

Evolution of cooperation in a finite homogeneous graph

Peter D. Taylor¹, Troy Day¹ & Geoff Wild¹

Recent theoretical studies of selection in finite structured populations^{1–7} have worked with one of two measures of selective advantage of an allele: fixation probability and inclusive fitness. Each approach has its own analytical strengths, but given certain assumptions they provide equivalent results¹. In most instances the structure of the population can be specified by a network of nodes connected by edges (that is, a graph)^{8–10}, and much of the work here has focused on a continuous-time model of evolution, first described by ref. 11. Working in this context, we provide an inclusive fitness analysis to derive a surprisingly simple analytical condition for the selective advantage of a cooperative allele in any graph for which the structure satisfies a general symmetry condition ('bi-transitivity'). Our results hold for a broad class of population structures, including most of those analysed previously, as well as some for which a direct calculation of fixation probability has appeared intractable. Notably, under some forms of population regulation, the ability of a cooperative allele to invade is seen to be independent of the nature of population structure (and in particular of how game partnerships are specified) and is identical to that for an unstructured population. For other types of population regulation our results reveal that cooperation can invade if players choose partners along relatively 'high-weight' edges.

In evolutionary biology an individual's behaviour is termed 'social' if it affects the reproductive success of other individuals in the population, and one of the most enduring puzzles is the existence of social behaviours such as cooperation and altruism. Hamilton's¹² pioneering work on inclusive fitness demonstrated that, if individuals tend to interact with genetic relatives, then such behaviours can often evolve. Interactions with relatives might occur as a result of kin recognition, but they might also occur simply as a result of limited dispersal^{13–16}.

Recent studies in evolutionary game theory^{8–10} have provided some interesting new results on the evolution of cooperation, by describing patterns of interaction among individuals in terms of graphs. A graph is simply a set of nodes (representing the individuals), each of which is connected to other nodes with edges (Box 1). These edges provide the relationships among individuals and are of two types: the dispersal patterns of offspring, and the patterns of social interaction among individuals. The probability of fixation of a cooperative allele can then be determined, as a function of the structure of the graph, so that we might understand how different kinds of networks of interactions affect the evolution of social behaviour^{8–10}. Here we demonstrate that Hamilton's notion of inclusive fitness¹² provides a natural way to understand evolution on such graphs, and that it provides simple analytical conditions for the evolution of any trait (including cooperation) for a large class of graphs. The primary process at work in such systems can thus be viewed as a case of interactions among related individuals as a result of limited dispersal. A schematic summarizing our main results is provided as Supplementary Fig. 1.

In the graphs considered here, the edges represent patterns of dispersal and social interactions given by the weights d_{ij} and e_{ij} respectively. Specifically, the weights d_{ij} determine (in a way made precise below) the probability that a birth at node i replaces the individual at node j . Furthermore, individuals i and j interact at each time step with probability e_{ij} . We assume $d_{ii} = e_{ii} = 0$, $\sum_j d_{ij} = \sum_j e_{ij} = 1$, and $d_{ij} = d_{ji}$ and $e_{ij} = e_{ji}$. We suppose that the fecundity $f_i = F(X_i, Y_i)$ of individual i (where F is the fecundity function specified by the model) is determined by its own phenotype X_i and by the average phenotype $Y_i = \sum_j e_{ij} X_j$ of the individuals with whom it interacts.

We assume that individuals are haploid with one of two alleles A or B, and offspring are identical to parents except for a small symmetric probability of mutation. We consider two versions of fecundity selection. In the BD process, births are allocated to the population at a fixed, fitness-independent rate and are given to individual i with relative probability f_i , replacing a neighbour j of i with probability d_{ij} . In the DB process, individuals die at a fixed, fitness-independent rate and a death at node j is replaced by an offspring from node i with relative probability $f_i d_{ij}$. In both cases, the population size remains constant. Take note that f_i measures fecundity, but this is only one component of fitness, the other being mortality.

Our results apply to an arbitrary fecundity function $F(X, Y)$ provided that the 'effect' of the A allele is both small and additive. For example, our results apply to the general matrix game¹⁰ $\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$ (where the first row gives the pay-off to an A player against an A or B opponent, and the second row gives the same pay-offs to a B player), provided both that the a_{ik} values are small and that $a_{11} + a_{22} = a_{12} + a_{21}$. We work here with the 'cost-benefit' matrix $\begin{bmatrix} b-c & -c \\ b & 0 \end{bmatrix}$. A second example is found in Box 2.

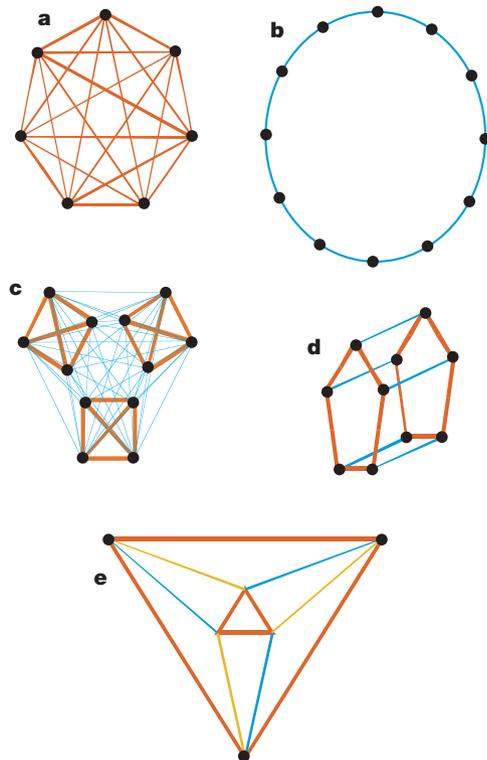
We consider graphs with a large amount of internal symmetry as described by an isomorphism. An isomorphism T of a graph is a bijection of the node set that preserves the dispersal and interaction parameters, that is, $d_{T(i)T(j)} = d_{ij}$ and $e_{T(i)T(j)} = e_{ij}$. A graph is called (node) transitive if, for every ordered pair of nodes (i, j) , there is an isomorphism T for which $T(i) = j$; it is called (node) bi-transitive if, for every ordered pair of nodes (i, j) , there is an isomorphism T for which $T(i) = j$ and $T(j) = i$. The graphs given in Box 1 are all transitive and all but panel e are bi-transitive.

Our objective is to measure the selective advantage of the allele A. We begin in the neutral population ($c = b = 0$) in which A and B are equally fit, and ask: what is the effect of increasing b and c above 0? We focus attention on three different selective measures. First, the change in b and c will cause the expected long-term frequency of A ($E(A)$; under mutation-selection balance) to differ from $E(B)$, the long-term frequency of B, and we might use that difference as a measure. Second, we define the fixation probability ρ_A of A (ρ_B of B) to be

¹Department of Mathematics and Statistics, Queen's University Kingston, Ontario K7L 3N6, Canada.

Box 1 | Transitive graphs

Roughly speaking, a graph is transitive if it globally 'looks the same' from any node; that is, if you placed an individual at a node and then blindfolded him and perhaps moved him to another node, he would be unable to tell, using only information about total configuration of edges and their weights, whether or not he had been moved. A graph is bi-transitive if it 'looks the same' from any pair of nodes. That is, if you placed two individuals at any two nodes and then blindfolded them and perhaps interchanged them, they would be unable to tell whether or not they had been interchanged. In the examples shown, different weights (both d and e weights) are represented by different colours, although the d values and the e values might be different. All graphs are transitive and all except panel e are bi-transitive.



Box 1 Figure 1 | Examples of transitive graphs. **a**, A 'complete' graph. **b**, A cycle. Nodes are joined only to immediate neighbours. **c**, An island structure¹⁶. Here there are three demes of size 4. Within each deme, all edges have equal weight; edges between demes have another weight. **d**, Two pentagonal cycles with constant edge weights. Edges between cycles have another weight. This is a version of the Petersen graph. **e**, This graph can be thought of in different ways, but we have drawn it to emphasize its relation to the Petersen graph in **d**. In this case there are two cycles of size 3 (triangles), and each node is joined to two nodes in the other triangle with edges of different weights. This graph is symmetric and transitive, but when the blue and amber edges have different d or e weights it is not bi-transitive. If one takes two nodes in different triangles, one can find an isomorphism that interchanges them, but this is not true for two nodes in the same triangle. Nevertheless, it turns out that equations (1) and (2) do hold for this graph.

the probability that a single randomly placed A allele in an otherwise B population (B allele in an otherwise A population) will become fixed in the absence of mutation. In the neutral case, $\rho_A = \rho_B = 1/N$ as all N individuals have an equal chance of contributing the gene that will ultimately become fixed, and we might measure the advantage of A with the difference $\rho_A - \rho_B$ ^{4,10}. Third, we might use the inclusive fitness effect¹² W_{IF} of the change from B to A (see Methods). To summarize, we might say that A has a selective advantage over B in any of the following situations: $E(A) > E(B)$, $\rho_A > \rho_B$, and $W_{IF} > 0$. It is known¹ that for sufficiently small mutation rates in a discrete-generations finite-population model, these three conditions are

Box 2 | Frank's island model of competition^{16,18,19}

In more general phenotypic models, fecundity is expanded in a Taylor series:

$$F(X, Y) = F_0 + \frac{\partial F}{\partial X} dX + \frac{\partial F}{\partial Y} dY$$

where we take the differential phenotype to be proportional to genotype x (frequency of A): $dX = \delta x$ where δ is small. This allows us to ignore higher order terms in the phenotypic change and we get weak selection and additivity all at once. In this case, our equations (1) and (2) apply with $c = -\delta \frac{\partial F}{\partial X}$ and $b = \delta \frac{\partial F}{\partial Y}$. In Frank's island model (Box 1 Fig. 1d with n demes of size m , so that population size is $N = nm$) the reproductive resources, $S = S(Z)$, available to a deme decrease with average deme phenotype Z , whereas an individual's share of the deme's resources is proportional to X/Z , its relative competitiveness in the deme; thus $F(X, Y) = \frac{X}{Z} S(Z)$. We take an individual's interactants to be its deme mates, so that $mZ = X + (m-1)Y$. With a BD protocol, equation (1) easily shows that, no matter what the pattern of offspring dispersal, the level of competitiveness X_0 will increase provided

$$\text{BD: } \frac{X_0(-S'(X_0))}{S(X_0)} < \frac{(m-1)n}{n-1} \quad (4)$$

For the DB protocol, we need to specify the dispersal pattern. If h is the probability an offspring remains on its natal deme, then equation (2) shows that X_0 will increase provided

$$\text{DB: } \frac{X_0(-S'(X_0))}{S(X_0)} < \frac{(m-1-h)n}{n(1+h)-2} \quad (5)$$

Provided $h > 1/N$, the right side of equation (4) exceeds that of equation (5), giving a higher evolutionarily stable level of competitiveness in the BD model.

equivalent to first order in the behavioural deviations b and c . The importance of this for us is that it allows us to use the more easily calculated inclusive fitness effect to measure the direction of change in expected frequency or fixation probability of A. We remark that when b and c are small, the second condition ($\rho_A > \rho_B$) can be shown to be equivalent to $\rho_A > 1/N$ in any finite population that can be modelled as a graph (P.D.T. *et al.*, manuscript in preparation).

This is not the case⁴ for the more general matrix $\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$ (with a_{hk} small) unless $a_{11} + a_{22} = a_{12} + a_{21}$.

The inclusive fitness effect of an action by a focal individual is defined to be the sum of the fitness effects of this action on all individuals in the population, each effect weighted by its relatedness to the focal individual. To give a simple example, a fecundity gift of b from i to a neighbour j will increase the probability that j will have an offspring but that offspring will replace another neighbour h , so that the inclusive fitness effect will be the extra fecundity to j minus the extra mortality to h , each weighted by the relatedness to i . Of course, if the action has other effects as well, such as a cost c to i , then the effects of that must be accounted for in the same way, and the weak selection assumption (small b and c) will allow us to add these two kinds of effects to obtain the overall inclusive fitness effect. These calculations (see Methods) give us the following simple expressions for the inclusive fitness effect of the allele A in any bi-transitive graph:

$$\text{BD model: } W_{IF} = -b - c(N-1) \quad (1)$$

$$\text{DB model: } W_{IF} = b[N\bar{d} - 2] - c(N-2) \quad (2)$$

where, in equation (2), $\bar{d} = \sum_j e_{ij} d_{ij}$ is the average d -weight of the edge between i and a random interactant, and under transitivity is independent of i . Alternatively, if we pick a random interactant j of i , then \bar{d} is the probability that i 's next offspring will displace j .

It is interesting that, in the BD model, the inclusive fitness effect is independent of the structure of the population and of the distribution $\{e_{ij}\}$ of interactants. It is therefore the same as in a random

mixing population in which all d -weights are $d_{ij} = 1/(N-1)$ for $i \neq j$. This generalizes known results^{13–15} for an infinite population with an island or stepping-stone structure, and reveals that, under BD, the ‘cooperative’ allele A can never be selected for positive values of b and c .

In the DB model, the condition does depend on i 's interactants, and when these are sufficiently ‘close’ to i (\bar{d} is large), A can be selectively advantageous for positive b and c with a high enough b/c ratio. The difference between these results for the BD and DB models has to do with where the competitive effects of a ‘gift’ from i to j are felt. Under BD these are felt by j 's neighbours (who, because they include i , have a higher average relatedness to i than does j), whereas under DB these are felt by the neighbours of j 's neighbours (who do not, in fact, have a higher average relatedness to i than does j).

These results extend previous results for the case in which selection is both weak and additive. A previous study¹⁰ uses analytical methods to calculate fixation probabilities on the cycle (Box 1 Fig. 1b) for both the BD and the DB models. Our equation (1) is their equation (2.4) and our equation (2), with $\bar{d} = 1/2$, is their equation (4.4). Their approach works well on the cycle essentially because a population that starts with a single A player will always have the property that the A players are found in a single connected cluster. For more complicated graphs, such as those that involve deme structure (Box 1 Fig. 1c, d), this is not the case and their approach appears to be less tractable. The inclusive fitness analysis continues to hold in these cases as well, however, allowing one to analyse evolution relatively easily in these more complex scenarios provided one has both weak selection and additivity (Box 2).

A previous study⁹ used numerical methods and pair approximation techniques to investigate the b - c matrix game in a DB model on a large variety of graphs. The main result of ref. 9 applies to graphs of degree k (every node has k edges with equal weight $d = 1/k$). In their model, partners are always chosen along a connecting edge (that is, $d_{ij} = e_{ij}$ for all ij), and in this case, for $k \ll N$, they find that $\rho_A > 1/N$ when $b/c > k$. They remark that this has the flavour of Hamilton's rule and, for bi-transitive graphs, we now see the connection. Equation (2) tells us that for interactions along all edges (for which $d_{ij} = e_{ij} = 1/k$) the inclusive fitness effect of A is positive when

$$\frac{b}{c} > \frac{k(N-2)}{N-2k} \quad (3)$$

For $k \ll N$ this indeed approximates the ref. 9 condition $b/c > k$. For example, with two connected cycles, each of size 18, and with $k = 3$, equation (3) gives $b/c > 3.4$, which is very nearly $b/c > k$. If the cycles are only of size 5 however (as in the Peterson graph, Box 1 Fig. 1d), then we no longer have $k \ll N$ and equation (3) gives $b/c > 6$. Figure 1 presents simulation results illustrating that equation (3) accurately predicts the spread of a cooperative allele across a range of values of N , even with moderate fitness effects.

Equations (1) and (2) reveal that the ability of cooperation to evolve depends critically on the nature of population regulation. For some forms of population regulation (the BD protocol) equation (1) demonstrates that population viscosity should not affect the evolution of cooperation under a much broader range of conditions than previously appreciated. At the same time, however, equation (2) demonstrates that viscosity under other forms of population regulation (the DB protocol) can facilitate the evolution of cooperation. This inequality clearly delineates the conditions under which this will occur for a quite general class of population structures. It shows that in a sufficiently ‘homogeneous’ population, if viscosity acts so that interactants have a high likelihood of displacing one another when they reproduce, then cooperation can evolve regardless of the precise form of population structure. Furthermore, although our main focus has been on cooperation, these results apply to the evolution of any trait. For example, in Box 2 we analyse Frank's island model of competition.

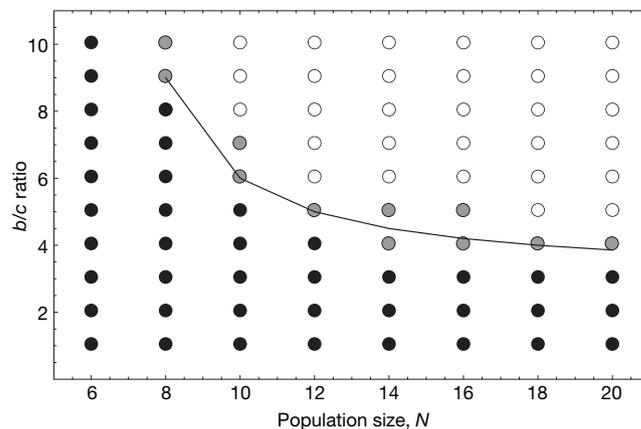


Figure 1 | Simulation results for the DB model with bi-transitive graphs of degree 3, and population sizes $N = 6$ to $N = 20$. The solid line is an analytical prediction from equation (3), above which the cooperative allele is predicted to invade and below which it is not. The population was initialized with one A allele at a randomly chosen node, and the DB process was simulated until fixation of either A or B occurred. Individual fecundities were calculated as $f_i = 1 - cI_i + \sum_j e_{ij} I_j b$, where I_j is an indicator variable equalling 1 if the allele at node j is A, and 0 otherwise. The b/c ratio was varied from 1 to 10, with $c = 0.1$ in all simulations. For each circle, 10,000 realizations of the simulation were run. The 95% confidence interval for the probability of fixation of A was then calculated as $\hat{\rho} \pm \sqrt{\hat{\rho}(1-\hat{\rho})/N}$ where $\hat{\rho} = \text{the number of fixations}/10^4$. If the confidence interval contained the neutral fixation probability, $1/N$, the circle was coloured grey (not different from neutral). If the confidence interval lay entirely below $1/N$ the circle was coloured black (no invasion). If the confidence interval lay entirely above $1/N$ the circle was coloured white (invasion). Similar results are obtained if we instead compare the fixation probability of allele A with that of allele B (rather than comparing it to $1/N$; T.D., unpublished data).

Considerable attention has been paid to the comparison of fixation probabilities on graphs under different matrix games. Such probabilities can be readily calculated only for a restricted class of simple graphs in which each state (number of A alleles) occurs in only one population configuration (for example, regular graphs and cycles). For more general scenarios, simulations and pair approximations have been used instead⁹. In this study, we use a different set of approximations (gene action is weak and additive), and demonstrate that inclusive fitness calculations can predict relative fixation probability in a large class of graphs. In particular, for graphs with a particular homogeneity property, and for small b and c , allele A will have a higher fixation probability than B ($\rho_A > \rho_B$) when the inclusive fitness effect W_{IF} in equations (1) and (2) is positive.

METHODS

Details of the methods used are found in Supplementary Information. The inclusive fitness calculation has two technical components: the calculation of relatedness¹⁷ and the calculation of the inclusive fitness effect of the A allele. For the first, we let G_{ij} be the coefficient of identity-by-descent between nodes i and j , and we find the expected change in these coefficients owing to a single breeding event (which displaces either i or j). The equilibrium condition is obtained by setting this change to be zero. We simplify this condition with the observation that bi-transitivity implies that the matrices $[d_{ij}]$ and $[G_{ij}]$ commute, and we get from this the two key relationships needed in the inclusive fitness analysis:

$$\sum_j d_{ij} G_{jk} = G_{ik} + \mu \quad (i \neq k)$$

$$\sum_j G_{jk} d_{jk} = 1 - \mu(N-1)$$

valid to first order in the mutation rate μ .

The inclusive fitness calculation begins with a uniform B population and replaces B with A in a focal actor i . The inclusive fitness effect is the weighted sum of the effects of this replacement on the fitness of each individual j , where the weights are the relatedness between i and j , and we show that these can be taken to be the coefficients G_{ij} . In these calculations, we must keep in mind that any

change in fecundity of an individual will affect both the birth rate and the death rate of neighbouring individuals. The precise effect on these individuals will differ between our two protocols, BD and DB.

Received 23 January; accepted 29 March 2007.

- Rousset, F. & Billiard, S. A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. *J. Evol. Biol.* **13**, 814–825 (2000).
- Taylor, P. D., Irwin, A. J. & Day, T. Inclusive fitness in finite deme-structured and stepping-stone populations. *Selection* **1**, 83–93 (2000).
- Proulx, S. R. & Day, T. What can invasion analyses tell us about evolution under stochasticity? *Selection* **2**, 1–16 (2001).
- Nowak, M. A., Sasaki, A., Taylor, C. & Fudenberg, D. Emergence of cooperation and evolutionary stability in finite populations. *Nature* **428**, 646–650 (2004).
- Wild, G. & Taylor, P. D. Fitness and evolutionary stability in game theoretic models of finite populations. *Proc. R. Soc. Lond. B* **271**, 2345–2349 (2004).
- Lessard, S. Long-term stability from fixation probabilities in finite populations: new perspectives for ESS theory. *Theor. Popul. Biol.* **68**, 19–27 (2005).
- Orzack, S. H. & Hines, W. G. S. The evolution of strategy variation: will an ESS evolve? *Evolution* **59**, 1183–1193 (2005).
- Lieberman, E., Hauert, C. & Nowak, M. A. Evolutionary dynamics on graphs. *Nature* **433**, 312–316 (2005).
- Ohtsuki, H., Hauert, C., Lieberman, E. & Nowak, M. A. A simple rule for the evolution of cooperation on graphs. *Nature* **441**, 502–505 (2006).
- Ohtsuki, H. & Nowak, M. A. Evolutionary games on cycles. *Proc. R. Soc. B* **273**, 2249–2256 (2006).
- Moran, P. A. P. *Statistical Processes of Evolutionary Theory* (Oxford, Clarendon, 1962).
- Hamilton, W. D. The genetical evolution of social behaviour, I and II. *J. Theor. Biol.* **7**, 1–52 (1964).
- Wilson, D. S., Pollock, G. B. & Dugatkin, L. A. Can altruism evolve in a purely viscous population? *Evol. Ecol.* **6**, 331–341 (1992).
- Taylor, P. D. Altruism in viscous populations – an inclusive fitness model. *Evol. Ecol.* **6**, 352–356 (1992).
- Taylor, P. D. Inclusive fitness in a homogeneous environment. *Proc. R. Soc. Lond. B* **249**, 299–302 (1992).
- Wright, S. Isolation by distance. *Genetics* **28**, 114–138 (1943).
- Michod, R. E. & Hamilton, W. D. Coefficients of relatedness in sociobiology. *Nature* **288**, 694–697 (1980).
- Frank, S. A. Kin selection and virulence in the evolution of protocells and parasites. *Proc. R. Soc. Lond. B* **258**, 153–161 (1994).
- Taylor, P. D. & Frank, S. How to make a kin selection argument. *J. Theor. Biol.* **180**, 27–37 (1996).

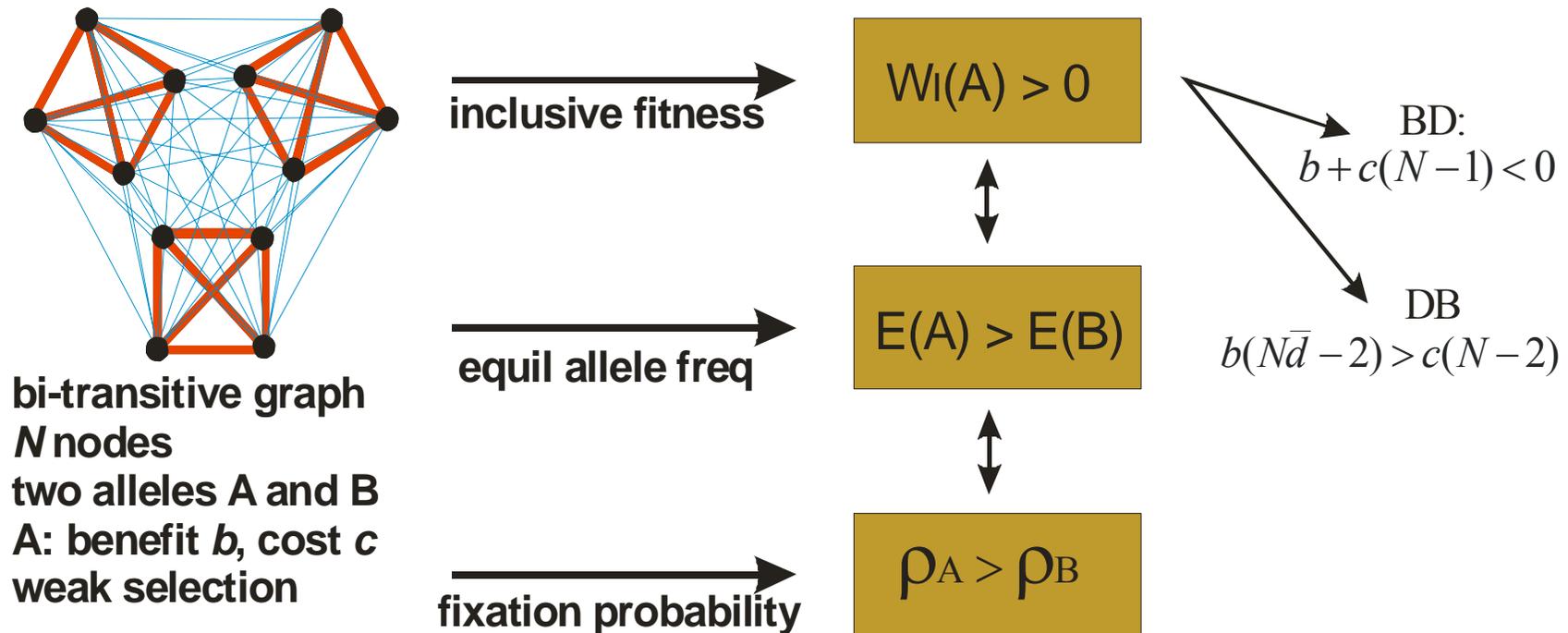
Supplementary Information is linked to the online version of the paper at www.nature.com/nature. A summary figure is also included.

Acknowledgements We thank D. Gregory for an exchange of ideas, and A. Gardner, J. Pepper and A. Grafen for many comments. This research was funded by grants to P.D.T. and T.D. from the Natural Sciences and Engineering Research Council (NSERC) of Canada.

Author Contributions All authors contributed equally to this work.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to P.D.T. (peter.taylor@queensu.ca).

Supplementary Methods



Supp Fig. 1.

In finite structured populations, the following three common measures of the selective advantage of an allele A are known to be equivalent under conditions in which gene action is additive and of small effect: the inclusive fitness effect of A, the relative equilibrium allele frequency of A and the relative fixation probability of A. In a large class of commonly studied populations of constant size, which includes cycles and island models (the latter illustrated in the figure) we have used an inclusive fitness analysis to establish a simple general condition for an altruistic allele A to be selectively favoured. The condition has different algebraic forms depending on whether birth precedes (BD) or follows (DB) death. This condition also generalizes to other additive models under weak selection (e.g. Box 2). The indicated class of populations are those whose graph-representation is bi-transitive. Essentially, this means that the “universe” looks the same from any two nodes, in the sense that a pair of observers on those nodes who switched places would not be able to tell whether they had been switched.

Technical Recap. In the graphs considered here, the edges represent patterns of dispersal and social interactions given by the weights d_{ij} and e_{ij} respectively. Specifically, when there is a birth by the individual at node i , we assume that the offspring replaces the individual at node j with relative probability d_{ij} , where $d_{ii} = 0$, $\sum_j d_{ij} = 1$ and $d_{ij} = d_{ji}$. Furthermore, individuals i and j interact at each time step with probability e_{ij} , where $e_{ii} = 0$, $\sum_j e_{ij} = 1$ and $e_{ij} = e_{ji}$. We suppose that the fecundity $f_i = F(X_i, Y_i)$ of individual i is determined by its own phenotype X_i and by the average phenotype $Y_i = \sum_j e_{ij} X_j$ of the individuals with whom it interacts. An *isomorphism* T of a graph is a bijection of the node set which preserves the dispersal and interaction parameters, i.e. $d_{T(i)T(j)} = d_{ij}$ and $e_{T(i)T(j)} = e_{ij}$. A graph is called (node) *transitive* if, for every ordered pair of nodes (i, j) , there is an isomorphism T for which $T(i) = j$ and it is called (node) *bi-transitive* if, for every ordered pair of nodes (i, j) , there is an isomorphism T for which $T(i) = j$ and $T(j) = i$.

Analysis of the relatedness recursions. In this section we assume neutrality ($b = c = 0$) so that all individuals have the same phenotype. Our argument applies to both the BD and the DB models. We let $d\alpha$ be the probability that any particular individual will reproduce in time dt . We suppose that a mutation occurs in the making of an offspring with probability μ and otherwise, with probability $1-\mu$, the offspring is identical by descent^{18,19} (IBD) to its parent. This model can be translated to our two-allele situation by assuming that every mutant allele is a new (not IBD) version of A or B independent of its ancestral state. If dG is the change in G in time dt , then

$$dG_{ik} = d\alpha \left[\sum_j d_{ji} [(1-\mu)G_{kj} - G_{ki}] + \sum_j d_{jk} [(1-\mu)G_{ij} - G_{ik}] \right] \quad (i \neq k) \quad (\text{S1})$$

This equation provides the two ways in which the coefficient between individuals i and k can change—if a neighbour of node i reproduces and colonizes node i and if a neighbour of node k reproduces and colonizes node k . At equilibrium, (S1) is zero.

If T is an isomorphism for which $T(i) = k$ and $T(k) = i$, then

$$\sum_j d_{ji} G_{jk} = \sum_j d_{jT(k)} G_{jT(i)} = \sum_j d_{T(j)T(k)} G_{T(j)T(i)} = \sum_j d_{jk} G_{ji} . \quad (\text{S2})$$

and we conclude that in a bi-transitive graph, the matrices $[d_{ij}]$ and $[G_{ij}]$ commute. It follows from this that at equilibrium, each of the summations in (S1) must be zero, and we conclude that to first order in μ :

$$\sum_j d_{ji} G_{jk} = G_{ik} + \mu \quad (i \neq k) \quad (\text{S3})$$

where we use the fact that $G_{ij} = 1$ to zeroth order in μ . Note that (S3) tells us that i is less related to k than it is, on average, to the neighbours of k , where the average is weighted by the dispersal coefficients of the edges at node k . If we now take eq. (S3) and sum over all $i \neq k$, we get, to first order in μ :

$$\sum_j G_{jk} d_{jk} = 1 - \mu(N - 1) . \quad (\text{S4})$$

Equations (S3) and (S4) are the key results needed in the inclusive fitness analysis.

Calculation of the Inclusive Fitness Effect. Take a uniform B-population, let a random actor i switch to allele A, and calculate the resulting change in fitness Δw_j of j . The inclusive fitness effect¹² W_{IF} of the allele A, is the sum of all these changes weighted by the relatedness to i . We use the central observation that when the actor has A instead of B it gives fecundity increment b to its partner at personal incremental cost c . In our calculations we use the coefficients G_{ij} in place of relatedness^{2,19} $R_{ij} = \frac{G_{ij} - G^*}{1 - G^*}$ where G^* is the population average G . To justify this, note that when the population size stays the same, the average fitness change from any interaction must be zero. In this case, a weighted sum of these fitness changes will be the same with weights G_{ij} and with weights $G_{ij} + C$ for any constant C .

Let i have fecundity $f_i = 1 + \varepsilon_i$ where our calculations will be to first order in the ε_i . We take the fitness increment Δw_j of j to be the expected change in its genetic representation following the next reproductive event. Our expressions for Δw_j will differ in the two fecundity models.

The BD model. The fitness increment of j is

$$\begin{aligned}\Delta w_j &= \frac{1}{N} \left[\frac{f_j}{1 + \bar{\varepsilon}} - \sum_{i \neq j} \frac{f_i d_{ij}}{1 + \bar{\varepsilon}} \right] = \frac{1}{N} \left[(1 + \varepsilon_j)(1 - \bar{\varepsilon}) - \sum_{i \neq j} d_{ij} (1 + \varepsilon_i)(1 - \bar{\varepsilon}) \right] \\ &= \frac{1}{N} \left[\varepsilon_j - \sum_{i \neq j} d_{ij} \varepsilon_i \right]\end{aligned}\quad (\text{S5})$$

to first order in the ε_i where $\bar{\varepsilon}$ is the average of the ε_i . The first term accounts for the probability that j wins the next reproductive event and the second accounts for the probability that there is another winner.

Increment to another. Suppose that i gives increment b to k for $k \neq i$. Then $\varepsilon_k = b$ and $\varepsilon_j = 0$ for $j \neq k$. Then from (S5) $\Delta w_k = b/N$ and $\Delta w_j = -d_{kj} b/N$ for $j \neq k$, and using (S3):

$$W_{\text{IF}} = \frac{b}{N} \left[G_{ik} - \sum_j d_{kj} G_{ij} \right] = \frac{b}{N} \left[G_{ik} - (G_{ik} + \mu) \right] = -\frac{b\mu}{N}$$

Increment to self. Suppose that i gives loss c to itself. Then $\varepsilon_i = -c$ and $\varepsilon_j = 0$ for $j \neq i$. Then from (S5) $\Delta w_i = -c/N$ and $\Delta w_j = d_{ij} c/N$ for $j \neq i$. Using (S4):

$$W_{\text{IF}} = -\frac{c}{N} \left[G_{ii} - \sum_j d_{ij} G_{ij} \right] = -\frac{c}{N} \left[1 - (1 - \mu(N-1)) \right] = -\frac{c\mu(N-1)}{N}$$

Putting these together, if i gives benefit b to k at cost c , the inclusive fitness effect (omitting the scaling factor μ/N) is the sum

$$W_{\text{IF}} = -b - c(N-1).\quad (\text{S6})$$

The DB model. The fitness increment of j is

$$\begin{aligned}\Delta w_j &= -\frac{1}{N} + \frac{1}{N} \sum_{i \neq j} \frac{f_j d_{ji}}{\sum_h f_h d_{hi}} = \frac{1}{N} \left[-1 + \sum_{i \neq j} d_{ji} (1 + \varepsilon_j) (1 - \sum_h \varepsilon_h d_{hi}) \right] \\ &= \frac{1}{N} \left[\varepsilon_j - \sum_{i \neq j} \sum_h d_{ji} d_{hi} \varepsilon_h \right]\end{aligned}\quad (\text{S7})$$

to first order in the ε_i . The first term accounts for the probability that j is selected to die and the second accounts for the probability that this falls to a neighbour of j .

Increment to another. Suppose that i gives increment b to k for $k \neq i$. Then $\varepsilon_k = b$ and $\varepsilon_j = 0$ for $j \neq k$. Then from (S7) $\Delta w_k = \frac{b}{N} [1 - \sum_i d_{ki} d_{ki}]$ and $\Delta w_j = \frac{b}{N} [-\sum_i d_{ji} d_{ki}]$ for $j \neq k$. Then

$$W_{\text{IF}} = \frac{b}{N} \left[G_{ik} - \sum_j \sum_h d_{jh} d_{kh} G_{ij} \right] = \frac{b}{N} \left[G_{ik} - \sum_{h \neq i} d_{kh} \sum_j d_{jh} G_{ij} - d_{ki} \sum_j d_{ji} G_{ij} \right]$$

Using (S3) twice and (S4), this simplifies as

$$W_{\text{IF}} = \frac{b\mu}{N} [d_{ki} N - 2].$$

Increment to self. Suppose that i gives loss c to itself. Then $\varepsilon_i = -c$ and $\varepsilon_j = 0$ for $j \neq i$. Then from (S7) $\Delta w_i = -\frac{c}{N} [1 - \sum_k d_{ik} d_{ik}]$ and $\Delta w_j = -\frac{c}{N} [-\sum_k d_{jk} d_{ik}]$ for $j \neq i$. Then:

$$W_{\text{IF}} = -\frac{c}{N} \left[G_{ii} - \sum_j \sum_k d_{jk} d_{ik} G_{ij} \right] = -\frac{c}{N} \left[1 - \sum_{k \neq i} d_{ik} \sum_j d_{jk} G_{ij} \right]$$

Using (S3) and (S4), this simplifies as

$$W_{\text{IF}} = -\frac{c\mu}{N} (N - 2).$$

Putting these together, if i gives benefit b to k at cost c , the inclusive fitness effect (omitting the scaling factor μ/N) is the sum

$$W_{\text{IF}} = b(d_{ki} N - 2) - c(N - 2).\quad (\text{S8})$$