

The evolution of trans-generational altruism: kin selection meets niche construction

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Abstract

A cornerstone result of sociobiology states that limited dispersal can induce kin competition to offset the kin selected benefits of altruism. Several mechanisms have been proposed to circumvent this dilemma but all assume that actors and recipients of altruism interact during the same time period. Here, this assumption is relaxed and a model is developed where individuals express an altruistic act, which results in posthumously helping relatives living in the future. The analysis of this model suggests that kin selected benefits can then feedback on the evolution of the trait in a way that promotes altruistic helping at high rates under limited dispersal. The decoupling of kin competition and kin selected benefits results from the fact that by helping relatives living in the future, an actor is helping individuals that are not in direct competition with itself. A direct consequence is that behaviours which actors gain by reducing the common good of present and future generations can be opposed by kin selection. The present model integrates niche-constructing traits with kin selection theory and delineates demographic and ecological conditions under which altruism can be selected for; and conditions where the 'tragedy of the commons' can be reduced.

Introduction

Explaining the emergence of traits by which individuals help others at a fitness cost to themselves is of fundamental importance to the understanding of sociality. Hamilton (1964) has demonstrated that such traits can be selected for if the beneficiaries share the same genes as the helpers. His theory emphasizes that relatedness between actor and recipient is the kernel of the process leading to the evolution of altruistic helping. Since Hamilton's breakthrough in the field, it remains to explore the interior and to understand the exact ecological and demographic conditions under which altruistic helping can be selected for. Identifying such conditions has not come without surprise. Indeed, essentially all natural populations are geographically structured in space (Balloux & Lugin-Moulin, 2002), a process

increasing the relatedness between locally interacting individuals and, thus, paving the way to kin selected benefits. However, limited dispersal also increases competition between interacting individuals (Wilson *et al.*, 1992), with the result that in a simple model where the population is of constant size, selection on helping is determined solely by direct fecundity benefits (Taylor, 1992a). Helping is selected for only if the actor's fecundity, that is, the number of juveniles counted before any competition stage, is increased. This result takes the form $B/N - C > 0$, where N is the group size, C is the fecundity cost of helping and B is the total fecundity benefit to the group, including the actor, so a benefit B/N is received by the actor. Surprisingly, Taylor's result holds whatever the structure of the population (e.g. island model of dispersal, stepping-stone dispersal) and whatever the type of effects (positive or negative) actors exert on the fecundity of recipients living in the same or in different patches (Taylor, 1992b; Rousset, 2004).

Relaxing some assumptions of Taylor's model allows identification of conditions under which helping can be

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selected for at a fecundity cost to the actor (i.e. $C > B/N$). These include introducing overlapping generations (Nowak *et al.*, 1994; Koella, 2000; Taylor & Irwin, 2000; Irwin & Taylor, 2001), various modes of kin discrimination within patches (Perrin & Lehmann, 2001; Lehmann & Perrin, 2002; Axelrod *et al.*, 2004; Jansen & van Baalen, 2006), an explicit patch demography (Van Baalen & Rand, 1998; Mitterdorf & Wilson, 2000; Le Galliard *et al.*, 2003), various modes of dispersal and effects of helping on various demographic variables determining patch dynamics (Lehmann *et al.*, 2006). All these models are essentially built on the assumption that actors and recipients interact during the same time period. For instance, it is the likelihood of direct interactions between parent and offspring that determine the direction of selection on helping in the presence of overlapping generations. Similarly, it is the high probability of meeting between siblings (or close relatives) that allows the co-evolution of helping and kin discrimination. Although these models include the possibility that an actor interacts with cousins, nephews or grandchildren (e.g. Taylor & Frank, 1996; Taylor & Irwin, 2000), the formulation of opportunities to posthumously benefit relatives of close or distant generations has been neglected. Here, I allow individuals to affect the fitness of others individual living in the future so that *intra*-temporal and *inter*-temporal effects on fitness jointly determine the evolutionary dynamics of helping. Inter-temporal fitness effects result from a variety of causes that are usually referred to as niche constructing behaviours (Odling-Smee *et al.*, 1996) or extended phenotypes (Dawkins, 1982). These traits are probably common in nature and by modifying environmental conditions that are transmitted through several generations (ecological inheritance), they can impact on the fitness of individuals living in the future. For instance, positive niche construction refers to phenotypic activities that increase the presence of a valuable resource, such as the construction of nests or burrow systems, which enhance the fitness of subsequent generations (Odling-Smee *et al.*, 2003). On the other side, negative niche construction is a consequence of severe depletion of resources or the build-up of detritus polluting the environment and is likely to result in a loss of fitness for individuals living in the future.

The present paper thus explores another ecological factor that may affect Taylor's rule ($B/N - C > 0$): when an actor helps relatives living in the future, benefits can feedback on the trait in a way that promotes helping at a direct fecundity cost to the actor. According to the model presented below and framed within the direct fitness approach (Taylor & Frank, 1996; Frank, 1998; Rousset & Billiard, 2000; Rousset, 2004), taking into account inter-temporal fitness effects has the potential to greatly enhance the kin-selective pressure on altruism in geographically structured populations. A direct corollary of this result is that behaviours where individuals gain by

destroying the common good available to future generations (negative niche construction) can be significantly opposed by kin selection, but only as long as individuals tend to be philopatric.

Model

Life-cycle

Let us posit that evolution occurs in a population following Wright's infinite island model of dispersal. Individuals are haploid and live in patches of finite size N . The timing of the life cycle is the following. (i) Reproduction occurs and each individual produces a very large number of juveniles. The fecundity of each individual depends on its own behaviour, on the behaviour of all other patch-mates and on the behaviour of all individuals living in that patch up to T generations in the past. (ii) Each juvenile disperses independently from each other with probability m to another patch. (iii) Regulation occurs and exactly N juveniles reach adulthood so the population is held at a constant size.

To determine whether helping will spread in such a population, I introduce a two-allele model. Individuals bearing a mutant allele express an act of helping that reduces their fecundity by some cost C . This act increases the fecundity of the set of all individuals living in the focal patch and in the focal generation by an amount B_0 . This benefit B_0 is the same as originally considered by Taylor (1992a). The act also increases the fecundity of the whole set of individuals living in the actor's patch t generations in the future by an amount B_t . Accordingly, the effects on fitness (B_1, B_2, \dots, B_T) are inter-temporal fitness effects. Individuals bearing a resident allele express no social trait.

Measuring selection on helping with inter-temporal effects on fitness

In the infinite island model of dispersal, the change in allele frequency (p) over one generation of the mutant allele with small phenotypic effect δ (weak selection) can be written as:

$$\Delta p = \delta S p (1 - p) + O(\delta^2), \quad (1)$$

where $O(\delta^2)$ is a remainder and S is Hamilton's inclusive fitness effect measuring the direction of selection on the mutant (Rousset, 2004, pp. 206–207). In the direct fitness framework (Taylor & Frank, 1996; Frank, 1998; Rousset & Billiard, 2000), the inclusive fitness effect is interpreted as a relatedness weighted sum of the effects of all individuals in the population on the fitness of a focal individual bearing the mutant allele. However, as described in the life-cycle, individuals living in the focal deme in time epochs prior to the focal individual's generation may also affect its fitness (e.g. positive or negative niche construction). We thus need an expression

of the inclusive fitness effect (S) that takes into account the effects on the focal individual's fitness of all those individuals living in the focal deme up to T generations in the past. In this situation, the fitness of a focal individual $w \equiv w(z_\bullet, \dots, z_t, \dots)$ can be expressed as a function of its own phenotype (z_\bullet) and the average phenotypes (z_t) of classes of actors located at different points in time (labelled t) prior to the focal generation. Inter-temporal fitness effects resulting from the expression of such phenotypes can directly be included into the classical derivation of the inclusive fitness effect (S) as giving the first order effect of selection on gene frequency change (Rousset & Billiard, 2000; Rousset, 2003, 2004). Such a derivation involves only the introduction of more complex notations in order to take the dimension of time into account, but no change in assumptions (see the Supplementary Material for this derivation). In the presence of inter-temporal effects on fitness, the inclusive fitness effect for the infinite island model of dispersal (eqn 11 of the Supplementary Material) then reads as:

$$S = \frac{\partial w}{\partial z_\bullet} + \sum_{t=0}^T \frac{\partial w}{\partial z_t} r_t, \quad (2)$$

which is similar in form to more classical situations (Taylor, 1990; Frank, 1998; Gandon & Michalakis, 1999; Rousset & Billiard, 2000). This equation sums up the effect of the action of all actors in the focal deme (living in the focal or in earlier generations) on the fitness of the focal individual. The effect of each category of actors (here individuals living at different time epochs) comes under the form of a weighted partial derivative of the fitness of the focal individual with respect to the average phenotype of individuals in that category. The weight r_t is the relatedness between the focal individual and an individual living t generations prior to the focal generation in the same deme. Such relatedness coefficients are conveniently evaluated as space-time probabilities of identity by descent (Epperson, 1999).

Fitness function

Here, the direct fitness of a focal individual (w) is derived by following the assumptions of the life-cycle spelt out above. The fitness depends on both the expected number of focal individual's offspring reaching adulthood in the focal deme (who compete against resident and immigrant juveniles) and on those reaching adulthood in a foreign deme by dispersing. It is thus given by the following expression:

$$w = f_\bullet \left[\frac{(1-m)}{(1-m)f_R + mf_d} + \frac{m}{f_d} \right], \quad (3)$$

where f_\bullet is the relative fecundity of the focal individual (fecundity relative to its baseline fecundity), f_R is the average relative fecundity of individuals in its deme (including itself) and f_d is the average relative fecundity of individuals living in different demes.

The relative fecundity of the focal individual is obtained by collecting the contribution of all individuals affecting her reproduction. It is given by

$$f_\bullet = 1 - Cz_\bullet + B_0 z_0^R + \sum_{t=1}^T B_t z_t, \quad (4)$$

where z_\bullet is the phenotype of the focal individual, z_0^R is the average phenotype of individuals living in the focal generation (including the focal actor), z_t is the average phenotype of those individuals living in the focal deme t generations prior to the focal generation and T is the time horizon of fitness effects. The average relative fecundity of individuals in the focal deme reads $f_R = 1 + (B - C)z_0^R + \sum_{t=1}^T B_t z_t$. Finally, the average relative fecundity of individuals living in different demes is given by $f_d = 1 + (B - C)\bar{z}_0 + \sum_{t=1}^T B_t \bar{z}_t$ where \bar{z}_t is the average phenotype of those individuals living in different demes t generations in the past.

Results

In order to obtain the direction of selection on the mutant allele, the selective pressure is evaluated at the phenotypic value of the resident allele that expresses no social behaviour ($z_\bullet = z_t = \bar{z}_t = 0$). Then, from the inclusive fitness effect (eqn 2) and the fitness function (eqn 3), we have:

$$S = -C + B_0 r_0^R - (1-m)^2 (B_0 - C) r_0^R + \sum_{t=1}^T B_t r_t - (1-m)^2 \sum_{t=1}^T B_t r_t, \quad (5)$$

which consists of five components. First, the direct cost (C) for a focal individual expressing an act of helping. Second, the benefit (B_0) received by the focal individual from all actors living in the focal patch in the focal generation (including the focal individual), which is weighted by the relatedness r_0^R between the focal individual and an individual sampled with replacement from the focal patch. Third, the cost resulting from the increase in competition faced by the focal individual's offspring resulting from all actors in the patch expressing helping in the focal generation (including the focal individual). This term depends on the factor $(1-m)^2$, which gives the probability that a focal individual's offspring compete against another juvenile produced in the focal patch. Fourth, the selective pressure on helping depends on the benefits received from all actors expressing acts of helping in prior generations. This term is weighted by the relatedness r_t between the focal individual and another individual sampled in the same patch at $t \geq 1$ generation(s) apart, which under the present haploid genetics reads:

$$r_t = (1-m)^t r_0^R. \quad (6)$$

(see eqn 12 of the Appendix). Finally, there is the cost associated with the increase in kin competition resulting

from individuals in prior generation helping the whole set of individuals in the focal patch, thus increasing the fecundity of the neighbours of the focal individual. This term is again weighted by $(1 - m)^2$, which gives the likelihood that juveniles produced in the same patch enter in competition.

Inserting the equilibrium coefficients of relatedness into the inclusive fitness effect (see Appendix) and simplifying leads to the result that helping spreads when:

$$\sum_{t=0}^T B_t \frac{(1 - m)^t}{N} > C \quad (7)$$

is satisfied. The right hand side is the direct cost of helping and the left hand side is a weighted stream of benefits. The weights are the probabilities that a random line of descent of the focal individual (proportional representation $1/N$) remained in the focal deme for at least t generations. The first generation ($t = 0$) corresponds to the focal individual itself and involves a weight of one, independent of migration as required by Taylor's result. By contrast, future benefits ($t > 0$) are weighted by terms decaying at geometric rate $(1 - m)$. The weights decay as time increases because in each generation the random line of descent of an individual leaves its deme with probability m (Fig. 1) so that the relatedness between individuals taken in different generation decreases at the rate $(1 - m)$ (eqn 6). Hence, exit of the current position of the gene lineage is ultimately certain. Whether a helping act satisfying inequality 7 can be considered as altruistic depends on whether it results in a negative effect on the fitness of a focal individual expressing the act (Hamilton, 1964; Grafen, 1984; Rousset, 2004), this effect on fitness is given here by

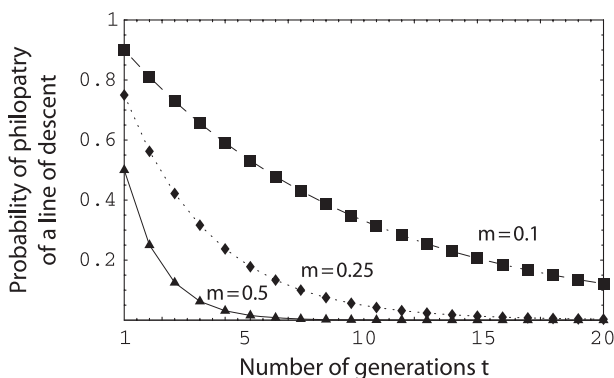


Fig. 1 Probability $(1 - m)^t$ that a random line of descent of an individual remains in the same deme for at least t generations plotted as a function of various migration rates. Black squares stand for $m = 0.1$, triangles stand for $m = 0.25$ and diamond for $m = 0.5$. The higher the migration rate, the lower the probability that a line of descent initiated by an individual remains in the same deme for several generations.

$$-c = -C + \frac{B_0}{N} - \frac{(1 - m)^2(B_0 + C)}{N}. \quad (8)$$

Comparing eqn 7 with eqn 8, we see that the introduction of inter-temporal effects on fitness greatly increases the scope for altruistic helping to be selected for because the effect of the focal individual on its fitness is independent of the inter-temporal fitness effects. Notice also that eqns 7 and 8 applies only as long as the migration rate is positive ($m > 0$). Indeed, when a patch is completely isolated (or under soft selection) all inter-temporal fitness effects cancel each other out. This occurs because exactly the same pool of individuals getting the benefits from earlier generations actually competes against each other, there is no component of group selection and all kin selected effects vanish (see Appendix A.3).

Inequality 7 can be illustrated more directly by using an explicit representation of the benefits B_t . Let us posit that the effect of the helping act involves the construction (or maintenance) of a communal nest resulting in a benefit B for the group of individuals living in the focal generation. The effect of this act on the fitness of individuals living in future generation decays with time according to the rate λ because the physical effect degrades ($\lambda < 1$). When $\lambda = 0$ the nest is erased from one generation to the next and $\lambda = 1$ would imply that the nest stays forever. This is a recency effect because recent generations of niche construction have a greater effect than earlier generations (Odling-Smee *et al.*, 2003, pp. 387–388). Under this scenario, we have $B_t = \lambda^t B$ and inserting this equation into in eqn 7 leads to helping being selected for when:

$$\frac{B}{N} + \frac{\lambda(1 - m)B}{N[1 - \lambda(1 - m)]} > C. \quad (9)$$

is satisfied. In the absence of ecological inheritance ($\lambda = 0$) we recover Taylor's rule. In the presence of ecological inheritance ($\lambda > 0$), the act has the potential to significantly feedback on its evolution and bolster the selective pressure on helping. This selective pressure varies directly with the rate of ecological inheritance (λ), and indirectly with the migration rate (m).

Inequality 7 can also be applied to the evolution of behaviours by which an individual pursues interests that increase its returns relative to neighbours by decreasing the value of the common good of later generations (negative niche construction). Such a trait is characterized by involving a fecundity benefit to the focal individual ($-C > 0$) and can be deleterious for all patch-mates and for the whole set of individuals living in the focal patch in the future ($B_0 < 0, B_1 < 0, \dots, B_T < 0$).

Discussion

Limited dispersal results in a concomitant increase in relatedness and competition between interacting

individuals. Taylor (1992a) demonstrated that in a simple model this can result in a situation where helping is selected for only if the actor's direct fecundity is increased. In the model presented here, one of Taylor's assumptions is relaxed so that *intra*-temporal, as well as *inter*-temporal, effects on fitness jointly determine the evolutionary dynamics of helping. Integrating inter-temporal fitness effects into the equations leads to a situation where the kin-competition pressure opposing the evolution of helping can be greatly reduced. The mechanism behind the decoupling of kin competition and kin selected benefits is that by posthumously helping relatives living in the future, a focal actor is helping individuals that are not in direct competition with itself. This positive effect of helping on inclusive fitness also implies that harming traits, by which an individual decreases the fitness of relatives living in the future, can be opposed by kin selection in geographically structured populations.

The results of the model presented here suggest that when an actor is affecting the fitness of individuals living in the future, for instance by modifying the distribution of local resources, the selective pressure on such a behaviour is changed. This selective pressure depends on the relatedness between actors and various classes of recipients living in different time periods. The relatedness between actors and recipients decreases by a multiplicative factor $(1 - m)$ with each additional intervening generation between them (eqn 6), because if we follow a random line of descent of an individual, it migrates to another deme with probability m in each generation. Accordingly, future benefits decay at geometric rate $(1 - m)$ and ultimately vanish because a gene lineage ultimately leaves its present position (in eqn 7). Although the model presented here assumes haploid genetics, the decrease of relatedness between actor and recipient sampled in different generations also follows the rate $(1 - m)$ under diploid genetics provided that both males and females have the same migration rate (eqn 20 of Appendix A.2). When the migration rate becomes unequal between both sexes, relatedness decays more rapidly, but importantly, it is generally not halved with each additional intervening generation between actor and recipient. Under haplo-diploid genetics, the situation is more complex and the rate of decrease of relatedness is only approximately given by $(1 - m)$ when both sexes have the same migration probability. Accordingly, the quantitative results reached for the selective pressure on helping under haploid genetics can apply to diploid genetics as a first approximation, but more specific formalization is required to match more specific life-cycles.

The recipients of the line of descent of a focal individual in the present model include its children, its grand children, its grand-grand children and so forth, so that the kin structure involved in the model is very similar to the one found in the presence of overlapping-generations, which is also known to promote altruism (Taylor & Irwin, 2000). In the presence of overlapping-

generations actors interact directly with various classes of relatives during the same time period and the physical consequences of helping is erased from one generation to the next. By contrast, in the present model, helping is envisioned as an extended effect, which result in a physical alteration of the habitat than can last over several generations. This generates a feedback that increases further the selective pressure on helping. But the model did not take into account the evolutionary consequence of niche construction on other traits. A candidate trait that may be directly affected by niche construction in the present context is dispersal, which optimal rate (Hamilton & May, 1977; Taylor, 1988; Gandon & Michalakis, 1999) might be affected by positive or negative niche construction and this points to directions for future explorations.

It is difficult to imagine that those organisms that modify their local biotic or abiotic habitat in which they reside will have absolutely no effect on individuals living in later generations (Odling-Smee *et al.*, 2003). Physical alterations of the environment including the constructions of nests, burrow systems, paths, dams or microbial biofilms will probably not be completely erased from one generation to the next and can thus potentially have an impact on the fitness of individuals living in later generations. Such persistence over time of the physical alteration of the habitat has been called ecological inheritance (Odling-Smee *et al.*, 2003) and is captured here by the inter-temporal fitness effects (B_1, B_2, \dots, B_T). These might represent the positive effects of the construction (or maintenance) of a nest or a burrow that benefits later generations. For instance, a number of monogynous social insects present temporal successions of reproductive individuals within colonies (André *et al.*, 2001), with the result that nests are not re-built afresh in each generation and exceed the life-span of a single individual. Such insects include primitive eusocial wasps (Gadagkar *et al.*, 1993), ponerine ants (Peeters, 1993), army ants (Gotwald, 1995); as well as queen-less ants, honey-bees and stingless bees (André *et al.*, 2001). Serial replacement of breeding individuals is also common in polygynous ants (Evans, 1996) or the euglossine bee *Euglossa townsendi* (Augusto & Garofalo, 2004). In all these organisms, it is difficult to rule out that individuals breeding in a nest constructed (or maintained) by other's living in prior generations do not benefit from the action of the latter's. These are examples that arguably involve some inter-temporal effects on fitness. Constructions extending over the life-span of individuals can also be found in mammals. It is very well exemplified by the complex burrow systems of black-tailed prairie dogs, which can extend over several kilometres and that are occupied by successive generations of individuals (Hoo-gland, 1995). Similar situations probably also involve the burrows of meerkats, the dams of beavers or the hanging nests of social weavers, to name a few. Inter-temporal effects on fitness probably also played a role in the

evolutionary environment of our own species. In particular, the transition from hunting and gathering to agriculture resulted in permanent or semi-permanent settlement that is associated with the domestication of plant and animals (Bellwood, 2004). This ecological transition leads to constructions such as houses, fortifications, agricultural fields or granaries, which pave the way to inter-temporal fitness effects and trans-generational bequests between relatives.

Behaviours by which individuals gain by pursuing interests that increase returns relative to neighbours and decrease the value of the common good are probably frequent in nature. This might result from severe depletion of resources or from the build-up of detritus polluting the environment (negative niche construction). This situation has been called the 'tragedy of the commons' (Hardin, 1968) and it has been suggested that self-restraint of resource use should be favoured by kin selection (Frank, 1995, 1998; Foster, 2004). The present analysis helps to understand the demographic conditions under which kin selection may promote improved efficiency of resource utilization, thus counter-selecting the evolution of negative niche construction. In the absence of any inter-temporal effects on fitness ($B_t = 0$ for $t \geq 1$), a behaviour that results in a benefit for the focal individual ($-C > 0$) and that is deleterious for the group ($B_0 < 0$), will be counter-selected only when it results in a net fecundity cost for the actor or when it decreases the survival of the group (Frank, 1995; Foster, 2004). The present model suggests that the kin selection pressure opposing the evolution of over-exploitation of resources can be greatly enhanced when such behaviours reduce the amount of resources for individuals living in future time periods. Then, these traits result in a fitness cost for subsequent generations ($B_1 < 0, \dots, B_T < 0$) and the kin selective pressure promoting self-restraint is promoted provided the rate of dispersal is low (in eqn 7). Hence, in the absence of any conditional expression of the trait, the gene lineages with the longest view in the future are those that tend to be philopatric. Examples of such situations may be found in mutualistic interactions involving situations where the life-span of the host exceeds that of the symbiont so that the phenotypic effect of a symbiont on the host may impact on the fitness of later generations of symbionts. For instance, ants of the genus *Pseudomyrmex* live on acacia plant and remove local vegetation in the vicinity of the plant and attack herbivores in contact with the plant, which reduce competition for the plant and is repaid by the provision of chambers to house the ants and various supplies of food (Sachs *et al.*, 2004). Individual ants not engaging in such defence activities might gain in terms of direct benefits but are likely to reduce the fitness of relatives living in later generations through the reduction of the survival ability or vigour of the plant. More generally, the phenotypic effects of parasites such as virus or bacteria on hosts might impact on the dynamics of infections in later

generations, with the consequence that the evolution of virulence depends on the within host demography and kin selection (Frank, 1994).

Classical population genetics and game theoretical models deal with situations where the change in frequency of an allele depends only on its current frequency. Although this frequency can be distributed among different classes of individuals, such as age-classes or geographical position, the future of the evolutionary process depends only on the present state. Past history is therefore irrelevant. The present paper focused on a situation where the selective pressure on helping depends on the distribution of gene frequencies in both space and time, a situation that is more likely to be the rule than the exception in nature (Odling-Smee *et al.*, 1996, 2003). Taking into account the posthumous legacies of helping traits on the fitness of individuals living in future generations allows decoupling further kin selected benefits and kin competition. This results in a higher selective pressure on altruism and allows to partially shunt down the tragedy of the commons.

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Supplementary Material

The following supplementary material is available for this article online:

Appendix S1. Evaluation of the selective pressure on a trait that results in both intra and inter-temporal effects on fitness.

This material is available as part of the online article from <http://www.blackwell-synergy.com>

Appendix

A.1. Space-time relatedness under haploid genetics

The selective pressure on helping given in the main text (eqn 5) depends on various relatedness coefficients (the r_i^s). These are probabilities of identity by descent between homologous genes and will be evaluated as is usually carried out for the infinite island model of dispersal (Taylor, 1988; Rousset, 2004), but in addition, a time structure will also be introduced into the model (Epperson, 1999).

Under haploid genetics, the probability that two homologous genes randomly sampled at the adult stage (after dispersal) are identical by descent is given by the following equation:

$$r_0 = (1 - m)^2 r_0^R, \quad (10)$$

where $(1 - m)^2$ is the probability that the two individual are of philopatric origin and r_0^R is the probability of

identity between two juveniles. This coefficient of relatedness depends on the probability $1/N$ that both juveniles descend from the same parent and is given by:

$$r_0^R = \frac{1}{N} + \left(\frac{N-1}{N}\right)r_0, \tag{11}$$

which also is equivalent to the probability of identity between two genes sampled with replacement at the adult stage in the same deme.

More generally, the probability of identity of two homologous genes sampled in the same deme at $t \geq 1$ generation(s) of interval can be expressed as a function of the migration rate and r_0^R according to:

$$r_t = (1 - m)^t r_0^R, \tag{12}$$

where $(1 - m)^t$ is the probability that when looking backwards in time, an ancestral line of a gene sampled in the present remained in the same deme for at least t generations. With probability $1/N$ the gene sampled at t generations in the past initiated this line of descent. With complementary probability $1 - 1/N$ the line of descent was initiated by another gene that has a probability of identity r_0 with the former gene. Comparing eqn 12 with eqn 10 reveals that the equilibrium relatedness between two genes sampled at one generation of interval (relatedness with the parental generation) exceeds the within generation relatedness.

Using the equilibrium coefficients of relatedness (eqn 10 and eqn 12), we find that the inclusive fitness effect (eqn 5) can be written as:

$$S = -C(1 - r_0) - (r_0 - r_0^R) \left[\sum_{t=0}^T B_t (1 - m)^t \right]. \tag{13}$$

Then, from eqn 11 used under the form $r_0^R = r_0 + (1 - r_0)/N$, we finally have:

$$S = \left[-C + \sum_{t=0}^T B_t \frac{(1 - m)^t}{N} \right] (1 - r_0). \tag{14}$$

A.2. Space-time relatedness under diploid and haplo-diploid genetics

Under diploid genetics and in the infinite island model of dispersal, the relatedness between a focal individual of sex i and another individual of sex j living t generation prior to the focal individual in the focal deme is given by:

$$r_{ij(t)} = \frac{2Q_{ij(t)}}{1 + F}, \tag{15}$$

where F is the probability that both homologous genes of the focal individual are identical by descent (i.e. inbreeding coefficient) and $Q_{ij(t)}$ is the probability that a gene randomly sampled in the focal individual of sex i is identical by descent with a randomly sampled homologous gene in an individual of sex j living t generations

prior to the focal generation in the focal deme (i.e. coancestry coefficient). These probabilities are assumed here to be evaluated after dispersal, so that $r_{ij(t)}$ measures the relatedness between adults. Noting that a gene sampled in an individual is either of philopatric or immigrant origin and that it descends either from a male (with probability $1/2$) or from a female breeding in the previous generation, we can see that the probabilities $Q_{ij(t)}$ satisfy the systems of recurrence equations for $t \geq 2$:

$$\begin{aligned} Q_{ff(t)} &= (1 - m_t) \left(\frac{1}{2} Q_{ff(t-1)} + \frac{1}{2} Q_{mf(t-1)} \right) \\ Q_{mf(t)} &= (1 - m_m) \left(\frac{1}{2} Q_{ff(t-1)} + \frac{1}{2} Q_{mf(t-1)} \right) \end{aligned} \tag{16}$$

and:

$$\begin{aligned} Q_{mm(t)} &= (1 - m_m) \left(\frac{1}{2} Q_{mm(t-1)} + \frac{1}{2} Q_{fm(t-1)} \right) \\ Q_{fm(t)} &= (1 - m_f) \left(\frac{1}{2} Q_{mm(t-1)} + \frac{1}{2} Q_{fm(t-1)} \right), \end{aligned} \tag{17}$$

where m_i designates the probability that an individual of sex i is of philopatric origin and the subscripts m and f stand for male and female, respectively. The initial conditions of these two systems of equations are the probabilities of identity between pairs of individuals sampled at one generation of interval (identity between the parental and the offspring generation), namely:

$$\begin{aligned} Q_{jj(1)} &= (1 - m_j) \left(\frac{1}{2} Q_{jj(0)}^R + \frac{1}{2} Q_{ij(0)} \right) \\ Q_{ij(1)} &= (1 - m_i) \left(\frac{1}{2} Q_{jj(0)}^R + \frac{1}{2} Q_{ij(0)} \right), \end{aligned} \tag{18}$$

where:

$$Q_{jj(0)}^R = \frac{1}{N_j} + \left(\frac{N_j - 1}{N_j} \right) Q_{ij(0)}, \tag{19}$$

is the probability of identity between two individuals of sex j sampled with replacement in the same generation and N_j is the number of individuals of that sex at the adult stage. It is well-known how to evaluate the various within generation probabilities ($Q_{ij(0)}$) of identity by descent (e.g. Taylor, 1988; Wang, 1997; Rousset, 2004). Solving the system of eqns 16 and 17, the coancestries are found to be given for $t \geq 1$ by:

$$\begin{aligned} Q_{jj(t)} &= (1 - m_j) \left(\frac{2 - m_m - m_f}{2} \right)^{t-1} \left(\frac{1}{2} Q_{jj(0)}^R + \frac{1}{2} Q_{ij(0)} \right) \\ Q_{ij(t)} &= (1 - m_i) \left(\frac{2 - m_m - m_f}{2} \right)^{t-1} \left(\frac{1}{2} Q_{jj(0)}^R + \frac{1}{2} Q_{ij(0)} \right). \end{aligned} \tag{20}$$

From these equations, we see that the probabilities of identity between pairs of individuals sampled in different epochs decays at geometric rate $(2 - m_t - m_m)/2$ as the number of generation between them increase. When the

dispersal probability is the same for each sex ($m_m = m_f = m$), this rate becomes $(1 - m)$, which is equivalent to the haploid case (eqn 12). As the coefficient of relatedness (eqn 15) between two individuals sampled in different generations depends only on the variation in the coefficient of coancestry between these individuals, relatedness decreases at the same rate as the coancestry coefficient.

Similar calculations of probabilities of identity by descent can be carried out for a haplo-diploid genetic system. It requires only to tune the second lines of eqns 16 and 17 by allowing males to inherit genes solely from females. The resulting equations are more complex and I present here only the case where the migration rate of both males and females is the same. In that situation, the coancestries are given by:

$$\begin{aligned}
 Q_{ff(t)} &= (1 - m)^t \left(\frac{2}{3} Q_{ff(0)}^R + \frac{1}{3} Q_{mf(0)} \right) + \frac{1}{3} \left(\frac{-(1 - m)}{2} \right)^t (Q_{ff(0)}^R - Q_{mf(0)}) \\
 Q_{mf(t)} &= (1 - m)^t \left(\frac{2}{3} Q_{ff(0)}^R + \frac{1}{3} Q_{mf(0)} \right) - \frac{2}{3} \left(\frac{-(1 - m)}{2} \right)^t (Q_{ff(0)}^R - Q_{mf(0)}) \\
 Q_{fm(t)} &= (1 - m)^t \left(\frac{2}{3} Q_{fm(0)} + \frac{1}{3} Q_{mm(0)}^R \right) - \frac{1}{3} \left(\frac{-(1 - m)}{2} \right)^t (Q_{mm(0)}^R - Q_{fm(0)}) \\
 Q_{mm(t)} &= (1 - m)^t \left(\frac{2}{3} Q_{fm(0)} + \frac{1}{3} Q_{mm(0)}^R \right) + \frac{2}{3} \left(\frac{-(1 - m)}{2} \right)^t (Q_{mm(0)}^R - Q_{fm(0)})
 \end{aligned}
 \tag{21}$$

From these equations we see that under haploid-diploid genetics the rate of decrease of the relatedness between two individual sampled at t generations of interval is not equal to $(1 - m)$ but will approach this value when t is large.

A.3. Soft selection

Here we present the selective pressure on helping in the presence of soft selection (regulation before dispersal), which is also equivalent to the case when the migration rate vanishes ($m \rightarrow 0$). Using the same notation as in eqns 3 and 4, the fitness is given by:

$$w = \frac{1 - Cz_\bullet + B_0 z_0^R + \sum_{t=1}^T B_t z_t}{1 + (B - C)z_0^R + \sum_{t=1}^T B_t z_t}, \tag{22}$$

because migrants to not affect the fitness of the focal individual. Using eqn 2 evaluated at $z_\bullet = z_t = 0$, we have:

$$S = -C(1 - r_0^R), \tag{23}$$

which is independent of any kin selection effects and is equivalent to the selective pressure obtained by Rousset (2004), (eq. 7.23, pp. 125) in the absence of any inter-temporal effects on fitness.

Supplementary material for “The evolution of trans-generational altruism: kin selection meets niche construction”

The selective pressure on a trait that results in both intra and inter-temporal effects on fitness will be evaluated in this supplementary material. This is done by extending the probability of fixation method developed in Rousset (2003) and Rousset (2004, chapter 6), whose analysis is followed here very closely. The results essentially demonstrate that individuals affecting the fitness of other individuals living in different time periods can be treated as different “classes” of actors in the same manner as is usually done in inclusive fitness theory for sex, age, geography or other kind of kin classes (Taylor, 1990, 1996; Taylor and Frank, 1996; Frank, 1998; Rousset and Billiard, 2000; Rousset, 2004). The selective pressure for the infinite island model of dispersal used in the main text is then obtained as a particular case of the approach.

A convergence measure of stability of a trait under selection can be obtained by analyzing the probability of fixation of a single mutant allele (say A) whose phenotypic effect deviates (with small magnitude δ) from the phenotype expressed by a resident allele (say a) fixed in the population. The direction of evolutionary change on the mutant is then determined by asking whether it has a larger or smaller probability of fixation than a neutral mutant. That is, does the phenotypic deviation δ results in a positive or negative effect on the probability of fixation of the mutant. This increment or decrement in the probability of fixation can be expressed as a function of the effect of the mutant on the between-generation change in expected average allele frequency $\Delta\bar{p}(t)$ in the population according to the equation

$$\phi = \text{E} \left[\sum_{t=0}^{\infty} \frac{d\Delta\bar{p}(t)}{d\delta} \right], \quad (1)$$

where the sum adds up until fixation of either the mutant or the resident allele (Rousset, 2003, p. 666).

Let us consider that evolution occurs in a population following the haploid island or isolation by distance model of dispersal. There are n_d demes, each with N adults so that the total population size is of constant size $N_T = n_d N$. For simplicity, we assume that dispersal is isotropic and homogeneous and that environmental conditions are the same in each deme. Accordingly, the fitness of each individual is independent of the geographical position of the deme in which it resides and its dispersal distribution is symmetric and the

same in each deme. Let a random sequence of mutant allele frequencies in the population since its appearance and up to time t be denoted by

$$\omega(t) \equiv \{\mathbf{p}(t), \mathbf{p}(t-1), \dots, \mathbf{p}(1), \mathbf{p}(0)\}, \quad (2)$$

where

$$\mathbf{p}(t) \equiv (p_1(t), \dots, p_{n_d}(t)) \quad (3)$$

is the vector of the frequencies of the mutant allele in the different demes at time t and $p_i(t)$ is the frequency of the mutant in deme i . In the presence of intra and inter-temporal effects on fitness, the change in allele frequency $\Delta\bar{p}(t)$ at generation t may depend on the whole history of allele frequencies $\omega(t)$ in the population up to time t . The change over one generation is thus conditional on the various realizations of deme gene frequencies and can be written as

$$\Delta\bar{p}(t) = \sum_{\omega(t)} (\mathbb{E}[\bar{p}(t+1)|\omega(t)] - \bar{p}(t)) \Pr(\omega(t)), \quad (4)$$

where $\Pr(\omega(t))$ is the probability of the occurrence of the sequence $\omega(t)$.

Following the argument given in Rousset (2003, eq. 4), the effect of the mutant on its probability of fixation is then given by

$$\phi = \mathbb{E}^\circ \left[\sum_{t=0}^{\infty} \frac{d}{d\delta} (\mathbb{E}[\bar{p}(t+1)|\omega(t)] - \bar{p}(t)) \right], \quad (5)$$

which is equivalent to eq. 5 of Rousset (2003) except that the expectation \mathbb{E}° over realization of deme gene frequencies in the neutral process is running here over all sequences $\omega(t)$ of present and past mutant gene distributions.

The sensitivity of average gene frequency change to mutant deviation in eq. 5 can be computed from the direct fitness of a focal individual $w \equiv w(z_\bullet, \dots, z_{k,h}, \dots)$, which is expressed here as a function the phenotype of the focal individual $z_\bullet = z_a + \delta$ and as a function of the average phenotypes $z_{k,h} = z_a + \delta p_{k,h}$ of individuals located in different demes (labeled k) at different points in time (labeled h) prior to the focal generation, where $p_{k,h}$ is the frequency of the mutant allele in such demes and z_a is the phenotype of the resident. Then, following the same development as Rousset (2003, eq. 9 to eq. 11), the first order effect of the mutant on its probability of fixation is given by

$$\phi = \mathbb{E}^\circ \left[\sum_{t=0}^{\infty} \left(\frac{\partial w}{\partial z_\bullet} + \sum_{h=0}^T \sum_{k=1}^{n_d} \frac{\partial w}{\partial z_{k,h}} p_k(t-h) \right) p_0(t) \right], \quad (6)$$

where $p_0(t)$ is the frequency of the mutant allele in a focal deme at time t , $p_k(t-h)$ is the frequency of the mutant in a deme at distance k from the focal deme at h generations prior to t (if $h > t$, $p_k(t-h) = 0$) and T is the time horizon of inter-temporal effects on fitness. Since we assumed a homogeneous environment and isotropic dispersal, only the spatial and time separation of gene frequencies relative to a focal deme in a focal generation matter to evaluate the selective pressure on the mutant. This is the reason why we do not have the sum outside the parentheses given in eq. 11 of Rousset (2003).

By the property that the partial derivatives of the fitness function sum up to zero (Rousset, 2004, eq. 6.9), eq. 6 can be written as

$$\phi = \sum_{k=1}^{n_d} \sum_{h=0}^T \frac{\partial w}{\partial z_{k,h}} \mathbb{E}^\circ \left[\sum_{t=0}^{\infty} (p_0(t)p_k(t-h) - p_0(t)) \right]. \quad (7)$$

The mutant appears as single copy in the population and its initial frequency in the deme where it appears is $1/N$. The probability that the mutant appears in a given focal deme is $1/n_d$, hence $\mathbb{E}^\circ [p_0] = 1/N_T$. The probability that a gene taken in a focal deme at time t and another gene taken in a deme at distance k from the focal deme at h generations prior to t are both mutants is given by

$$\begin{aligned} \mathbb{E}^\circ [p_0(t)p_k(t-h)] &= \frac{1}{N_T} \sum_{g=0}^t C_{k,h}(g) \\ &= \frac{1}{N_T} \sum_{g=h}^t C_{k,h}(g), \end{aligned} \quad (8)$$

where $C_{k,h}(g)$ is the probability that a gene taken in a focal deme and another gene taken in a deme at distance k from the focal deme at h generations prior to the focal generation coalesce in a common ancestor living in generation g prior to h ($g \geq h$). We can now

write

$$\begin{aligned}
\mathbb{E}^\circ \left[\sum_{t=0}^{\infty} (p_0(t) - p_0(t)p_k(t-h)) \right] &= \frac{1}{N_T} \sum_{t=0}^{\infty} \left(1 - \sum_{g=h}^t C_{k,h}(g) \right) \\
&= \frac{1}{N_T} \sum_{t=0}^{\infty} \left(\sum_{g=h}^{\infty} C_{k,h}(g) - \sum_{g=h}^t C_{k,h}(g) \right) \\
&= \frac{1}{N_T} \sum_{t=0}^{\infty} \sum_{g=t+1}^{\infty} C_{k,h}(g) \\
&= \frac{1}{N_T} \sum_{t=0}^{\infty} t C_{k,h}(t) \\
&= \frac{T_{k,h}}{N_T}, \tag{9}
\end{aligned}$$

where the second equality is obtained by using the identity $\sum_{g=h}^{\infty} C_{k,h}(g) = 1$, which amounts to say that two genes sampled at k generations of interval must eventually coalesce in a common ancestor if we look sufficiently far enough into the past. The last two steps are in fact strictly equivalent to those given in eq. 14 of Rousset (2003) and $T_{k,h}$ designates the average coalescence time between two genes, one sampled in the focal deme and the other sampled in a deme at distance k from the focal deme at h generations prior to the focal generation.

Then, following again the line of arguments spelt out in Rousset (2003), the effect of the mutant on its probability of fixation is given by

$$\phi = \lim_{\mu \rightarrow 0} \frac{S}{1 - r_0}, \tag{10}$$

where r_0 is probability of identity of a pair of genes within a deme and S is the inclusive fitness effect measuring the direction of selection on the mutant allele. The inclusive fitness effect takes here the form

$$S = \frac{\partial w}{\partial z_{\bullet}} + \sum_{h=0}^T \sum_{k=1}^{n_d} \frac{\partial w}{\partial z_{k,h}} r_{k,h}, \tag{11}$$

where $r_{k,h}$ is the probability that a gene sampled in a focal individual is identical to a homologous gene sampled in an individual of class k living h generations prior to the focal generation. In the infinite island model of dispersal (that is when $n_d \rightarrow \infty$), we have $r_{k,h} = 0$ for all k except $r_{0,h} \geq 0$ and the inclusive fitness effect gives the first order effect of selection on gene frequency change (Rousset, 2004, pp. 206–207). The resulting change in average

mutant allele frequency p in the population can then be written as

$$\Delta p = \delta S p(1 - p) + O(\delta^2), \quad (12)$$

where $O(\delta^2)$ is a remainder of phenotypic effects on fitness of second order in δ .

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