

$$p'_{ij} = \frac{n'_{ij}}{n'_j} = p_{ij} \left( 1 + \delta_i - \sum_k \delta_k p_{kj} \right). \quad (\text{C4})$$

The fitness of the adult on site  $i$  with a mutant at site 0 is

$$w'_i = s + (1 - s) \sum_j p'_{ij}, \quad (\text{C5})$$

and together with (C1) and (C4) we obtain the inclusive fitness effect of the mutant

$$\Delta w_{IF} = \sum_i \Delta w_i r_i = (1 - s) \sum_{ij} r_i p_{ij} \left( \delta_i - \sum_k \delta_k p_{kj} \right). \quad (\text{C6})$$

Symmetry allows us to write  $p_{ij} = p_{j-i}$  and  $p_{-j} = p_j$ ; the probability of dispersal to a site depends only on the separation between the two sites and not the absolute position of the sites. The simplified expression is (2).

*Survival effects.* Writing the survival of an adult on site  $i$  as  $s_i = s$  we can introduce an effect of the mutant, altering the survival probability by a small relative change  $\delta_i$ ,

$$s'_i = s_i(1 + \delta_i). \quad (\text{C7})$$

We leave  $n_{ij}$  and  $p_{ij}$  as before, and note that  $p_{ij}$  can be interpreted as the probability an individual from site  $i$  wins on site  $j$  conditioned on the death of the individual at site  $j$ . The fitness of an individual on site  $i$  is

$$w_i = s_i + \sum_j p_{ij}(1 - s_j) \quad (\text{C8})$$

and after a mutant is introduced at site 0, the fitness is

$$\begin{aligned} w'_i &= \sum_j p'_{ij}(1 - s'_j) + s'_i = \sum_j p_{ij}(1 - s_j(1 + \delta_j)) + s_i(1 + \delta_i) \\ &= w_i - \sum_j \delta_j p_{ij} s_j + s_i \delta_i. \end{aligned} \quad (\text{C9})$$

The inclusive fitness effect  $\Delta w_{IF} = \sum_i r_i \Delta w_i$  is (8).

#### APPENDIX D. ITERATED PRISONER'S DILEMMA.

The average payoff to a  $p$  actor playing a  $q$  player is

$$W(p, q) = pq \left( \frac{R}{1-w} \right) + (1-p)q \left( T + \frac{Pw}{1-w} \right) \quad (\text{D1})$$

$$+ p(1-q) \left( S + \frac{Pw}{1-w} \right) + (1-p)(1-q) \left( \frac{P}{1-w} \right). \quad (\text{D2})$$

The cost to an actor of using the mutant strategy  $p' = p + \delta$  is

$$C = -(W(p', p) - W(p, p)) = -\delta_0 \quad (\text{D3})$$

and the benefit to its neighbours is

$$B = W(p, p') - W(p, p) = N\delta_1. \quad (\text{D4})$$

We use capital letters as a reminder that these are the net cost  $C$  to the actor and the benefit  $B$  which is divided, on average, among the  $N$  neighbours not including the actor. Substituting (D3, D4) into (5, 7, 10, 12) to obtain an altruism relatedness threshold  $-\delta_0/(N\delta_1)$  and solving for  $p$  to first order in  $\delta$  using the payoffs from Table 2 we obtain the following threshold

$$p = \frac{1-w}{3w-1} \cdot \frac{(\frac{-\delta_0}{N\delta_1})(3+N) - 4}{1 + (\frac{-\delta_0}{N\delta_1})(N-2)}. \quad (\text{D5})$$

If  $w > 1/3$  then increased altruism (frequency of playing TFT) is selected for  $p$  greater than this threshold and decreased altruism is selected for smaller  $p$ . If  $w < 1/3$  then AD is the ESS.

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Table 1.

Notation used in the main altruism model. In a homogeneous lattice, variables with two indices depend only on the separation between sites and are sometimes written to reflect this, e.g.  $r_{j-i} = r_{ij}$ . In two dimensions this is a vector difference and we index with these differences, e.g.  $r_{0,\pm 1} = r_{\pm 1,0}$  is the relatedness of nearest-neighbours.

$d$	dispersal rate,
$\delta_i$	effect of altruist at the origin on the fecundity or survival of an individual on site $i$ ,
$k$	dispersal cost; a fraction $1 - k$ arrive at the new site,
$N$	number of neighbours,
$n_{ij}$	average number of offspring competing for site $j$ who come from site $i$ ,
$n_j = \sum_i n_{ij}$	average number of offspring competing for site $j$ ,
$p_{ij} = n_{ij}/n_j$	probability an offspring competing for site $j$ came from site $i$ ,
$r_{ij}$	equilibrium relatedness between an adult on site $i$ and an adult at site $j$ ,
$s$	the probability an adult survives to breed in the next generation,
$w_i, \Delta w_i$	fitness (and change in fitness due to the mutant) of an adult on site $i$ .

Table 2.

Payoffs for the iterated prisoner's dilemma where TFT is the cooperative strategy 'tit-for-tat' and AD is 'always defect'. The parameters  $T, R, P, S$  are the payoffs for the prisoner's dilemma and satisfy  $T > R > P > S$ . The probability of playing the prisoner's dilemma again with the same partner is  $w$ . We use  $T = 5, R = 3, P = 1, S = 0$  for numerical examples. If  $w = 0$  the game reduces to the prisoner's dilemma.

		Partner	
		TFT	AD
Actor	TFT	$R/(1 - w)$	$S + Pw/(1 - w)$
	AD	$T + Pw/(1 - w)$	$P/(1 - w)$

FIGURE CAPTIONS

Figure 1.

Site classes on the two dimensional stepping-stone lattice labelled with relatedness to the centre (black) site. Shaded sites are in the interaction neighbourhood of an individual on the centre site.

Figure 2.

Altruism threshold  $-\delta_0/(N\delta_1)$  as a function of survival  $s$ . Results for fecundity (solid) and survival (dashed) effects in one (A) and two (B) dimensions. Thick lines are for zero-cost dispersal and thin lines for a small dispersal cost ( $k = 0.2$ ). The horizontal dotted line is the altruism threshold for random-mixing populations or  $s = 0$ .

Figure 3.

Altruism thresholds  $\frac{b}{N+1}/c$  as a function of survival  $s$ . Results for fecundity (solid) and survival (dashed) effects in one (A) and two (B) dimensions. Thick lines are for zero-cost dispersal and thin lines for a small dispersal cost ( $k = 0.2$ ). The horizontal dotted line is the threshold for random-mixing populations or  $s = 0$ .

Figure 4.

Threshold values of TFT frequency  $p$  as a function of survival  $s$  for the iterated prisoner's dilemma game with a probability of re-encounter of  $w = 3/5$  in one- (A) and two-dimensional (B) stepping-stone populations. The horizontal dotted line is the threshold for random-mixing populations (17) or  $s = 0$  and other lines are as in Figure 2. Increased frequency of TFT is favoured above the appropriate line. For no-cost dispersal in one dimension, TFT is the only ESS for  $s > \frac{3(P-S)}{2T-3P+S} = \frac{3}{7}$  with fecundity effects and AD is the only ESS for  $s < \frac{9-13w}{1+3w} = \frac{3}{7}$  with survival effects.

Figure 5.

Threshold values of TFT frequency  $p$  as a function of the probability of re-encounter  $w$  for the iterated prisoner's dilemma game with survival probability of  $s = 2/5$  in one- (A) and two-dimensional (B) stepping-stone populations. The dotted line is the threshold for randomly-mixing populations (17) or  $s = 0$  and other lines are as in Figure 2. Increased frequency of TFT is favoured above the appropriate line.

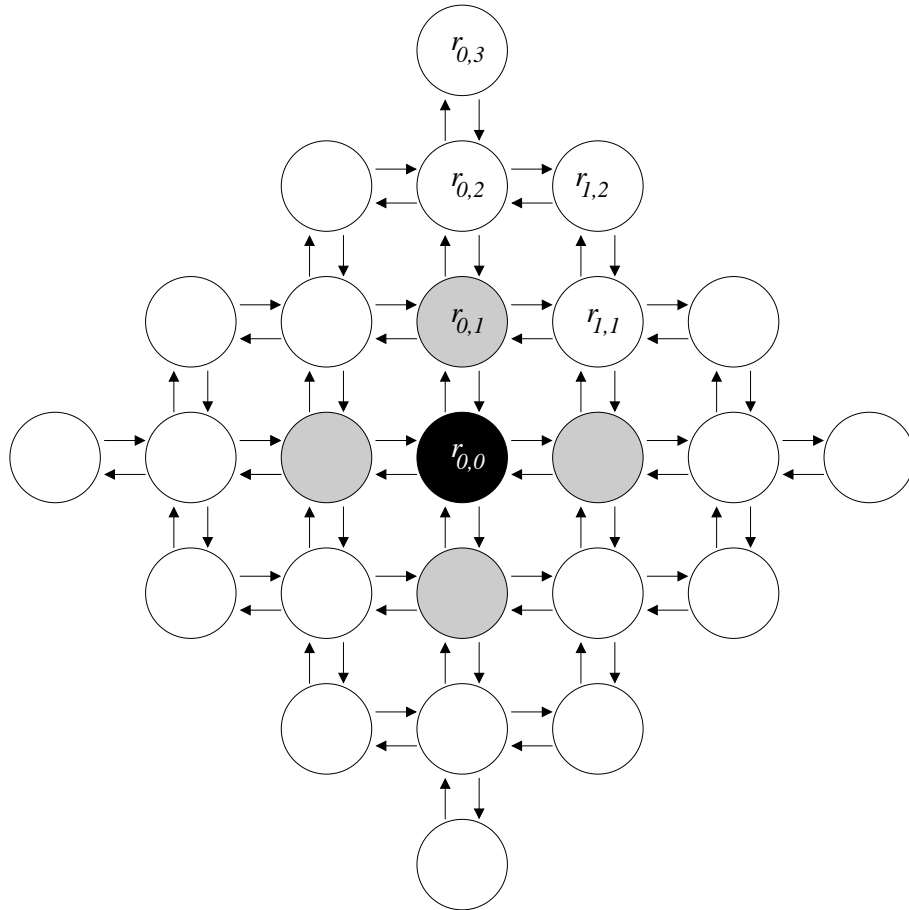


Figure 1. (Irwin / Taylor)

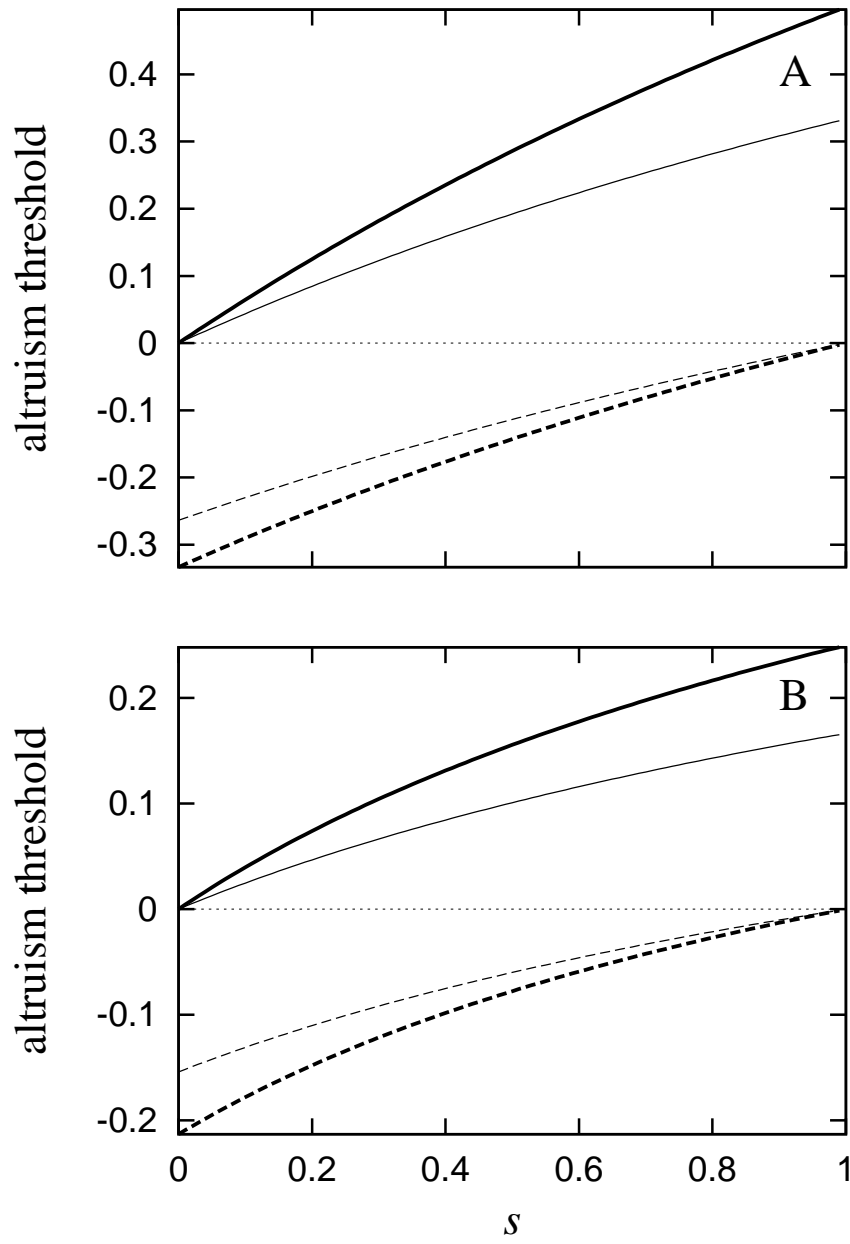


Figure 2. (Irwin / Taylor)

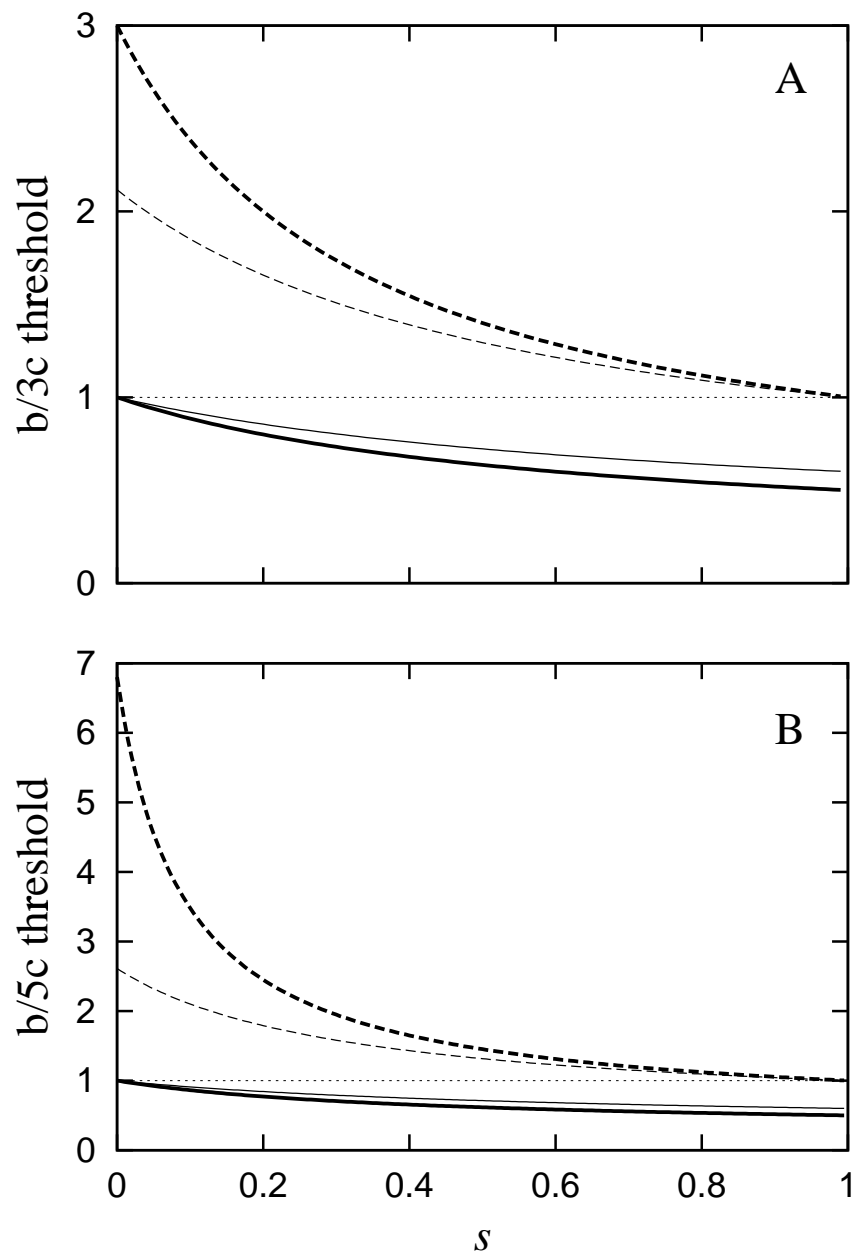


Figure 3. (Irwin / Taylor)

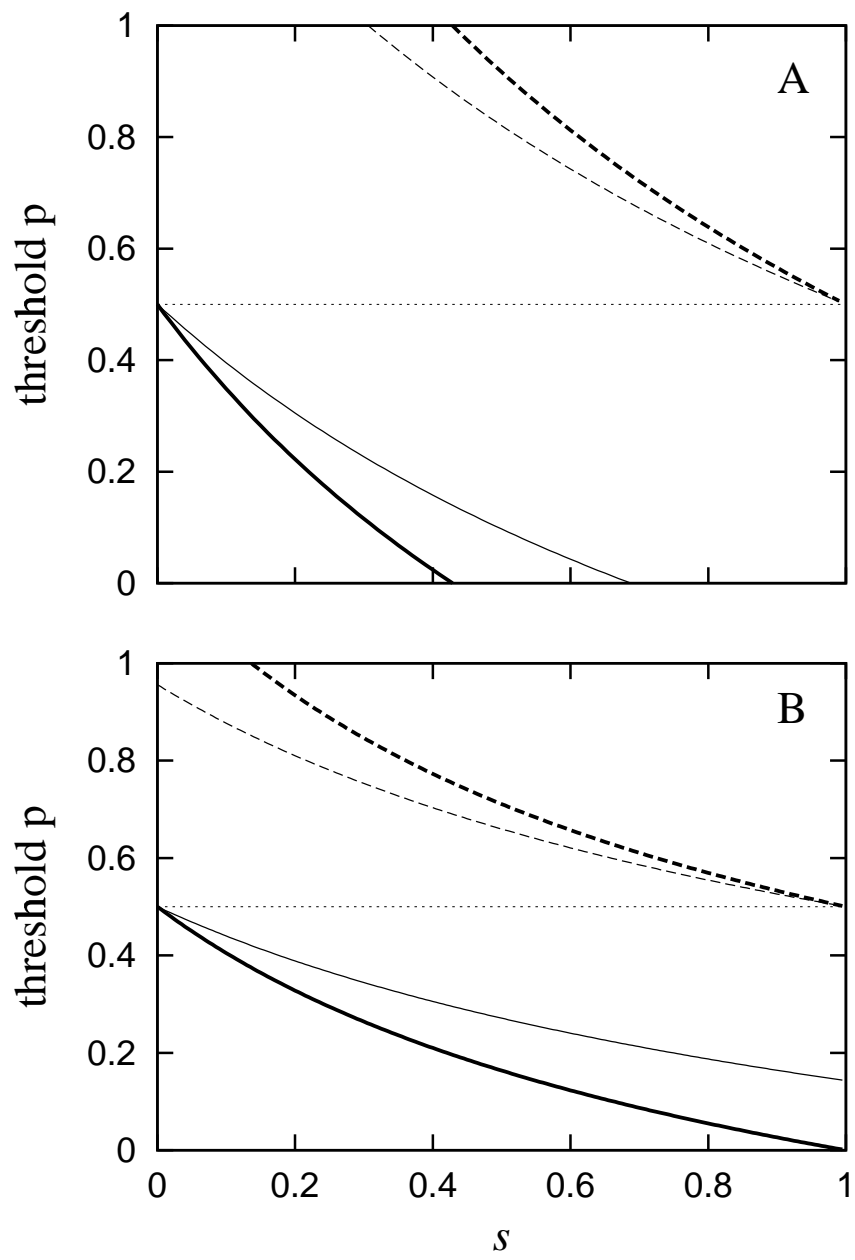


Figure 4. (Irwin / Taylor)

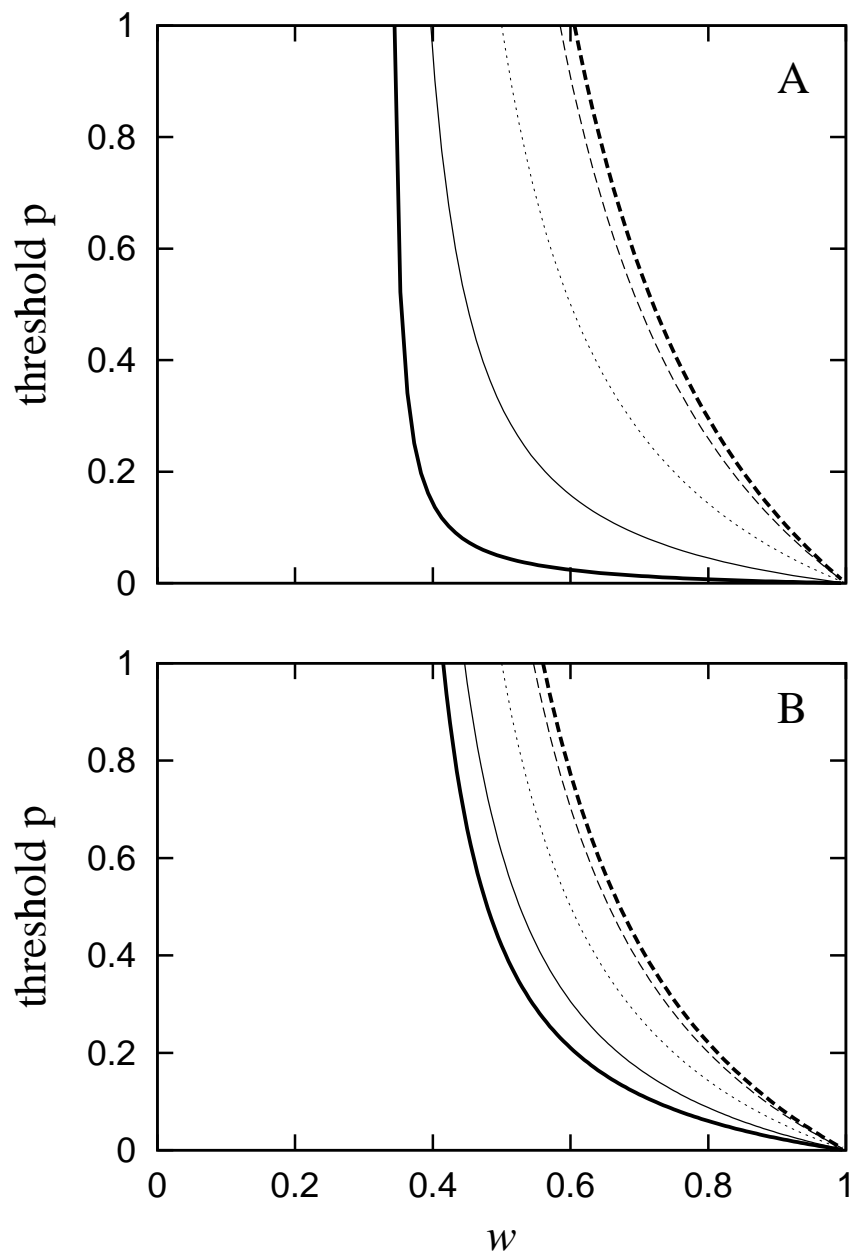


Figure 5. (Irwin / Taylor)