

## Selection in Ephemeral Networks

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**ABSTRACT:** A model of “ephemeral” population structure is presented that applies not only to biological systems in which discrete groups form but also to networks without group boundaries. The evolution of altruistic behaviors is discussed. Nonrandom interaction and nonlinear fitness structures are modeled; together, these factors can produce stable polymorphisms of altruistic and selfish types, as well as bistability. Empirical applications of the model may be found in microbes, marine invertebrates, annual plants, and other organisms.

*Keywords:* altruism, association, internal equilibria, network, nonlinear fitness, population structure.

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### Introduction

Evolutionary processes can be strongly affected by population structure. Such structure can take various forms. A first distinction can be made between persisting and ephemeral structure (Wilson 1983). Sewall Wright’s (1932) “demes”—groups whose boundaries stay intact for many generations—are an example of persisting structure. Ephemeral groups, in contrast, form and dissolve in each generation (Wilson 1975; Matessi and Jayakar 1976; Kerr and Godfrey-Smith 2002a). A distinction crosscutting this first one concerns the form of the population structure. Many models, like those cited above, describe populations divided into discrete groups. Another tradition of work investigates populations with interactions between neighbors but without group boundaries. These include models of “viscous” populations (Hamilton 1964, 1975) and recent models of evolution on networks (Nowak and May 1992; Taylor 1992; Wilson et al. 1992; Mitteldorf and Wilson 2000; Lieberman et al. 2005; Ohtsuki et al. 2006). These models of neighbor interactions concern persisting population structure. There has been less discussion of populations in which individuals interact with neighbors

in the absence of group boundaries but the population structure is dissolved and reestablished in each generation.

Here we give a general model of the evolutionary consequences of ephemeral population structure. The model is designed to deal with cases where a population is divided into groups and cases where neighbors interact but there are no group boundaries. The term “network” is applied generally here; group structures may be treated as networks with a particular pattern of connectivity.

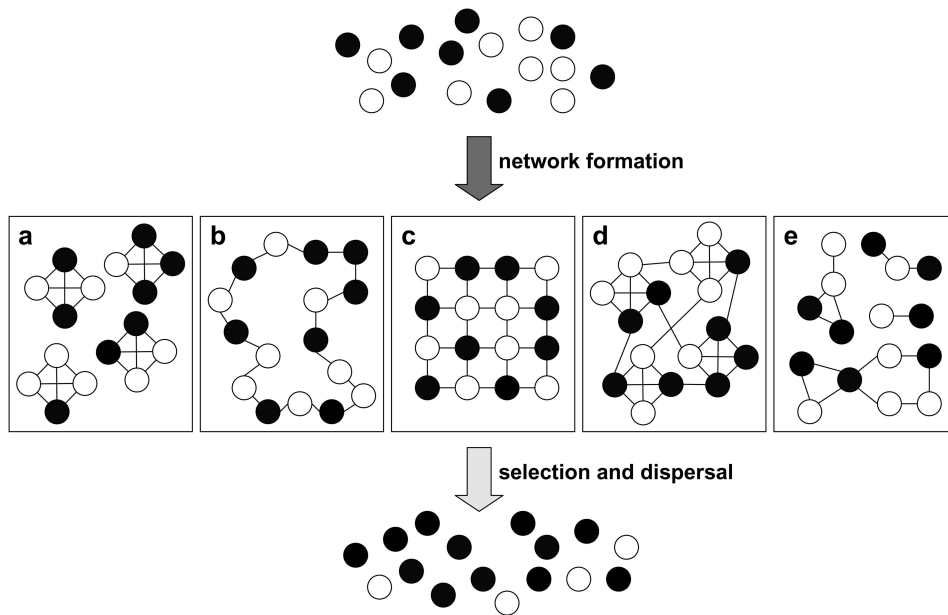
### Modeling Framework

We assume an infinite population of asexually reproducing semelparous individuals, of types *A* and *B*, who settle into a spatial structure with well-defined neighbor relations that affect fitness. This structure might comprise a collection of discrete groups, a line, a lattice, or some other network. These structures may be represented as graphs (undirected graphs in all our examples) where individuals are nodes and fitness-affecting interactions are edges. Some possible forms of population structure are represented in figure 1.

While natural networks contain heterogeneity in neighbor number, for simplicity here we assume regular networks; all individuals have the same number of neighbors, *n*. We also assume that there is no mutation. With reproduction and the death of the parents, the population structure dissolves. The offspring then form a new network.

Three components of such a model can be distinguished: the fitness structure, the neighborhood distributions, and the network formation rule. The fitness structure is an assignment of fitnesses to each of the types as a function of the possible neighborhoods they may encounter. In our models, the (absolute) fitness of the *A* type when surrounded by *i* neighbors of the *A* type is symbolized  $\alpha_i$ . The fitness of the *B* type when surrounded by *i* neighbors of the *A* type is  $\beta_i$ . The neighborhood distribution for a type at time *t* is the frequency distribution of fitness-affecting neighborhoods encountered by that type at that time step. The fitness structure, the neighborhood distributions, and the frequencies of the types suffice for the prediction of evolutionary change over one

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**Figure 1:** Life cycle of a population with ephemeral structure. Individual types are represented as filled or open circles (network nodes), and fitness-affecting interactions are represented as connections between the circles (network edges). The first step in the life cycle involves network formation. We compare five kinds of networks. *a*, Individuals form discrete groups in which interactions occur within but not between groups. *b*, Individuals form a “looped-chain” network in which every individual has two neighbors but multiple groups do not exist. *c*, Individuals interact with neighbors in a densely packed lattice. *d*, Hybrid between *a* and *b*: individuals do not form discrete groups, but parts of the network form densely interconnected pockets. *e*, Individuals form a fragmented network in which discrete groups exist but interaction within the groups is not complete. In *c–e*, the number of neighbors in the network varies from individual to individual, whereas this is constant in *a* and *b*. In some cases, these irregular networks can be made regular either by extending to infinity or by wrapping the network (e.g., forming a torus in *c*). After the network forms, fitness-affecting interactions occur and the network dissolves.

time step or generation. Specifically, let  $f_i^A(t)$  be the frequency with which *A* individuals encounter a neighborhood with *i* *A*s at time step *t*. Similarly, let  $f_i^B(t)$  be the frequency with which *B* individuals encounter a neighborhood with *i* *A*s at that time step. If  $p(t)$  and  $p(t+1)$  are the frequencies of the *A* type at *t* and *t+1*, respectively, then the equations for evolutionary change are

$$p(t+1) = p(t) \sum_{i=0}^n f_i^A(t) \frac{\alpha_i}{\bar{W}(t)},$$

$$\bar{W}(t) = p(t) \sum_{i=0}^n f_i^A(t) \alpha_i + (1-p(t)) \sum_{i=0}^n f_i^B(t) \beta_i. \quad (1)$$

This information does not suffice to predict further rounds of change, however. Above, we assumed that the neighborhood frequency distributions were known for time *t*; in effect, the analysis started in the middle step of figure 1 and ended with the composition of a new offspring pool. Further information is needed to determine how those individuals will settle into a new network. This may take the form of a network formation rule, a rule describing

how a population characterized by the frequencies of types will form a network.

Suppose, for example, that the network formation rule is that individuals settle randomly into a two-dimensional lattice (fig. 1*c*; extended to infinity). If each focal individual is affected by its four neighbors in cardinal (N, S, E, W) directions, then the neighborhood distribution for each type will be binomial with parameters 4 and  $p(t)$ .

## Results

We will focus on fitness structures in which the *A* type is an “altruist.” The cases below all satisfy the following conditions.

*Neighbor altruism.* *A* is an altruist if and only if

$$\alpha_i < \beta_i \text{ for } i \in \{0, 1, 2, \dots, n\}, \quad (2)$$

$$\alpha_i < \alpha_{i+1} \text{ for } i \in \{0, 1, 2, \dots, n-1\}, \quad (3)$$

$$\beta_i < \beta_{i+1} \text{ for } i \in \{0, 1, 2, \dots, n-1\}. \quad (4)$$

From inequality (2), in any given neighborhood, the *B*

type fares better than *A*. From inequalities (3) and (4), both types benefit from the addition of more *A* individuals to their neighborhoods.

Within this category, a linear case has been much discussed (Wilson 1975, 1990; Nunney 1985):

$$\begin{aligned} \alpha_i &= z - c + b\left(\frac{i}{n}\right), \\ \beta_i &= z + b\left(\frac{i}{n}\right). \end{aligned} \tag{5}$$

Here  $z$  is a baseline fitness,  $c$  is the cost to the bearer of a trait that is exhibited only by *A*, and  $b$  is the benefit received by an individual when its entire neighborhood is filled with *A* types. In the linear model, each additional *A* neighbor increments the fitness of a focal individual by the same amount ( $b/n$ ). When  $c$  and  $b$  are both positive, the *A* type is an altruist in the sense of inequalities (2)–(4). Hereafter, we also assume that  $b > c$ .

In this note we investigate a more general class of functions that include the familiar structure in equations (5) as a special case but allow that fitness may be a nonlinear function of the number of *A* types in an individual’s neighborhood ( $i$ ). Specifically, we look at concave (down) and convex functions, corresponding to, respectively, diminishing and increasing returns from adding *A* neighbors. Convex and concave cases are represented in equations (6) and (7), respectively.

$$\begin{aligned} \alpha_i &= z - c + b\left(\frac{i}{n}\right)^{k+1}, \\ \beta_i &= z + b\left(\frac{i}{n}\right)^{k+1}, \end{aligned} \tag{6}$$

$$\begin{aligned} \alpha_i &= z - c + b\left[1 - \left(1 - \frac{i}{n}\right)^{k+1}\right], \\ \beta_i &= z + b\left[1 - \left(1 - \frac{i}{n}\right)^{k+1}\right]. \end{aligned} \tag{7}$$

Here  $k$  measures the deviation from linearity. At  $k = 0$ , equations (6) and (7) reduce to equations (5), and we have the linear case. As  $k$  increases from 0, the fitness functions get either more convex (eqq. [6]) or more concave (eqq. [7]). These functions are evaluated at integer values of  $i$  between 0 and  $n$ , inclusive. Each function can be obtained from the other by flipping across its horizontal and vertical midpoints (app. A in the online edition of the *American Naturalist*).

The average fitnesses of *A* and *B* types are given by

$$\begin{aligned} W_A(t) &= E(\alpha) = \sum_{i=0}^n f_i^A(t) \alpha_i, \\ W_B(t) &= E(\beta) = \sum_{i=0}^n f_i^B(t) \beta_i. \end{aligned} \tag{8}$$

The type with the higher average fitness increases in frequency.

For the case of altruist fitness structures discussed above, it is possible to derive a general condition for increase of the *A* type in terms of  $c$ ,  $b$ , and statistical moments of the neighborhood distribution. Let  $x(t)$  and  $y(t)$  be random variables giving the fraction of *A* types in the neighborhood of an *A* type and a *B* type, respectively, at time  $t$ . Similarly, let  $u(t)$  and  $v(t)$  be random variables for the fraction of *B* types in the neighborhood of an *A* type and *B* type, respectively, at time  $t$ . (In all that follows, we drop  $t$  from time-dependent variables.) Under convex fitness structures given by equations (6), altruists increase in frequency if

$$E(x^{k+1}) - E(y^{k+1}) > \frac{c}{b}. \tag{9}$$

Under the concave fitness structures given by equations (7), altruists increase in frequency if

$$E(v^{k+1}) - E(u^{k+1}) > \frac{c}{b}. \tag{10}$$

Results about some special cases follow immediately. First, if the neighborhood distributions for *A* and *B* are the same ( $x$  and  $y$  are the same random variable), then *A* decreases in frequency. This includes the case of random network formation. Second, if fitnesses are linear, then the only feature that affects evolutionary outcomes is the mean of each neighborhood distribution (Kerr and Godfrey-Smith 2002*b*; Fletcher and Doebeli 2009). Setting  $k = 0$  in equation (9) or (10) shows that the altruist increases in frequency if

$$E(x) - E(y) > \frac{c}{b}. \tag{11}$$

If  $k = 1$  in equations (6) or (7), then both means and variances of the neighborhood distributions are important. As  $k$  increases, higher-order statistical moments of these distributions become relevant.

Results (9)–(11) apply for any regular network, including those with group boundaries, densely packed lattices, and others. In the language of the “Modeling Framework” section, these results make use of information about the

fitness structure and the neighborhood distribution but not the network formation rule. As a consequence, these results describe change over only a single generation. To extend the model beyond a single generation, we will need a network formation rule.

The simplest example of a network formation rule is random settlement of individuals into the network. Then, the distribution of neighborhoods experienced by both types is binomial, with parameters  $n$  and  $p$ :

$$f_i^A = f_i^B = \binom{n}{i} p^i (1-p)^{n-i}. \quad (12)$$

This is a case in which  $x = y$  for all values of  $p$ ; it is hence a case in which the  $A$  type always decreases in frequency. The  $B$  type can invade a population of  $A$ 's, fix, and resist invasion by  $A$ . This is analogous to well-known results that hold for ephemeral group-structured populations (reviewed in Kerr and Godfrey-Smith 2002a).

We now turn to nonrandom network formation rules. In some cases, a tendency for positive or negative correlation between types can be represented with a parameter  $F$ , which is used along with  $p$  to generate the "experienced" frequency of  $A$  neighbors for each of the two types (Hamilton 1975; Nunney 1985). We will call this a simple-assortment model. Here an individual's neighbors are each chosen independently but with different probabilities for the two types. For an  $A$  individual, the chance of each neighbor being of the  $A$  type is  $p_A$ ; for a  $B$  individual, the chance of each neighbor being of the  $A$  type is  $p_B$ . These probabilities are

$$\begin{aligned} p_A &= F + p(1-F), \\ p_B &= p(1-F). \end{aligned} \quad (13)$$

Here we assume that  $0 \leq F \leq 1$  (although some negative values are possible, with the lower bound determined by the overall frequencies of the types). Simple assortment involves two strong assumptions. First,  $F$  remains constant as  $p$  changes. Second, neighbors are assigned to any focal individual independently of each other.

To illustrate the constraints inherent in the second assumption, imagine the sequential filling of places in a network. After the placement of a focal individual, each neighbor is determined independently. It is as if a coin were independently flipped for each neighbor. The coin comes up heads with probability  $F$ . If heads, the neighbor is the same type as the focal. If tails, the neighbor is chosen at random from the population. Equations (13) then apply. This scenario is unproblematic if the network contains no loops. When a network has loops, the assignments of some

individuals to the network are constrained probabilistically by the outcome of several prior assignments, not just one.

Networks without loops include lines, discrete pairs, and some tree structures. Most networks do contain loops, and then simple assortment does not strictly apply. In some of these cases, loops may be scarce, however, and only a small fraction of individuals are affected (e.g., fig. 1b). In those cases, the simple-assortment model may apply as an approximation. For instance, sparsely populated lattices may contain few loops. Interestingly, there are also biologically relevant networks filled with loops, where a corresponding simple-assortment model gives the right evolutionary prediction despite a violation of some of its assumptions (for an example involving reproduction within discrete groups, see app. B in the online edition of the *American Naturalist*).

If the simple-assortment model can be used, then

$$\begin{aligned} f_i^A &= \binom{n}{i} p_A^i (1-p_A)^{n-i}, \\ f_i^B &= \binom{n}{i} p_B^i (1-p_B)^{n-i}. \end{aligned} \quad (14)$$

Suppose that the fitness structure is linear. Then, using formulas (5), (8), (13), and (14), we find that the fitness of  $A$  is higher than that of  $B$  if and only if

$$F > \frac{c}{b}. \quad (15)$$

This condition has an obvious kinship with Hamilton's (1964, 1975) rule. The condition can also be derived from equations (11) and (13) by noting that under simple assortment,  $E(x) = p_A$  and  $E(y) = p_B$ . The relation between the two average fitnesses in the linear case does not depend on  $p$ , and there can be no internal equilibria (aside from total neutrality when  $F = c/b$ ). So if inequality (15) holds,  $A$  excludes  $B$ , and if  $F < c/b$ , then  $B$  excludes  $A$ .

When the fitness structure is nonlinear, the relations between the average fitnesses may now be frequency dependent, and additional possibilities such as internal equilibria appear. Suppose that the fitness structure is as in equations (6) with  $k = 1$ . Then, under the simple-assortment model,  $A$  increases in frequency if

$$\frac{F}{n} \{1 + (n-1)[2p(1-F) + F]\} > \frac{c}{b}. \quad (16)$$

When  $n = 1$ , inequality (16) reduces to inequality (15) because nonlinearity can play no role. When  $n > 1$ , the benefit accrued by adding successive  $A$  neighbors follows

an accelerating function. For some parameter values, the result is that each type is favored when common and unstable internal equilibria are possible (see app. A). When  $F = 0$ , then inequality (16) does not hold for any value of  $p$ , and the  $A$  type is lost. When  $F = 1$ , then inequality (16) holds for all values of  $p$ , and the  $A$  type fixes.

If the fitness structure is as in equations (7) with  $k = 1$ , then  $A$  increases in frequency if

$$\frac{F}{n} \{1 + (n-1)[2 - F - 2p(1 - F)]\} > \frac{c}{b}. \quad (17)$$

The benefit derived from adding successive  $A$  neighbors now diminishes. The result may be that each type is favored when rare: when  $p$  is low, the  $A$  type benefits from having a few rather than no  $A$  neighbors; when  $p$  is high, the benefit to both types saturates, and  $A$  suffers from the direct cost of altruism. As a result, there may be stable internal equilibria (app. A). As above, when  $F = 0$  or  $F = 1$ ,  $A$  is lost or fixes, respectively.

### Discussion

A summary of our results is given in table 1. Random interaction prevents the evolution of altruism, a result found in many models. The distinction between linear and nonlinear fitness structures does not affect this result. Positive assortment of types generally favors altruism. Whether altruism can prevail will depend on the relation between the degree of assortment and the details of the fitness structure.

When a simple-assortment model can be used, expressions can be derived that give conditions for the increase and decrease in frequency of an altruist type in terms of  $F$ , a parameter measuring the tendency for like to interact with like. When fitness structures are nonlinear, these conditions may be frequency dependent and may result in stable or unstable polymorphic equilibria. In some cases of interest, including densely packed lattices and discrete groups, a simple-assortment assumption may not apply. However, if the fitness structure can be approximated by equations such as equations (6) or (7), a limited number of central moments (means, variances, etc.) from the neighborhood distributions are sufficient to predict evo-

lutionary change. For instance, when the fitness structure is linear (eqq. [5]), only the means of the neighborhood distributions are needed for evolutionary predictions. These may be knowable even when other features of the distributions are not.

Our model is idealized, but it may provide insight into evolutionary processes in various organisms. The combination of local interaction and dispersal at reproduction is characteristic of many marine invertebrates. Acorn barnacles (order *Sessilia*) are an example. Following reproduction, the offspring disperse as larvae in the sea. After a swimming stage, the larvae settle on rocks, forming a roughly two-dimensional population structure. Larval settlement is active and guided by the topography of the surface and chemical cues (Crisp 1961). A number of species are gregarious, preferring to settle near conspecifics, and there is also some evidence of kin aggregation (Knight-Jones 1953; Veliz et al. 2006). Other marine organisms also form networks with features represented in our model. Active settlement into a network based on genotype, for example, has been observed in marine invertebrates, such as the colonial hydroid *Hydractinia symbiolongicarpus* (Grosberg et al. 1996).

Microbes often live in spatially structured networks, such as biofilms. In some cases the construction of the biofilm itself can be seen as a cooperative trait, for which “free rider” strains are known (e.g., in the bacterium *Pseudomonas fluorescens*; Rainey and Rainey 2003). Within these systems, various public goods such as exoenzymes (secreted enzymes that function extracellularly) may be produced, again with known defector variants (Greig and Travisano 2004). In such cases, because growth saturates with the concentration of enzymatic products, the fitness structure is inherently concave, as in equations (7) (Gore et al. 2009). Thus, our model predicts that polymorphisms between altruistic producers and selfish types are possible, given nonrandom network formation.

Many biological systems naturally produce nonrandom network formations through within-group reproduction before selection occurs. The relationship between this life cycle and simple assortment is treated in appendix B. When the fitness structure is linear, a system of this kind behaves as if simple assortment applied, with the  $F$  parameter now representing a coefficient of relatedness. Such

Table 1: Summary of results for ephemeral networks

	Linear fitness structure	Nonlinear fitness structure
Random network formation	Altruist lost	Altruist lost
Nonrandom network formation	Only means of neighborhood distributions matter	Higher-order moments of distributions may matter
Within simple-assortment model	No frequency dependence, no polymorphic equilibria	Frequency dependence, polymorphic equilibria possible

a life cycle may apply to organisms that form nests (e.g., eusocial insects) and various social microbes such as the amoeba *Dictyostelium discoideum* and the bacterium *Myxococcus xanthus* (Velicer et al. 2000; Strassmann and Queller 2007).

Plants have significant interactions between neighbors (including shading and interaction between roots), and some annuals may approximate the periodic dispersal stage of our model. Last, the model may have some application to colonially nesting birds, in which spatially organized networks of breeding pairs are formed anew on breeding sites each year and behavioral interactions between neighbors may be very significant.

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