

Group selection and kin selection: Two concepts but one process

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In a recent paper, Traulsen and Nowak use a multilevel selection model to show that cooperation can be favored by group selection in finite populations [Traulsen A, Nowak M (2006) *Proc Natl Acad Sci USA* 103:10952–10955]. The authors challenge the view that kin selection may be an appropriate interpretation of their results and state that group selection is a distinctive process “that permeates evolutionary processes from the emergence of the first cells to eusociality and the economics of nations.” In this paper, we start by addressing Traulsen and Nowak’s challenge and demonstrate that all their results can be obtained by an application of kin selection theory. We then extend Traulsen and Nowak’s model to life history conditions that have been previously studied. This allows us to highlight the differences and similarities between Traulsen and Nowak’s model and typical kin selection models and also to broaden the scope of their results. Our retrospective analyses of Traulsen and Nowak’s model illustrate that it is possible to convert group selection models to kin selection models without disturbing the mathematics describing the net effect of selection on cooperation.

Traulsen and Nowak (1) (T&N) present a multilevel selection model and demonstrate that a mutant helping allele can be favored to fixation, when introduced as a single copy in a population monomorphic for selfishness if

$$\frac{b}{c} > 1 + \frac{N}{n_g} + \frac{\lambda}{q}, \quad [1]$$

where c is the cost of helping, b the benefit of helping for group members (excluding the actor), N the group size, n_g the number of groups, λ the migration rate between groups, and q the probability of group splitting (T&N, inequality ineq. 2). In their conclusion, T&N challenge the view that kin selection is an appropriate interpretation of their results and state that:

“It would be interesting to see how the mathematical methods of kin selection can be used to derive our central results given by eqs. 1–3 and what assumption are needed for such a derivation. The problem is that typical methods of kin selection are based on traditional considerations of evolutionary stability, which are not decisive for games in finite populations.”

Further, in a recent comment on the various possible mechanisms leading to the evolution of cooperation, Nowak (2) states that the group selection model of T&N results in a different process than kin selection. These are surprising statements, given that many authors have emphasized that group selection models are not different from kin selection models (3–8), and that kin selection theory has been extended to finite populations that can follow very diverse demographic regimes (8–14). To us, the mechanism favoring cooperation in T&N’s model is clearly kin selection. Indeed, kin selection operates whenever interactions occur among genetic relatives, that is, among individuals who tend to share a more recent common ancestor than individuals sampled randomly from the whole population. This may happen when interactions take place within families before the dispersal of offspring, or when dispersal is limited (population structure), so that relatives remain near each other. This is clearly the case in the “group selection” scenario

considered by T&N, because dispersal is limited, interactions occur among relatives.

In this paper, we first address T&N’s challenge and carry out a retrospective analysis of their model by deriving ineq. 1 using the kin selection approach for finite populations developed by Rousset (8, 15). Next, we consider a slightly different life cycle that resembles more the life cycles usually represented in classical kin selection formalizations. This allows us to highlight the few differences and broad similarities between T&N’s model and “typical” kin selection models. This second formalization suggests that ineq. 1 in fact holds for a large spectrum of life cycles, provided that $M_e \equiv \lambda/q$ is interpreted as the “effective number of migrants.”

Results

T&N’s Model. To derive ineq. 1 by using inclusive fitness theory (16), we endorse exactly the same assumptions as T&N. The population is subdivided into n_g groups, which grow in size as individuals within them reproduce. In any one time step, a single individual from the entire population is chosen for reproduction with a probability proportional to its payoff. When a group has reached a threshold size N , it either divides into two daughter groups with probability q (in which case a random group from the population is eliminated), or it does not divide (with complementary probability $1 - q$), in which case a random individual in the group is eliminated. Social interactions occur only among members of the same group, and individuals bearing a mutant allele (say A) express an act of helping, which decreases their payoff by c and generates a benefit b , which is shared by all other group members (thus excluding the actor). Selfish individuals then tend to replicate faster than helpers within groups, but groups comprising helpers grow faster and have a greater chance of dividing before going extinct. T&N also introduce migration between groups, by assuming that once an individual has reproduced, one of its offspring may migrate to another group with probability λ . If the group exceeds the critical size N after the arrival of the migrant, the group splits with probability q , or a random individual is eliminated from the group.

T&N analyze their model in the limiting case where both migration and group division are very rare ($q \ll 1$ and $\lambda \ll 1$), so they can assume in their calculations that the population behaves as if all its groups constantly remain at the threshold size N . With these assumptions, fixation within groups occurs on a faster time scale than migration and group division. The fixation probability π of a newly arisen mutant in the population can then be expressed as the product of the fixation probability π_g of a single mutant in a group (before migration or group division occurs) times the fixation

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Abbreviations: T&N, Traulsen and Nowak (ref. 1); ineq., inequality.

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probability π_p of the mutant at the level of the population conditional on its fixation at the level of a single group (e.g., T&N). The direction of evolutionary change of the mutant can then be determined by asking whether it has a larger or smaller probability of fixation than a single neutral mutant (8, 9, 17). The change of the fixation probability for a mutant with small phenotypic deviation δ relative to the resident allele (weak selection) is given by the derivative of the probability of fixation with respect to the phenotypic deviation δ , evaluated at $\delta = 0$. This yields

$$\frac{d\pi}{d\delta} = \frac{d\pi_g}{d\delta} \pi_p^\circ + \frac{d\pi_p}{d\delta} \pi_g^\circ, \quad [2]$$

where $\pi_g^\circ = 1/N$, and $\pi_p^\circ = 1/n_g$ are the fixation probabilities in the absence of selection (neutral case; that is, $\delta = 0$).

In the supporting information (*SI Appendix*), we show that Eq. 2 represents, in fact, a specific application of the inclusive fitness framework for finite populations of Rousset and coworkers (8, 9, 14, 15). Further, the effects of the mutant on its probability of fixation both at the level of a single group ($d\pi_g/d\delta$) and at the level of the population conditional on its fixation at the level of a single group ($d\pi_p/d\delta$) can be calculated by the direct fitness method for constructing kin selection models (6, 9, 18). In particular, Eq. 19 of *SI Appendix* reveals that the effect of the mutant on its probability of fixation at the level of a single group can be expressed as

$$\frac{d\pi_g}{d\delta} = \frac{\partial w_{ij}^g}{\partial z_{ij}} K_g, \quad [3]$$

where w_{ij}^g is a direct fitness function giving the expected number of individuals descending from individual j in group i (possibly including ij himself) between two reproductive events causing neither a migration nor a group division, z_{ij} is the phenotype of individual ij , and K_g is a positive constant that depends on demographic assumptions (e.g., iteroparity vs. semelparity, group size). Because reproduction occurs at a faster time scale than migration or group division, the function w_{ij}^g measures fitness on a “small” time interval, whereas migration or group division can be seen as being spaced by a “large” time interval. Eq. 3 informs us that the direction of selection on the probability of fixation of a single mutant at the level of the group depends only on the effect of the phenotype of individuals on their own fitness ($\partial w_{ij}^g/\partial z_{ij}$) and is independent of the behavior of the other individuals from the group. Because by definition the act of helping results in a fitness cost, selection disfavors the fixation of helping at the level of the group.

Eq. 21 of *SI Appendix* shows that the effect of the mutant on its probability of fixation at the level of the population can be written as

$$\frac{d\pi_p}{d\delta} = \left(\frac{\partial w_{ij}^p}{\partial z_{ij}} + \frac{\partial w_{ij}^p}{\partial z_i} R \right) K_p, \quad [4]$$

where w_{ij}^p is a direct fitness function giving the expected number of individuals descending from individual j in group i (possibly including ij himself) between two reproductive events causing either a migration or a group division. The function w_{ij}^p thus measures fitness on the “large” time interval, during which many reproductive events have occurred within groups, so that all groups are genetically monomorphic by the time migration or group division occurs. Eq. 4 also depends on z_i , which is the average phenotype of individuals in group i , R , which measures by how much two individuals randomly sampled from the same group are more related than two individuals sampled randomly from the whole population (Eq. 11 of *SI Appendix*), and K_p , which is a positive constant depending on demographic assumptions on the population (e.g., migration, population size).

Eq. 4 tells us that the effect of the mutant on its probability of fixation at the level of the population now depends both on the

effect $\partial w_{ij}^p/\partial z_{ij}$ of the phenotype of the individual on its fitness and the effect $\partial w_{ij}^p/\partial z_i$ of the mean group phenotype on the focal individual's fitness, weighted by the coefficient of relatedness among group members. Substituting the fitness effects (Eqs. 3 and 4) into the measure of selection $d\pi/d\delta$ (Eq. 2) reveals that this equation fits within Hamilton's definition of the inclusive fitness effect (16), which is a relatedness-weighted sum of the effects of the phenotypes of different actors on the fitness of a focal individual. The mutant allele is selected for when the inclusive fitness effect is positive (16), which is when $d\pi/d\delta > 0$.

A consequence of the assumptions of T&N's model is that relatedness is always equal to one ($R = 1$) and thus takes its maximal value. Indeed, because migration and group division are very rare, all lineages from a group trace back to a single ancestor during the time between two migration/division events. This result in a situation where the effect of migration affects not relatedness but only the fitness function w_{ij}^p and the weight K_p of the inclusive fitness effect. Following T&N's life cycle assumptions, we evaluate, in the *SI Appendix*, the fitness functions w_{ij}^g and w_{ij}^p ; and the two weights K_g and K_p . We find that the inclusive fitness effect is positive when

$$\frac{b}{c} > 1 + \frac{N + \frac{n_g \lambda}{q}}{n_g - 2 - \frac{\lambda}{Nq}}, \quad [5]$$

which is precisely ineq. 34 of T&N. This inequality represents their main and exact weak selection result, which holds for any group size and number (see Eq. 43 of *SI Appendix*). If $n_g \gg 1$ and $N \gg 1$, it simplifies to ineq. 1. Our derivation of ineq. 5 by the direct fitness method allows us to illustrate that it is possible to translate group selection models to kin selection models without disturbing at all the mathematics describing the net effect of selection on helping behaviors.

Typical Kin Selection Model. The assumptions used by T&N to obtain ineq. 1 imply that individuals are iteroparous, with no more than one individual dying per unit time, and that a breeding individual produces only one offspring (i.e., the Moran process). By contrast, traditional multilevel and kin selection models rely on different life-history assumptions, namely that all adult individuals produce at the same time a very large number of juveniles and then die (3, 8, 19–24). To complement T&N's analysis and to highlight the similarities and differences between their model and typical kin selection models, we derive a multilevel selection model for a finite population with nonoverlapping generations. We consider a population where individuals live in n_g groups of constant size N that are connected by migration. Each individual produces a large number of juveniles, the exact number depending on its own phenotype and the phenotypes of other group members. As in T&N's model, individuals bearing a mutant allele express an act of helping, which decreases their fecundity by c and increases the fecundity of their neighbors by b . All adults die, and juveniles from the same group assemble to form daughter groups of size N . The number of daughter groups produced by a group is proportional to the average fecundity in the group, and the individual contribution to a daughter group is proportional to individual fecundity relative to group fecundity. Groups then compete against each other to form the next generation of adults, which migrate randomly with probability λ to another of the n_g groups. As in T&N's model, the entire evolutionary dynamics is driven by individual fitness, and the effect of a mutant on its probability of fixation is given by

$$\frac{d\pi}{d\delta} = \left(\frac{\partial w_{ij}}{\partial z_{ij}} + \frac{\partial w_{ij}}{\partial z_i} R \right) K, \quad [6]$$

where w_{ij} is the fitness function giving the expected number of successful offspring of individual j in deme i , and K is a positive constant depending on the demographic assumptions on the population (Eq. 10 of *SI Appendix*). The function w_{ij} measures fitness between two reproductive events, which occur at exactly the same time scale as migration and group division. The crucial difference between Eq. 6 and the inclusive fitness effect obtained for T&N's model (Eq. 4) is the way relatedness affects selection on the mutant allele. Because of the separation of the time scale between fixation within groups and migration or group division, relatedness is always equal to one during the period of competition between groups in T&N's model. By contrast, relatedness depends on the demographic parameters of the population in the typical kin selection model, because fixation at the level of the group is very unlikely to precede migration or group division. For large deme size and low migration ($n_g \gg 1$ and $\lambda \ll 1$ and see Eq. 50 in *SI Appendix*), relatedness is given by

$$R = 1 - (N - 1) \left(\frac{1}{n_g} - 2\lambda \right). \quad [7]$$

Relatedness takes its maximum value when there is a very large number of groups ($n_g \rightarrow \infty$), and when migration is absent ($\lambda = 0$). Relatedness decreases as n_g decreases, because individuals from different groups may bear the same allele inherited from a common ancestor. Substituting the relatedness and the fitness function (Eq. 51 in *SI Appendix*) into the inclusive fitness effect (Eq. 6) reveals that, if $n_g \gg 1$ and $\lambda \ll 1$, helping spreads when

$$\frac{b}{c} > 1 + \frac{N}{n_g} + M_e, \quad [8]$$

where $M_e = 2N\lambda$ is the average number of migrants in a group. This condition of invasion is similar to ineq. 1, with the only difference that the number of migrants is given by $M_e = \lambda/q$ in T&N's model. This difference is explained by the differences in life cycles. Indeed, in our semelparous model, group splitting occurs in each generation (and all group splits), and all individuals can migrate. Relatedness then depends on the square of the migration rate and on group size (see Eq. 48 in *SI Appendix*), yielding $2N\lambda$ as the number of migrants, as is usually the case for haploid models with population structure (8, 25, 26). Our results suggest that provided M_e is interpreted as the "effective number of migrants", and that ineq. 8 applies to a continuum of life cycles, ranging from few group divisions and migrations occurring per unit time to frequent ones and from only one or a few individuals reproducing per unit time (overlapping generations) to all individuals in the population reproducing (non-overlapping generations). This is so because, in all these situations, competition occurs strictly and randomly between groups. Hence, the various within-group demographics will affect only quantitatively the condition under which selection favors helping. So long as competition occurs randomly between groups, ineq. 8 should also apply to simple metapopulation models with extinction and recolonization of groups, to other genetic systems (e.g., diploidy and haplo-diploidy), and to other mating systems (e.g., selfing and polygyny), because all these variations will affect only the effective number of migrants M_e , through the alteration of the effective migration rate and effective group size (8).

Our analyses also allow us to clarify why helping evolves in T&N's model, and how it relates to previous kin theoretical models for the evolution of helping in subdivided populations. Helping evolves in the two multilevel selection models analyzed in this paper, because competition occurs between groups *sensu stricto*. Indeed, the round of competition between groups that follows a group division event occurs at the level of the population, so that local competition between individuals for resources is prevented to occur. This results in a demographic situation where kin competition cannot hamper the spread of helping, a result that our typical kin selection model

suggests is true whatever the life-history assumptions concerning individuals within groups (e.g., overlapping generations vs. non-overlapping generations and haploidy vs. diploidy). By contrast, when competition occurs *sensu stricto* between individuals, genetically related neighbors are also more likely to compete for the same local resources because some individuals remain philopatric during the round of competition (see ref. 27 for a direct comparison between models involving competition between groups or between individuals). In this case, kin competition can at least partially offset the benefits of helping. For instance, helping at a fecundity cost to the actor is selected for under overlapping generations (28), but the fecundity benefits of helping are completely canceled out by the concomitant increase in kin competition under nonoverlapping generations (23, 29, 30).

Conclusion

We derived in this paper two multilevel selection models for the evolution of helping in finite populations. The first is a retrospective analysis of the model of T&N, who suggest that helping does not evolve through kin selection in their formalization. Using inclusive fitness theory (16), we recovered the main result of T&N as a specific application of kin selection theory for structured populations of finite size (8, 9, 14, 15). It is quite obvious that the mechanism that allows cooperation to evolve under T&N's life cycle is kin selection; interactions occur within groups, and individuals from the same group are related (i.e., they share a more recent common ancestor than individuals sampled randomly from the whole population). Hence, T&N's model falls into the scope of Hamilton's inclusive fitness theory, which is a general method for analyzing selection that can also be used to study the evolution of social interactions among nonkin (31, 32).

To illustrate the similarities and differences between T&N's life cycle with overlapping generations (the Moran scheme of reproduction) and more typical kin selection formalizations, we developed a multilevel selection model for nonoverlapping generations with frequent group divisions and arbitrary migration rates (3, 19–24). The analysis of this model suggests that ineq. 8 in fact holds for a variety of life cycles ranging from rare group divisions and migrations occurring per unit time to frequent ones and from overlapping to nonoverlapping generation situations, provided the parameter M_e is interpreted as the "effective number of migrants." Further, so long as competition occurs randomly and strictly between groups, ineq. 8 will also apply to simple metapopulation models with extinction and recolonization of groups and to other genetic systems and mating systems, because all these variations will affect only the average number of migrants M_e . To us, the two models investigated in this paper do not represent different mechanisms for the evolution of helping behaviors but only involve different sets of life-history assumptions and approximations, of which there are infinitely many.

The statement that helping evolves by a different mechanism ("group selection" or "multilevel selection") will only bring confusion in a domain of knowledge that was rather clear 20 years ago. This emphasizes the need for researchers to relate their work to the existing literature, especially when discussing the possible novelty of mechanisms leading to the evolution of cooperation and altruism (33, 34). To avoid semantic confusion both within and across disciplines (35), it appears more useful to reckon that, whenever interactions occur at a local spatial scale, and dispersal is limited, then interactions occur among genetic relatives, and thus kin selection is operating. Finally, it is also important to keep a tight link between modeling and biology and to develop models that are aimed at representing life cycles that occur in nature. As was pointed in a recent comment on social evolutionary theory (36), "For the study of cooperation and altruism, we think that the time has come to value work more highly that brings theory and observation into closer contact, compared with work that merely adds another twist to modeling."

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Supporting appendix for the paper “Group selection and kin selection. Two concepts but one process”

Inclusive fitness effect

Probability of fixation

We first give a brief summary of the argument developed by Rousset (1; 2) to compute the first derivative of the probability of fixation of a new allele (say A) with respect to its phenotypic effect. Call π the probability of fixation of allele A , and $E[p(t)]$ the expected frequency of A at time t , where $t = 0$ is the time at which the allele enters the population. We have:

$$\pi = E[p(\infty)] = p(0) + \sum_{t=0}^{\infty} E[p(t+1) - p(t)], \quad (1)$$

which can be expressed as:

$$\pi = p(0) + \sum_{t=0}^{\infty} \sum_{\mathbf{x}} E[\Delta p(t) | \mathbf{p}(t) = \mathbf{x}] \Pr[\mathbf{p}(t) = \mathbf{x}] \quad (2)$$

where $\mathbf{p}(t)$ is a vector giving the frequency of allele A in all interaction groups (or demes, or families) at time t , the second sum is over all possible values \mathbf{x} that this vector may take, $\Pr[\mathbf{p}(t) = \mathbf{x}]$ is the probability that $\mathbf{p}(t)$ equals \mathbf{x} , and $E[\Delta p(t) | \mathbf{p}(t) = \mathbf{x}]$ is the expected change in frequency of A between times t and $t+1$ given that $\mathbf{p}(t) = \mathbf{x}$. Call δ the phenotypic deviation of allele A relative to the phenotypic effect of the resident allele. When $\delta = 0$, the allele has the same phenotypic effect as the resident allele and is neutral, in which case $E[\Delta p(t) | \mathbf{p}(t) = \mathbf{x}] = 0$. Therefore, we have:

$$\left. \frac{d\pi}{d\delta} \right|_{\delta=0} = \sum_{t=0}^{\infty} \sum_{\mathbf{x}} \left. \frac{dE[\Delta p(t) | \mathbf{p}(t) = \mathbf{x}]}{d\delta} \right|_{\delta=0} \Pr^{\circ}[\mathbf{p}(t) = \mathbf{x}] \quad (3)$$

where $\Pr^{\circ}[\mathbf{p}(t) = \mathbf{x}]$ is the probability that $\mathbf{p}(t)$ equals \mathbf{x} in a neutral model ($\delta = 0$). Allele A is selected for when its probability of fixation is greater than the probability of fixation of a neutral allele, namely, when $d\pi/d\delta > 0$.

Example

We now consider a specific application of the result of the last section by assuming that the population is subdivided into n_g groups, each comprising N adult individuals so that

the population is of total constant size $n_g N$. We assume that migration can occur between groups but, for simplicity, there is no isolation by distance. Call z_{ij} the phenotype of individual j in group i , z_i the average phenotype in group i , and z the average phenotype in the whole population. Without loss of generality, we can assume that individuals bearing allele A have phenotype δ , while the carriers of the resident allele (say allele a) have phenotype 0. Therefore, we have $z_{ij} = \delta p_{ij}$, $z_i = \delta p_i$, and $z = \delta p$, where p_{ij} , p_i and p are the frequencies of A in individual ij , in group i and in the whole population, respectively (p_{ij} equals 0 or 1 if individuals are haploid). The “fitness” w_{ij} of individual ij is defined as its expected number of offspring who will be part of the next adult generation; w_{ij} may depend on z_{ij} , z_i , and z . Note that with such a definition of fitness, the average fitness equals one ($E[w_{ij}] = 1$) and the expected change in frequency of A over one generation is given by (getting rid of t for simplicity):

$$E[\Delta p] = \frac{1}{n_g N} \sum_{i=1}^{n_g} \sum_{j=1}^N w_{ij} p_{ij} - p. \quad (4)$$

As w_{ij} depends on z_{ij} , z_i and z , which themselves depend on δ , one obtains (using the fact that $p_{ij}^2 = p_{ij}$):

$$\begin{aligned} \left. \frac{dE[\Delta p]}{d\delta} \right|_{\delta=0} &= \frac{1}{n_g N} \sum_{i=1}^{n_g} \sum_{j=1}^N \left(\frac{\partial w_{ij}}{\partial z_{ij}} \frac{dz_{ij}}{d\delta} + \frac{\partial w_{ij}}{\partial z_i} \frac{dz_i}{d\delta} + \frac{\partial w_{ij}}{\partial z} \frac{dz}{d\delta} \right) p_{ij} \\ &= \frac{\partial w_{ij}}{\partial z_{ij}} p + \frac{\partial w_{ij}}{\partial z_i} \overline{p_i^2} + \frac{\partial w_{ij}}{\partial z} p^2, \end{aligned} \quad (5)$$

where $\overline{p_i^2}$ is the average of p_i^2 over all groups i , and where the partial derivatives are evaluated at $z_{ij} = z_i = z = 0$. Finally, using the fact that the sum of the partial derivatives of the fitness function sum up to zero (3), one obtains:

$$\left. \frac{dE[\Delta p]}{d\delta} \right|_{\delta=0} = \frac{\partial w_{ij}}{\partial z_{ij}} (p - p^2) + \frac{\partial w_{ij}}{\partial z_i} (\overline{p_i^2} - p^2). \quad (6)$$

From equations 3 and 6, one arrives at:

$$\left. \frac{d\pi}{d\delta} \right|_{\delta=0} = \frac{\partial w_{ij}}{\partial z_{ij}} (S - S_0) + \frac{\partial w_{ij}}{\partial z_i} (S_0 - S_1) \quad (7)$$

with

$$S = \sum_{t=0}^{\infty} E^\circ [p(t)], \quad S_0 = \sum_{t=0}^{\infty} E^\circ [\overline{p_i^2}(t)], \quad S_1 = \sum_{t=0}^{\infty} E^\circ [p^2(t)], \quad (8)$$

where $E^\circ [x(t)]$ is the expected value of x at time t in the neutral case ($\delta = 0$). In the case where allele A is present as a single copy in the whole population at time zero, these

expectations are given by:

$$E^\circ [p(t)] = \frac{1}{n_g N}, \quad E^\circ [\overline{p_i^2}(t)] = \frac{Q_0^R(t)}{n_g N}, \quad E^\circ [p^2(t)] = \frac{Q_1^R(t)}{n_g N} \quad (9)$$

where $Q_0^R(t)$ and $Q_1^R(t)$ are the probabilities that the ancestral lineages of two homologous genes sampled with replacement from the same group, and from the whole population (respectively) at time t coalesce between time 0 and time t . These probabilities of identity between pairs of homologous genes are functions of the parameters describing population structure (e.g., number of groups, group size, migration rates). This finally gives:

$$\left. \frac{d\pi}{d\delta} \right|_{\delta=0} = \left(\frac{\partial w_{ij}}{\partial z_{ij}} + \frac{\partial w_{ij}}{\partial z_i} R \right) \frac{Z}{n_g N}, \quad (10)$$

where the first term in the parentheses measures the effect of the phenotype of an individual on its fitness, the second term measures the effect of the group phenotype on that individual's fitness and

$$R = \frac{\sum_{t=0}^{\infty} [Q_0^R(t) - Q_1^R(t)]}{\sum_{t=0}^{\infty} [1 - Q_1^R(t)]} \quad (11)$$

is the coefficient of relatedness measuring by how much two individuals sampled with replacement from the same group are more related than two individuals sampled randomly from the whole population. Lastly,

$$Z = \sum_{t=0}^{\infty} [1 - Q_1^R(t)] \quad (12)$$

is a constant of proportionality that is always positive and depends on the demographic assumption on the population (e.g., number of groups, group size, migration rates). The effect of the mutant on its probability of fixation $d\pi/d\delta$ fits within Hamilton's definition of the inclusive fitness effect (4), which is a weighted sum of the effects of the phenotypes of different actors on the fitness of a focal individual. The probability of fixation of allele A is greater than the probability of fixation of a neutral allele if the inclusive fitness effect is positive, that is, when

$$\frac{\partial w_{ij}}{\partial z_{ij}} + \frac{\partial w_{ij}}{\partial z_i} R > 0. \quad (13)$$

T&N's model

Inclusive fitness effect and T&N's model

In order to apply the previous formalism to T&N's model, it proves convenient to measure a "generation" by the time between two migration or group division events because fixation

within groups occurs on a faster time scale compared to migration and group division. More precisely, time 0 corresponds to the time at which allele A enters the population (as a single copy), while times 1, 2, 3, ... are the times just before reproduction events that will cause either a migration or a group division. Therefore, at any time unit all groups are genetically homogeneous, and all lineages from the same group coalesce during time t and time $t+1$. The method described previously can be applied here, the only difference being that we have to treat the first time interval separately: indeed, during time 0 and time 1, coalescence occurs within all groups (so that the mutant allele either fixes within its group or disappears), but no migration or group division occurs, while during all other time intervals, one migration or group division event occurs. Therefore, equation 10 becomes:

$$\left. \frac{d\pi}{d\delta} \right|_{\delta=0} = \left(\frac{\partial w_{ij}^p}{\partial z_{ij}} + \frac{\partial w_{ij}^p}{\partial z_i} R \right) \frac{Z}{n_g N} + \left. \frac{dE[\Delta_0 p]}{d\delta} \right|_{\delta=0} \quad (14)$$

where w_{ij}^p is a fitness function giving the expected number of individuals descending from individual ij (possibly including himself) after a reproductive event causing either a migration or a group division. Here, we have $R = \sum_{t=1}^{\infty} [Q_0^R(t) - Q_1^R(t)] / \sum_{t=1}^{\infty} [1 - Q_1^R(t)]$, $Z = \sum_{t=1}^{\infty} [1 - Q_1^R(t)]$, and $E[\Delta_0 p]$ is the expected change in frequency of allele A between time 0 and time 1 given by:

$$\begin{aligned} E[\Delta_0 p] &= \pi_g \left(\frac{1}{n_g} - \frac{1}{n_g N} \right) + (1 - \pi_g) \left(-\frac{1}{n_g N} \right) \\ &= \frac{1}{n_g} \pi_g - \frac{1}{n_g N} \end{aligned} \quad (15)$$

where π_g is the probability of fixation of a single allele at the level of a single group. The derivative of the probability of fixation of allele A with respect to its phenotypic effect δ can be obtained by an application of the method exposed in the last section and by following T&N's assumption that the mutation appears in a group of size N . We then have:

$$\left. \frac{d\pi_g}{d\delta} \right|_{\delta=0} = \sum_{h=0}^{\infty} \sum_x \left. \frac{dE[\Delta p(h) | p(h) = x]}{d\delta} \right|_{\delta=0} \Pr^\circ[p(h) = x] \quad (16)$$

where $p(h)$ is the frequency of allele A in the group at time h after its appearance, where h is the "fast" time scale of reproductive events within the group (i.e. $h = 0, 1, \dots$ are the times just before the first, second... reproductive events within the group), which is small enough so that allele A fixes within the group before the first migration or group division. The second sum in eq. 16 is over all possible values x that the frequency of allele A may take in the group it appears in, $\Pr[p(h) = x]$ is the probability that $p(h)$ equals x , and

$E[\Delta p(h)|p(h) = x]$ is the expected change in frequency of A between times h and $h + 1$ given that $p(h) = x$. Without loss of generality, call the group where the mutation arises group i and call w_{ij}^g the expected number of successful offspring of individual ij (possibly including himself) after a reproductive event that causes neither a migration nor a group division. Noting that the fitness of individual ij is affected only by its own phenotype z_{ij} and the average phenotype z_i in group i , the expected change in frequency of A over one generation is given by (getting rid of h for simplicity)

$$E[\Delta p] = \frac{1}{N} \sum_{j=1}^N w_{ij}^g p_{ij} - p_i. \quad (17)$$

As w_{ij} depends on z_{ij} and z_i only, which themselves depend on δ , one obtains (using the fact that $p_{ij}^2 = p_{ij}$):

$$\begin{aligned} \left. \frac{dE[\Delta p]}{d\delta} \right|_{\delta=0} &= \frac{1}{N} \sum_{j=1}^N \left(\frac{\partial w_{ij}^g}{\partial z_{ij}} \frac{dz_{ij}}{d\delta} + \frac{\partial w_{ij}^g}{\partial z_i} \frac{dz_i}{d\delta} \right) p_{ij} \\ &= \frac{\partial w_{ij}^g}{\partial z_{ij}} p_i + \frac{\partial w_{ij}^g}{\partial z_i} p_i^2, \end{aligned} \quad (18)$$

where the partial derivatives are evaluated at $z_{ij} = z_i = 0$. Finally, using the fact that the sum of the partial derivatives of the fitness function sum up to zero ($\partial w_{ij}^g / \partial z_i = -\partial w_{ij}^g / \partial z_{ij}$) and following the same stream of calculations as in the previous section shows that

$$\left. \frac{d\pi_g}{d\delta} \right|_{\delta=0} = \frac{\partial w_{ij}^g}{\partial z_{ij}} \frac{Z_g}{N}, \quad (19)$$

with $Z_g = \sum_{h=0}^{\infty} [1 - Q_0^R(h)]$, where $Q_0^R(h) = NE^\circ [p_i^2(h)]$ and the sum being over the “fast” time scale of reproductive events within the group.

With this result, the inclusive fitness effect (eq. 14) can be written as

$$\begin{aligned} \left. \frac{d\pi}{d\delta} \right|_{\delta=0} &= \frac{\partial w_{ij}^g}{\partial z_{ij}} \frac{Z_g}{n_g N} + \left(\frac{\partial w_{ij}^p}{\partial z_{ij}} + \frac{\partial w_{ij}^p}{\partial z_i} R \right) \frac{Z}{n_g N} \\ &= \frac{d\pi_g}{d\delta} \frac{1}{n_g} + \frac{d\pi_p}{d\delta} \frac{1}{N}, \end{aligned} \quad (20)$$

where

$$\left. \frac{d\pi_p}{d\delta} \right|_{\delta=0} = \left(\frac{\partial w_{ij}^p}{\partial z_{ij}} + \frac{\partial w_{ij}^p}{\partial z_i} R \right) \frac{Z}{n_g} \quad (21)$$

and π_p is the probability of fixation of the mutant at the level of the population conditional on having fixed at the level of a single group.

In order to recover T&N's result that $d\pi/d\delta$ approximately equals $1+(N/n_g)+(\lambda/q)$ when N and n_g are large, we now calculate explicitly the terms Z_g , w_{ij}^g , R , Z and w_{ij}^p appearing in the inclusive fitness effect (eq. 20). In so doing, we follow exactly the assumptions that are implicit in eqs. 2-3 and eqs. 26-27 of T&N's and that are the following: 1) whenever reproduction occurs within a group without a migration or a group division, the new offspring replaces a randomly chosen individual from the group, 2) whenever a group division occurs, one of the two offspring group survives with probability one, while a group among the n_g remaining in the population is removed at random, 3) whenever a migration event occurs, migration is random to the n_g groups of the population, so that a migrant returns to its natal group with probability $1/n_g$ and, finally, 4) a migrant replaces a randomly chosen individual from the group where it immigrates.

Explicit functionals for fixation within the group

The term $Z_g = \sum_{h=0}^{\infty} [1 - Q_0^R(h)]$, where h is the “fast” time scale of reproductive events, can be obtained as follows: $1 - Q_0^R(h)$ is the probability that the ancestral lineages of two homologous genes sampled with replacement from the same group at time h do not coalesce within the group between time 0 and time h . If the two genes are sampled from the same individual (probability $1/N$), they coalesce immediately, and so:

$$[1 - Q_0^R(h)] = \left(1 - \frac{1}{N}\right) [1 - Q_0^D(h)], \quad (22)$$

where $1 - Q_0^D(h)$ is the probability that the ancestral lineages of two homologous genes sampled from two different individuals in the same group at time h do not coalesce. A recursion for $[1 - Q_0^D(h)]$ between pairs of genes is obtained as follows: the probability that two individuals sampled without replacement come from the same parent just before the last reproductive event is $2(1/N)(1 - 1/N)1/(N - 1) = 2/N^2$, where $1/N$ is the probability of sampling the new individual produced by the reproductive event, $1 - 1/N$ is the probability that the parent is still alive, and $1/(N - 1)$ is the probability of sampling the parent. Hence:

$$[1 - Q_0^D(h)] = \left(1 - \frac{2}{N^2}\right) [1 - Q_0^D(h - 1)]. \quad (23)$$

Using the fact that $1 - Q_0^D(0) = 1$, one obtains after simplification:

$$Z_g = \frac{N(N - 1)}{2}. \quad (24)$$

It now remains to evaluate the fitness function w_{ij}^g , which gives the expected number of individuals descending from individual j in group i (possibly including ij himself) after a reproductive event that does not lead to a migration or group division. Remember that $z_{ij} = \delta$ if individual ij carries allele A , while $z_{ij} = 0$ if he carries allele a . Because we only need the first derivative of w_{ij}^g with respect to z_{ij} (taken in $z_{ij} = z_i = 0$), it is sufficient to express w_{ij}^g to the first order in z_{ij} and z_i . From the assumptions on the costs and benefits of T&N's model, the probability that individual ij is chosen for reproduction in its group is:

$$\frac{1}{N} \left[1 - \left(c + \frac{b}{N-1} \right) (z_{ij} - z_i) \right] \quad (25)$$

and the probability that individual ij is not killed after the reproductive event is $(N-1)/N$. Combining these two terms, we obtain:

$$w_{ij}^g = \frac{N-1}{N} + \frac{1}{N} \left[1 - \left(c + \frac{b}{N-1} \right) (z_{ij} - z_i) \right]. \quad (26)$$

Inserting this equation and eq. 24 into eq. 19, yields:

$$\left. \frac{d\pi_g}{d\delta} \right|_{\delta=0} = -\frac{1}{2} \left(c + \frac{(b-c)}{N} \right). \quad (27)$$

Explicit functionals for fixation in the whole population

The coefficient of relatedness $R = \sum_{t=1}^{\infty} [Q_0^R(t) - Q_1^R(t)] / \sum_{t=1}^{\infty} [1 - Q_1^R(t)]$ equals one here, since at any time unit t between a migration or a group division (i.e., "large" time scale), the ancestral lineages of two genes sampled from the same group coalesce within groups with probability one (i.e., $Q_0^R(t) = 1$ for all $t \geq 1$). The term $Z = \sum_{t=1}^{\infty} [1 - Q_1^R(t)]$ can be obtained as follows: $1 - Q_1^R(t)$ is the probability that the ancestral lineages of two homologous genes sampled with replacement from the whole population at time t do not coalesce between time 0 and time t (i.e., probability of non-identity). If the genes are sampled from the same group (probability $1/n_g$), they will coalesce, and so:

$$[1 - Q_1^R(t)] = \left(1 - \frac{1}{n_g} \right) [1 - Q_1^D(t)] \quad (28)$$

where $1 - Q_1^D(t)$ is the probability that the ancestral lineages of two genes sampled from two different groups at time t do not coalesce. A recursion for the probability of non-identity $[1 - Q_1^D(t)]$ between pairs of genes is obtained as follows: with probability $q/(\lambda + q)$, a group division occurred just after time $t - 1$. With probability $2/n_g^2$, the two groups where the

genes are sampled at time t are the offspring groups of the group that has divided; in this case, the two lineages will coalesce. In the other case, the lineages coalesce with probability $Q_1^D(t)(t-1)$. Then, with probability $\lambda/(\lambda+q)$, a migration occurred just after time $t-1$. Since migration is random to any group (including the parental group), the probability that two genes sampled at random from the population after migration descend from the same group before migration is given by $2/n_g^2$. But now, we have to multiply $2/n_g^2$ by the probability that a migrant fixes within a group (in the neutral case), which is $1/N$. We thus have:

$$[1 - Q_1^D(t)] = \left[\frac{q}{\lambda+q} \left(1 - \frac{2}{n_g^2}\right) + \frac{\lambda}{\lambda+q} \left(1 - \frac{2}{n_g^2 N}\right) \right] [1 - Q_1^D(t-1)] \quad (29)$$

Using the fact that $1 - Q_1^D(1) = 1$, one obtains after simplification:

$$Z = \frac{n_g(n_g - 1)(q + \lambda)N}{2(qN + \lambda)}. \quad (30)$$

We now evaluate the fitness function w_{ij}^P , which is the expected number of offspring present in the population at time $t+1$ just before a reproductive event causing either a migration or a group division, and that descend from individual j in group i who is present in the population at time t , just before a reproductive event causing either a migration or a group division. Since all groups become genetically homogeneous between two such reproductive events, we have $z_{ij} = z_i$, and we can thus express w_{ij}^P as a function of z_{ij} and z only. Taking into account both migration and group division, w_{ij}^P can be expressed as:

$$w_{ij}^P = \frac{q}{\lambda+q} w_{ij}^Q + \frac{\lambda}{\lambda+q} w_{ij}^A \quad (31)$$

where w_{ij}^Q is the fitness of individual ij given that a group division occurs just after time t , while w_{ij}^A is the fitness of ij given that a migration occurs just after time t . Because we only need the first derivative of w_{ij} with respect to z_{ij} (taken in $z_{ij} = z = 0$), it is sufficient to express w_{ij}^Q and w_{ij}^A to the first order in z_{ij} and z .

From the assumptions on the costs and benefits of helping of the model of T&N, the probability that individual ij is chosen for reproduction is given by (to the first order in z_{ij} and z):

$$\frac{1}{n_g N} [1 + (b - c)(z_{ij} - z)]. \quad (32)$$

After reproduction, group i is made of $N+1$ individuals. If the group splits, the two offspring groups survive regulation with probability $1 - 1/n_g$, in which case the two offspring

of individual ij will be the ancestors of all the individuals in the two offspring groups of group i (at the next time unit) with probability $2/[(N+1)N]$ (in which case the fitness of ij is $2N$), while only one of his offspring will be the ancestor of all the individuals in one of the two offspring groups of group i with probability $4(N-1)/[(N+1)N]$ (in which case the fitness of ij is N). With probability $1/n_g$, only one offspring group of group i survives regulation, in which case one of the two offspring of individual ij will be the ancestor of all the individuals in the group with probability $2/(N+1)$ (in which case the fitness of ij is N). Therefore, if individual ij is chosen for reproduction and if group i splits, the fitness of ij is $2N(2n_g - 1)/[n_g(N+1)]$.

The probability that another individual from group i is chosen for reproduction is (given that $z_{ij} = z_i$, and to the first order in z_{ij} and z):

$$\frac{N-1}{n_g N} [1 + (b-c)(z_{ij} - z)]. \quad (33)$$

In that case, and if group i splits, individual ij will be the ancestor of all the individuals in one of the two offspring groups of group i with probability $2/(N+1)$ if both offspring groups survive regulation, while ij will be the ancestor of all individuals in the offspring group of group i with probability $1/(N+1)$ if only one of the offspring groups survives regulation (in both cases the fitness of ij is N). Therefore, if another individual than ij is chosen for reproduction in group i and if the group splits, the fitness of ij is $N(2n_g - 1)/[n_g(N+1)]$.

Finally, the probability that an individual from another group is chosen for reproduction is (to the first order in z_{ij} and z):

$$1 - \frac{1}{n_g} [1 + (b-c)(z_{ij} - z)]. \quad (34)$$

In that case (and if this other group splits), group i persists with probability $1 - 1/n_g$, in which case individual ij will be the ancestor of all the N individuals in group i at the next time unit with probability $1/N$. Hence, if an individual from another group than i is chosen for reproduction, the fitness of ij is $1 - 1/n_g$.

Combining all three cases just described gives:

$$w_{ij}^Q = 1 + \frac{1}{n_g} (b-c)(z_{ij} - z). \quad (35)$$

We now express w_{ij}^A , which is the fitness of individual ij , given that a migration occurs just after time t . With a probability given by equation 32, individual ij is chosen for reproduction.

One of his offspring remains in group i , while the other migrates. With probability $1/n_g$ the migrant returns in its natal group, in which case with probability $1 - 1/N$ the offspring that remained in group i will survive regulation. Each of the surviving offspring of individual ij will be the ancestor of all the N individuals in group i with probability $1/N$ at the next time unit. Hence, the fitness of individual ij is given by $2 - 1/N$ when the migrant offspring returns to the natal deme. With probability $1 - 1/n_g$ the migrant enters a different group than group i . Then, from eq. 27 and eq. 2, the immigrant will be the ancestor of all the N individuals in group k at the next time unit with probability (to the first order in z_{ij} and z_k):

$$\pi_g(z_{ij}, z_k) = \frac{1}{N} - \frac{1}{2} \left(c + \frac{(b-c)}{N} \right) (z_{ij} - z_k). \quad (36)$$

Thus, the fitness of individual ij , given that he is chosen for reproduction and that one of his offspring migrates to another deme is:

$$1 + \frac{1}{n_g - 1} \sum_{k \neq i} \left[1 - \frac{1}{2} (b + c(N-1)) (z_{ij} - z_k) \right] \quad (37)$$

which, given that

$$\frac{1}{n_g - 1} \sum_{k \neq i} z_k = \frac{n_g z - z_i}{n_g - 1} \quad (38)$$

and that $z_i = z_{ij}$, simplifies to:

$$2 - \frac{n_g}{2(n_g - 1)} (b + c(N-1)) (z_{ij} - z). \quad (39)$$

With a probability given by equation 33 it is another individual than ij that is chosen from group i for reproduction. If this reproductive events is followed by a migration, one of the offspring of the reproducing individual remains in group i , while the other migrates. The migrant returns to its natal group with probability $1/n_g$, in which case ij will be the ancestor of all the individuals of group i with probability $1/N$ if he survives regulation, which occurs with probability $1 - 1/N$ (in which case his fitness is N). If the migrant reaches another group (probability $1 - 1/n_g$), individual ij will be the ancestor of all the individuals of group i at the next time unit with probability $1/N$ (in which case his fitness is also N).

Finally, with a probability given by equation 34, an individual from another group (say group k) is chosen for reproduction. If one of his offspring migrates, he will arrive in group i with probability $1/n_g$. Then, with probability $1 - 1/N$, individual ij survives regulation and

with probability $1 - \pi_g(z_k, z_{ij})$ the immigrant lineage eventually disappears from group i . In that case, individual ij will be the ancestor of all the N individuals of group i at the next time unit with probability $1/(N - 1)$. From all this, the fitness of individual ij , given that an individual from another group is chosen for reproduction, and that this reproduction is followed by a migration is given by:

$$1 - \frac{1}{n_g} \pi_g(z_{ij}, z_k) \quad (40)$$

Taking all cases into account and simplifying, one obtains that w_{ij}^Λ is given by (to the first order in z_{ij} and z):

$$w_{ij}^\Lambda = 1 - \frac{c}{n_g} (z_{ij} - z). \quad (41)$$

Since all groups are genetically homogeneous at time units $t > 0$ ($R = 1$), we can write $z_{ij} = z_i$, the term $\partial w_{ij}^p / \partial z_{ij} + R \partial w_{ij}^p / \partial z_i$ that appears in equation 21 is then given directly by $\partial w_{ij}^p / \partial z_{ij}$. Equations 31, 35 and 41 give:

$$\frac{\partial w_{ij}^p}{\partial z_{ij}} = \frac{q(b - c) - \lambda c}{(\lambda + q)n_g}. \quad (42)$$

Finally, one obtains from equations 20, 24, 27, 30 and 42 that the inclusive fitness effect of allele A is positive when:

$$\frac{b}{c} > 1 + \frac{N + \frac{n_g \lambda}{q}}{n_g - 2 - \frac{\lambda}{Nq}}, \quad (43)$$

which is precisely eq. 34 of T&N and represents their exact result, holding for any group size and number. If $n_g \gg 1$ and $N \gg 1$, the inclusive fitness effect boils down to

$$\frac{b}{c} > 1 + \frac{N}{n_g} + \frac{\lambda}{q}. \quad (44)$$

Typical kin selection model

Relatedness

We calculate here the terms R and w_{ij} appearing in the inclusive fitness effect for the life-cycle without overlapping generations described in our main text (eq. 6). The coefficient of relatedness is obtained from eq. 11 and involves expressions for the probabilities of identity between two homologous genes sampled with replacement from the same group $Q_0^R(t)$ and

sampled with replacement from the total population $Q_1^R(t)$, where t corresponds to the time between two reproductive events during which group division, regulation and migration occurred. With probability $1/N$ the same individual is sampled twice from the same group and with probability $1/n_g$ the same group is sampled twice from the population. Whereby:

$$\begin{aligned} Q_0^R(t) &= \frac{1}{N} + \left(\frac{N-1}{N}\right) Q_0^D(t), \\ Q_1^R(t) &= \frac{1}{n_g} Q_0^R(t) + \left(\frac{n_g-1}{n_g}\right) Q_1^D(t), \end{aligned} \quad (45)$$

where is $Q_0^D(t)$ the probability of identity between two homologous genes sampled from different individuals in the same group and $Q_1^D(t)$ is the probability of identity between two homologous genes sampled from two individuals residing in different groups.

Note that $Q_0^R(t)$ and $Q_1^R(t)$ in eq. 45 can also be interpreted as the probabilities of identity between different offspring sampled in the same and different groups right after reproduction and regulation but before migration, and expressed in terms of the identities between individuals of the parental generation. After reproduction and regulation, each individual of the offspring generation migrates independently from each other with probability λ to another random group. The probability q_s that two individuals sampled in the same group after dispersal descend from the same group before dispersal is given by:

$$q_s = (1 - \lambda)^2 + \frac{\lambda^2}{n_g - 1}, \quad (46)$$

while the probability q_d that two individuals sampled in different groups after dispersal descend from the same group before dispersal is:

$$q_d = \frac{1 - q_s}{n_g - 1}, \quad (47)$$

We then have:

$$\begin{aligned} Q_0^D(t) &= q_s Q_0^R(t-1) + (1 - q_s) Q_1^R(t-1) \\ Q_1^D(t) &= q_d Q_0^R(t-1) + (1 - q_d) Q_1^R(t-1). \end{aligned} \quad (48)$$

Using the fact that $Q_0^R(0) = 0$ and $Q_1^D(0) = 0$, one obtains after simplification:

$$R = \frac{n_g - 1}{N n_g - (N - 1)(n_g - 1)(q_s - q_d) - 1}. \quad (49)$$

Substituting the explicit values of q_s and q_d into the last equation, keeping only terms of leading order when the number of groups becomes large and the migration rate becomes

small ($n_g \gg 1$ and $\lambda \ll 1$), relatedness simplifies to:

$$R = 1 - (N - 1) \left(\frac{1}{n_g} + 2\lambda \right). \quad (50)$$

Fitness function

The fitness w_{ij} of individual ij is given by the ratio of the individual's fecundity relative to average fecundity in the population. To the first order in z_i , z_{ij} and z , this is:

$$w_{ij} = 1 - \left(c + \frac{b}{N-1} \right) z_{ij} + \frac{bN}{N-1} z_i - (b-c) z \quad (51)$$

Substituting this fitness function and eq. 49 into eq. 13, we find that allele A is selected for when:

$$\frac{b}{c} > 1 + \frac{N(1 + n_g(1 - q_s))}{n_g q_s - 2}. \quad (52)$$

In a panmictic population (i.e., $\lambda = 1 - 1/n_g$), this condition of invasion becomes:

$$\frac{b}{c} > 1 - n_g N. \quad (53)$$

If $b > c$, the equality can be satisfied only when $b < 0$. Helping group neighbors can no longer evolve, but harming them at a direct fecundity cost can.

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