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Kin competition and the evolution of cooperation

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Abstract

Kin and multilevel selection theories predict that genetic structure is required for the evolution of cooperation. However, local competition among relatives can limit cooperative benefits, antagonizing the evolution of cooperation. We show that several ecological factors determine the extent to which kin competition constrains cooperative benefits. In addition, we argue that cooperative acts that expand local carrying capacity are less constrained by kin competition than other cooperative traits, and are therefore more likely to evolve. These arguments are particularly relevant to microbial cooperation, which often involves the production of public goods that promote population expansion. The challenge now is to understand how an organism's ecology influences how much cooperative groups contribute to future generations and thereby the evolution of cooperation.

Keywords

social evolution; multilevel selection; kin selection; group selection; altruism; viscous population; Hamilton's Rule; relatedness; local competition; scale of competition; hard selection; soft selection; density dependence; limited dispersal; Price equation; public good

Limited dispersal and the evolution of cooperation

Explaining the evolution of cooperative or altruistic traits is a fundamental challenge in evolutionary theory. Cooperative traits impose a cost on individuals exhibiting the trait to the benefit of other individuals. Consequently, within-group natural selection disfavors cooperative individuals, favoring instead individuals that cheat or freeloader by avoiding the costs of cooperation while continuing to receive the benefits provided by cooperative individuals^{1, 2}. Despite this, cooperation is commonplace in nature, being found in a variety of biological systems including primates³, social insects⁴ and bacteria⁵, suggesting that costs of cooperation can be overcome.

Hamilton posed the first evolutionary explanation of how cooperation can evolve despite its direct costs^{1, 6}, known as Hamilton's rule (see Glossary). He showed that cooperative traits can evolve whenever the benefits that recipients accrue weighted by genetic relatedness outweigh the costs that actors pay^{1, 6}. Accordingly, relatedness is required for the evolution of cooperative traits; that is, individuals must tend to interact within family groups or with

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other genetically similar individuals. Relatedness among interacting individuals can arise due to limited dispersal or assortative interactions based on genetic similarity^{1, 6}. Limited dispersal can be a particularly powerful means of generating relatedness because it does not require active kin recognition but can yield substantial between-group genetic variation¹. Groups with a higher proportion of cooperative individuals can then have higher productivity and this increased productivity can be sufficient to overcome the costs of cooperation (see Box 1)⁷.

Box 1

Kin competition in social evolutionary theory

Kin and multilevel selection theories are the two most prominent frameworks for the evolution of cooperation. While these complementary approaches partition fitness differently, they are fully interchangeable frameworks for social evolution^{18, 19}. Multilevel and kin selection models both emphasize the importance of genetically structured interactions, wherein individuals are more likely to cooperate with individuals with whom they are more genetically similar^{69, 70}. Despite their similarities, these frameworks address the potential antagonistic effects of kin competition on the evolution of cooperation in different ways.

Kin selection theorists have incorporated kin competition's antagonistic effect into Hamilton's rule using a variety of approaches⁹. One approach is to augment the cost of cooperation with an additional term accounting for the decrease in fitness associated with kin competition, weighted by the relatedness of the actor to the individuals experiencing this fitness cost^{11, 14}. The effect can also be put into the benefit term by devaluing the benefit to a degree that depends on the scale of competition⁷¹. Alternatively, the effect can be captured in the relatedness term by defining relatedness relative to the subpopulation of competitors (rather than the global population)¹³.

Just as Hamilton's rule is the centerpiece of kin selection theory, partitioning selection into within- and between-group components is essential to multilevel selection approaches to social evolution^{72, 73}. Though cooperative traits are expected to be selected against within groups whenever there is variation within groups, they can be selectively favored between groups if cooperative groups are more productive than less cooperative groups⁷². Between-group responses to selection depend on the degree of genetic structure among groups. Low relatedness corresponds to a high proportion of genetic variation within groups, while high relatedness corresponds to a high proportion of genetic variation between groups⁷⁴. Considering this, it is not surprising that the formal equivalence of kin and multilevel selection models has been demonstrated by many researchers^{19, 72, 75}.

The multilevel selection approach emphasizes that cooperative groups must be more productive in order for the cooperative trait to spread by between-group selection. If the population density of all groups is regulated at the local scale to the same density, then the spread of cooperation is stymied because uniform local density dependence precludes cooperative groups from being more productive than less cooperative groups (Figure

1a)^{7, 12, 29}. This directly parallels kin selection models that incorporate the effect of kin competition by devaluing cooperative benefits⁷¹.

Viscous populations are characterized by limited dispersal. Discussions of population viscosity and the evolution of cooperation have emphasized the potential for kin competition to limit the evolution of cooperation in viscous populations^{8–10}. While cooperative individuals are more likely to benefit kin in viscous populations, they also compete for limiting resources with these same kin. Early theoretical work found that such kin competition can strongly antagonize the benefits of kin cooperation and inhibit the evolution of cooperation in viscous populations^{9, 11–15}. Consistent with this, empirical studies have failed to find a relationship between relatedness and aggressiveness in fig wasps¹⁶ and bruchid beetle larvae¹⁷, suggesting that the effects of kin competition might negate any kin-selected benefits associated with being less aggressive toward kin.

We critically evaluate the importance of kin competition in constraining the evolution of cooperation and demonstrate that the evolution of cooperation is facilitated when the cooperative trait increases local population productivity. In addition, we explicitly examine the ecological factors influencing the evolution of cooperation and conclude that for many systems limited dispersal facilitates, not antagonizes, the evolution of cooperation. This conclusion stems from the fact that ecological factors can influence the degree of kin competition, the benefits of cooperation, and the degree to which individuals cooperatively interact with kin.

Ecological factors influence social evolution

Results from kin and multilevel selection theories have shown that kin competition can antagonize the evolution of cooperation. Many theoreticians have demonstrated that these frameworks are complementary descriptions of the same evolutionary processes^{18, 19} (Box 1). The Price equation has proven a particularly useful conceptual tool for identifying the common foundations of kin and multilevel selection theories^{18–20} (Box 2). Extending this approach, we show that when cooperative traits increase the pre-dispersal population size of local groups there can be additional pathways for cooperative benefits that promote the evolution of cooperation (Figures 1 and 2; Box 2). That is, increased local carrying capacity or relaxed local density dependence can facilitate the evolution of cooperation within viscous populations even in the face of kin competition. In studies emphasizing the negative effect of local scale competition, the relationship between population size and fitness is thought to be negative because of increased kin competition, potentially reducing the rate of genetic change. We describe multiple circumstances in which this relationship can be positive, thereby facilitating the evolution of cooperation.

Box 2

Hamilton's rule when cooperative behavior influences population expansion

The effect of genetically determined population expansion on the response to selection can be incorporated into a kin selection model using Queller's method⁷⁶. A simplified

version of the Price equation²⁰ describes selection's effect on the population average genetic composition

$$\Delta \bar{G} = Cov(G_i, W_i) \quad \text{Eqn. 1}$$

where G_i and W_i represent the i th individual's genes underlying the trait and fitness, respectively.

For a social trait that influences population size the relative fitness of an individual depends on its own genes (G_i), its neighbor's genes (G'_i), and the pre-dispersal size of the individual's group (N_{Di}) (Figure 2). Thus, an individual's fitness can be described by the following least squares regression:

$$W_i = \alpha_1 + \beta_{WG \cdot G'_i N_D} G_i + \beta_{WG'_i \cdot GN_D} G'_i + \beta_{WN_{Di} \cdot GG'_i} N_{Di} + \varepsilon_1 \quad \text{Eqn. 2}$$

wherein G'_i describes the average genic value of the group and each of the partial regression coefficients, of the form $\beta_{WX \cdot YZ}$, describes the linear relationship between fitness and the X variable holding the other variables (Y and Z) constant, while α and ε represent the intercept and residuals of the model, respectively. The average genic value of the group and the genic value of the focal individual also influence population size, represented by a second regression:

$$N_{Di} = \alpha_2 + \beta_{N_{Di} G'_i \cdot G_i} G'_i + \beta_{N_{Di} G \cdot G'_i} G_i + \varepsilon_2 \quad \text{Eqn. 3}$$

This assumes a simple form of density-regulation where population size depends only on the genetic composition of the group. Combining Equations 1, 2, and 3 gives the following expression for the response to selection:

$$\Delta G = \beta_{WG \cdot G'_i N_D} Var(G_i) + \beta_{WG'_i \cdot GN_D} Cov(G_i, G'_i) + \beta_{WN_{Di} \cdot GG'_i} \beta_{N_{Di} G'_i \cdot G_i} Cov(G_i, G'_i) + \beta_{WN_{Di} \cdot GG'_i} \beta_{N_{Di} G \cdot G'_i} Var(G_i)$$

$$\text{Eqn. 4}$$

A modified form of Hamilton's rule can be recovered from Equation 4 by simply dividing through by $Var(G_i)$:

$$0 < \beta_{WG \cdot G'_i N_D} + \beta_{WG'_i \cdot GN_D} \beta_{G'_i G} + \beta_{WN_{D_i} \cdot GG'} \beta_{N_{D_i} G \cdot G'_i} + \beta_{WN_{D_i} \cdot GG'} \beta_{N_{D_i} G'_i \cdot G_i} \beta_{G'_i G}$$

or

$$0 < c + br + de_i + de_g r,$$

see Table

I Eqn. 5

As identified by Queller, the first two terms of Equation 5 are analogous to the cost (c) and the benefit term ($b \cdot r$), giving Hamilton's rule when there are no paths through N_{D_i} ⁷⁶.

The third and fourth terms of Equation 5 describe the direct and indirect feedbacks on genetic change through population size, respectively. The direct feedback depends on how fitness changes as a linear function of group size ($\beta_{WN \cdot G'G}$ or d) and how population size changes as a linear function of a focal individual's genes ($\beta_{NG \cdot G'}$ or e_i). The effect through indirect feedback similarly depends on the benefits or costs accrued through growth or decline of the individual's group (d) and how group size changes as a linear function of neighbor's genes ($\beta_{NG' \cdot G}$ or e_g), and is also mediated by relatedness. These additional terms potentially augment cooperative benefits thereby facilitating the evolution of cooperation in viscous populations despite kin competition.

Table I

Variables used in deriving modified version of Hamilton's rule for cooperative traits that influence population growth or decline

Regression coefficient	Interpretation	Simplified notation
$\beta_{WG \cdot G'N}$	Fitness cost of cooperation	c
$\beta_{WG' \cdot GN}$	Fitness benefit of cooperation stemming from effects on neighbors	b
$\beta_{G'G}$	Relatedness	r
$\beta_{WN \cdot G'G}$	Fitness benefit or cost resulting from group elasticity	d
$\beta_{NG \cdot G'}$	Elasticity of group size in response to focal individual's genes	e_i
$\beta_{NG' \cdot G}$	Elasticity of group size in response to neighbor's genes	e_g

In this section, we examine the ecological conditions that promote the evolution of cooperation despite kin competition in viscous populations. Ecological factors such as the scale of density dependence, population elasticity, and patterns of dispersal influence the degree to which cooperative groups can contribute to the next generation and thus shape the selective pressures acting on cooperative traits.

Scale of population density dependence

The manner in which population density is regulated can alter the evolutionary process. This is particularly true when selection occurs both within- and between-groups because density regulation can influence how much each group contributes to the next generation²¹. Kin competition is most antagonistic to the evolution of cooperation when cooperative groups are constrained in their productivity²². For this reason, the evolution of cooperation is unlikely when the scale of cooperation is larger than or equal to the scale at which group size is regulated to a fixed carrying capacity (see Figure 1a)^{21, 23}. Such scenarios can occur when reproductive potential is locally fixed (Box 3).

Box 3

Taylor's kin selection model of cooperation with competition

Taylor presented a simple patch-structured model of the evolution of cooperation wherein cooperation increases the competition for space experienced by the progeny of a cooperator¹¹. This model envisions cooperative acts that increase the number of offspring produced on a local patch by n_b at the cost of cooperative mothers who produce n_c fewer offspring. The fitness of a focal cooperative asexual female depends on her indirect benefits of cooperating ($R \cdot n_b$), her direct cost of cooperating (n_c), and the cost of having related individuals displaced by the extra individuals present on the patch because of the cooperative act ($sR \cdot s(n_b - n_c)$), with s being the probability that an individual remains in its natal patch and R being the average relatedness in the patch. The model assumes that $s(n_b - n_c)$ individuals are above carrying capacity, which is fixed by the number of breeding sites on the patch (F). The focal female's relatedness to these displaced individuals is given by sR .

Assuming females are equally productive, the probability that any two individuals on the patch are siblings is given by $\frac{1}{F}$. The probability that two individuals are non-sibling relatives is given by $\frac{F-1}{F} s^2 R$. These probabilities sum to give relatedness. The cooperative trait is predicted to spread when the net fitness gain of a cooperative individual is greater than zero. With the costs, benefits, and relatedness described above this occurs when females accrue a net benefit to themselves ($\frac{n_b}{F} > n_c$) because kin selected benefits are exactly cancelled by the effects of kin competition.

This model makes a number of simplifying assumptions that enhance the degree to which kin competition antagonizes the evolution of cooperation. In this model, individuals compete locally for a fixed number of breeding sites in a fully saturated environment (see Figure 1a). Relaxing the restrictive conditions of Taylor's model has provided a useful approach for subsequent investigations of conditions facilitating the evolution of cooperation^{31, 33}. Allowing population elasticity (either through increased local density or effective dispersal to other patches) or allowing a more global scale of competition can greatly facilitate the spread of cooperation in viscous populations by enhancing the

degree to which cooperative groups contribute to the next generation (Box 2, Figure 1b and 1c).

Hamilton provided an example of this when he pointed out that competition among siblings for resources within the same mammalian womb slows the rate of evolution of a cooperative behavior between these siblings¹. Siblings only have “a local standard-sized pool of reproductive potential” available to them via the provisioning of their mother¹. Despite the high assurance that the genes of individuals within the same womb covary, cooperative behaviors directed toward siblings within the same womb are unlikely to evolve because the scale of cooperation equals that of competition and the available resources are fixed. Considering this, it is perhaps unsurprising that sibling rivalry sometimes results in hostile interactions among mammalian and avian siblings within the same womb or in the same nest^{24, 25}. In fact, while local competition resulting from limited dispersal antagonizes the evolution of cooperation, it can also favor the evolution of spiteful interactions^{25, 26} and the dispersal of individuals away from the natal site^{27, 28}.

Early discussion of the evolution of cooperation with kin competition focused on ecologies that are restrictive to the evolution of cooperation (see Box 3). This led to the common view that special conditions are required to explain the evolution of cooperative behaviors that occur without subsequent dispersal. Taylor’s patch-structured model of altruism in a viscous population has been one of the most influential theoretical investigations of the effects of kin competition on the evolution of cooperation¹¹ (Box 3). The main result of this work demonstrates that under the assumed life-history and ecological conditions the effects of kin competition fully offset the benefits of cooperation. Researchers have argued that patterns of sibling competition in organisms with inelastic local competition (Figure 1a), such as beetles¹⁷ and fig wasps¹⁶ competing at natal sites, are consistent with the predictions of Taylor’s model.

The effect of kin competition is weakened when density dependence is more global than the local scale of cooperation because global density dependence allows cooperative groups to be more productive than less cooperative groups^{7, 16} (Figure 1b). Griffin et al.²⁹ experimentally tested this prediction by examining how the scale of density dependence influences the evolution of cooperative siderophore production in *Pseudomonas aeruginosa*. Many bacterial pathogens facultatively produce extracellular siderophores that aid neighboring cells in acquisition of limiting iron by ligating free or bound iron in the external environment. As expected, cooperative siderophore-producing strains spread under global but not local density dependence²⁹. As with any cooperative behavior, siderophore producers pay the cost of production and thus are selected against within their groups regardless of the scale of density dependence. However, under global density dependence there is increased potential for between-group benefits of the behavior to override this cost.

Many factors determine the degree to which cooperative groups are able to be more productive. When cooperative benefits are directed to recognized kin or excluded from non-kin, cooperation likely occurs at a more local scale than does competition and there is a positive genetic covariance (relatedness) among interacting individuals³⁰. The scale of

cooperation can also be more restricted than the scale of competition whenever cooperative behaviors are timed to occur before dispersal^{11, 31}. This is notably the case when juveniles cooperate at or near the natal site before then dispersing away from the site. Here cooperatively interacting individuals enjoy the benefits of viscosity (e.g. enhanced relatedness) but minimize its drawbacks (i.e. kin competition) since by separating after cooperating they have less opportunities to compete with their kin. However, there is still potential for kin competition if available breeding sites are limited^{32, 33}.

Population elasticity

Group productivity can vary in elastic populations²². In such populations, cooperative behaviors can affect a variety of factors that influence how much a group contributes to the next generation by increasing the group's population density, range, migrant output, or survivorship^{22, 32, 34–37}. The organism's ecology determines which of these effects can vary depending on the genetic composition of the group. A cooperative behavior can increase group productivity by increasing the group's local carrying capacity (Figure 1c) or when population density is regulated at a scale broader than the scale of cooperation (Figure 1b). In each case, the scope of cooperative benefits is greater than it is when fixed reproductive potential constrains the productivity of the group (i.e. groups are locally inelastic). These additional benefits increase the degree to which group (and kin) selection favors the cooperative trait (Box 2).

Competition for breeding sites (space) illustrates how the selective dynamics of cooperation depends on the potential for groups to export the benefits of cooperation. When breeding sites are fixed and fully occupied, competition for space is particularly fierce¹¹ (Box 3). However, when empty sites are available kin competition is likely to be less severe and as a consequence the fitness of cooperative individuals is less compromised³³. In this case, there are more sites available thereby reducing competition such that the increased demand for sites due to cooperation does not necessarily come at the expense of the fitness of the cooperative individual. The availability of empty sites facilitates the evolution of cooperation by allowing the export of cooperative benefits from cooperative groups, so that such groups can be more productive than non-cooperative groups.

The benefits of cooperation often stem from the increased reproductive potential of groups of individuals. In many species, males are less constrained in their reproductive potential because they are able to attain higher fitness via increased access to females^{38, 39}. Because of this, coalitions of males that cooperatively court can have more reproductive potential than males courting alone, even though subordinate males in coalitions have lower reproductive success than solo males⁴⁰. For example, coalitions of related male turkeys have overall more success than do solo males, as the net effect of cooperating is positive⁴⁰. This is despite subordinate males in coalitions having poor reproductive success due to competition with the coalition's dominant male.

Cooperative behaviors that increase the local carrying capacity of a group also allow for increased group productivity. Microbial cooperation is often associated with public goods that can increase the local carrying capacity (reviewed in ref.⁵). Examples include the production of siderophores⁴¹, viral replication enzymes⁴², specialized resources^{43, 44}, and

secreted exoenzymes⁴⁵. In these cases, a cooperative group is able to grow to a higher local density than can a non-cooperative group. The effects of this increased group productivity can offset the consequences of kin competition (Figure 1c). For example, Kümmerli et al. have shown experimentally that cooperation can spread when highly productive siderophore producing groups are able to export these cooperative benefits because of an advantage in colonizing new subpopulations, but fails to spread without this colonization advantage⁴⁶.

Agrobacterium tumefaciens, a common plant pathogen, provides an illustrative example. The Ti plasmid of *A. tumefaciens* confers the ability to cause plant tissues to produce opines, a specialized resource that only cells harboring a Ti plasmid can catabolize⁴⁷. Expressing the virulence system is costly to the individual cell and the benefits of this cooperative act are available to any Ti plasmid bearing cell near the infection. As consequence, an *Agrobacterium* subpopulation in the vicinity of an infected plant has a higher local carrying capacity than a group in the non-disease environment⁴³. Because opines can only be catabolized by cells bearing the virulence plasmid, this organism employs a greenbeard-like 'recognition' that ensures that cooperative benefits are only available to genetically similar individuals. These individuals are likely to have both virulence and opine catabolic functions due to linkage of these genes on the Ti plasmid. The cooperative pathogenesis of *A. tumefaciens* increases both the competitive ability and carrying capacity of cells with a Ti plasmid at the site of the infection allowing increased group productivity.

The mutualistic association among rhizobia and legumes similarly results in increased carrying capacity of the bacteria near the nodule due to increased plant exudates^{48, 49}. As with the *Agrobacterium* system, these increased plant exudates sometimes include specialized resources (rhizopines) that can only be catabolized by other rhizobia⁵⁰. Recently, several authors have argued that the evolution of cooperation among rhizobia is strongly hindered by kin competition at the nodule^{51, 52}. These arguments ignore the consequences of population elasticity and greenbeard-like recognition which are likely to swamp out the effects of kin competition. Similar increases in local carrying capacity potentially play roles in the evolution of other root symbionts including arbuscular mycorrhizal fungi⁵³.

Patterns of dispersal

Many of the factors restricting the importance of kin competition in viscous populations can be thought of as the effects of metapopulation and life-history features. We have discussed some of the ways in which these attributes can influence the impact of kin competition (e.g. its effects are limited when individuals disperse after cooperating) and the benefits of cooperative traits (e.g. empty sites increase the potential for benefits through increased group productivity).

Patterns of dispersal play a large role in shaping the genetic structure of populations⁵⁴. In viscous populations, limited dispersal generally promotes both the genetic similarities among interacting individuals and the degree of kin competition⁹. Notably, kin-structured dispersal strongly promotes the maintenance of a high degree of relatedness thereby promoting the evolution of cooperative traits^{55–57}. A wide range of organisms exhibit kin-structured dispersal including vertebrates⁵⁸, plants⁵⁹, insects^{60, 61}, and bacteria⁶². Thus, kin-

structured dispersal can be important to the evolution of cooperation in many systems. To date, support for this remains largely theoretical and a topic for future empirical research.

Viscosity and social evolution in macro- versus micro-organisms

At the simplest level, in order for kin competition to hinder the spread of cooperation, individuals must compete and cooperate with the same individuals. However, ecological factors alter the degree to which kin competition antagonizes the evolution of cooperation. Whenever cooperative groups are more productive than less cooperative groups there is potential for between-group selection to favor the spread of the cooperative trait. This is likely when population density is globally regulated and/ or if local density dependence is non-uniform. Either way, cooperative groups are more productive in terms of migrants, expansion, or persistence (Box 2). Higher group productivity augments the benefits associated with cooperative traits, potentially offsetting the negative effects of kin competition (Table 1). We have reviewed the ecological factors that determine the impact of kin competition and argue that for many biological systems population viscosity is more likely to promote the evolution of cooperation than hinder it.

The widespread notion that kin competition limits the evolution of cooperation in viscous populations is likely an outgrowth of early models focusing on competition in a saturated environment^{11, 12} and macro-organisms with relatively inelastic populations¹⁶. Social evolution researchers are increasingly turning their attention to microbial cooperation (reviewed by ref.⁵). Some authors have suggested that the evolution of some forms of microbial cooperation should be expected to be constrained by the fact that cooperation and competition occur at the same spatial scale^{51, 52}. However, microbial populations are generally more elastic than those of macro-organisms, thus limiting the potential for kin competition to outweigh the benefits of cooperation. For example, while the number of breeding sites and mates that sibling birds are competing for are fixed, there is considerably more potential for the behavior of microbes to increase the availability of resources in their environment through cooperative acts (e.g. siderophores increasing iron availability, bacterial pathogens increasing release of resources from hosts, and root symbionts increasing plant exudates). We therefore conclude that for many cooperative systems, particularly microbial ones, limited dispersal is more likely to favor, rather than hinder, the evolution of cooperation by facilitating interactions among kin.

There is a growing body of theoretical work showing that patterns of spatial structure determined by migration alter ecological and evolutionary dynamics^{23, 63–65}. In this paper, we review how the interplay of these dynamics influences the evolution of cooperation. Many aspects of this interplay have been underappreciated. To move forward, future research must begin to account for the ways in which ecological factors influence the costs and benefits of cooperative traits. This is particularly important as the frameworks of social evolution are applied to organisms with varied life-histories such as plants^{66, 67}, fungi^{53, 68}, and microbes⁵. Moreover, future studies on all organisms should examine the importance of ecological factors that play strong roles in social evolution.

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Glossary

Carrying capacity

maximum sustainable population size

Global density dependence

when the density of a population is determined at a broad spatial scale; for example, where there is a well mixed food source or where predation is by a roaming predator

Group productivity

contribution of a group to the next generation; this can depend on migrant dispersal, group survival, or changes in the group's range

Hamilton's rule

prediction that a costly trait benefiting other individuals evolves only when the relatedness weighted benefits of the trait outweigh its direct costs ($r \cdot b > c$); the cost (c) and benefit (b) describe how the relative fitnesses of the cooperative individual and beneficiaries, respectively, change because of the trait's expression

Kin selection

framework of social evolution that emphasizes the costs (c), benefits (b), and genetic relatedness (r) of social interactions (see Hamilton's rule)

Local density dependence

when the density of a population is determined by locally acting density regulating processes; for example, where resources are distributed on a local scale

Multilevel selection (group selection)

evolutionary framework that partitions the effects of selection into within-group and between-group components

Population elasticity

potential for group productivity to change

Scale of competition

spatial scale over which competitive interactions influencing an individual's fitness occur

Scale of cooperation

spatial scale over which cooperative interactions influencing an individual's fitness occur

Relatedness

measure of the statistical association among the genes of interacting individuals (see Hamilton's rule)

Viscous population

population characterized by limited dispersal such that individuals tend to live near their natal site

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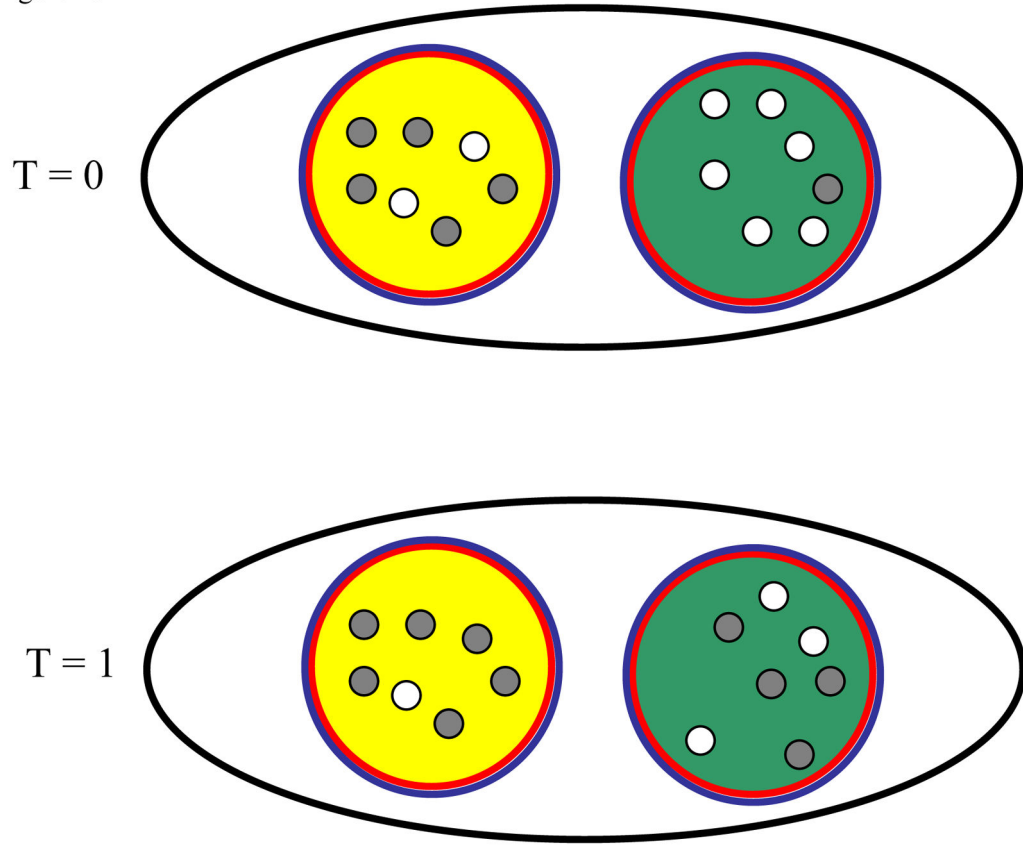
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Figure 1a



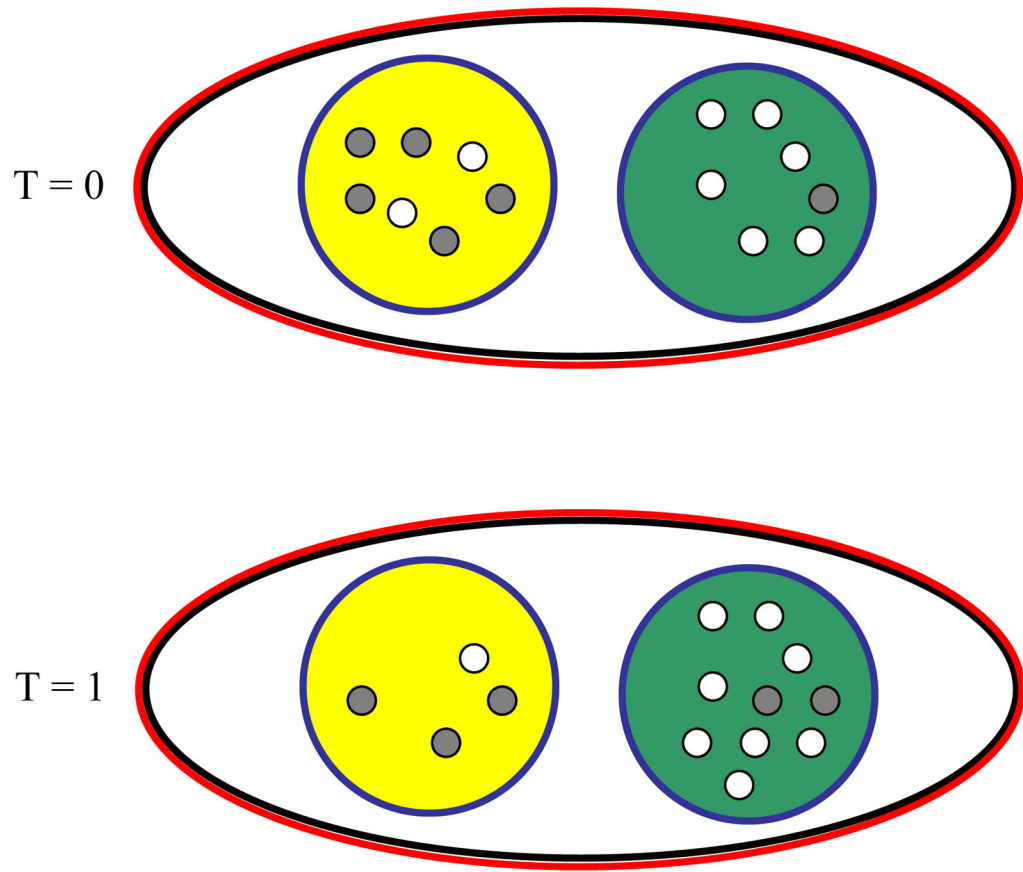
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Figure 1b



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Figure 1c

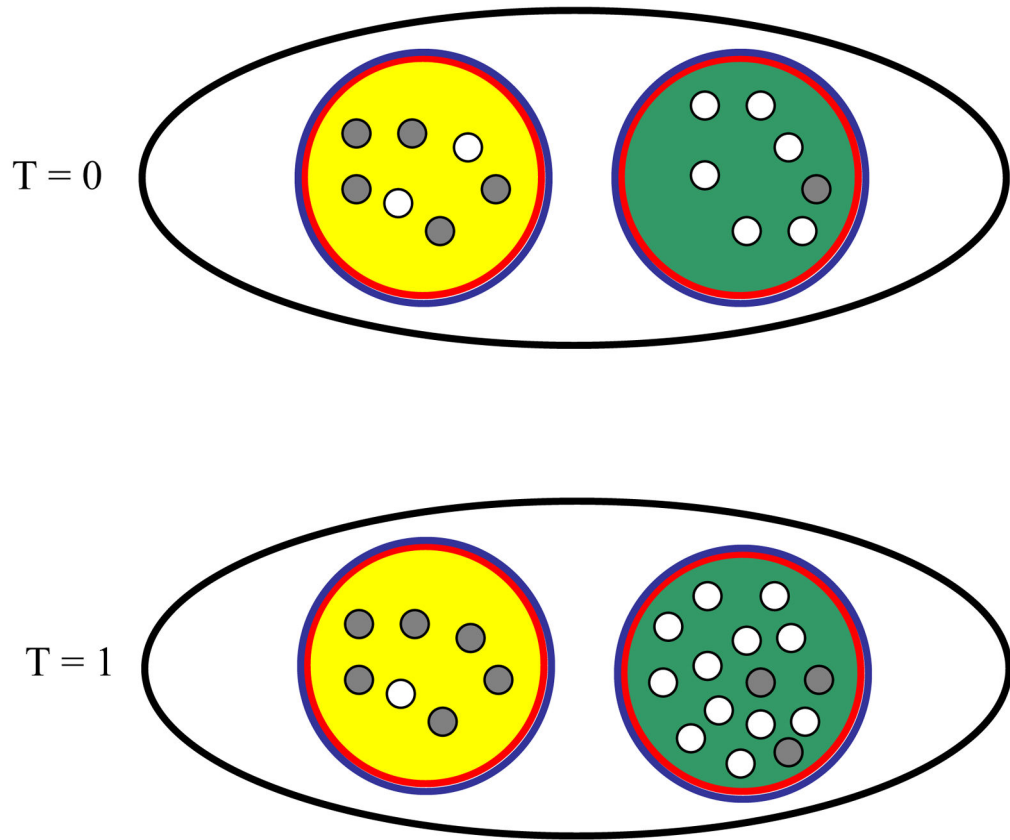
**Figure 1.**

Illustration of how local density dependence (a), global density dependence (b), and local carrying capacity elasticity (c) influence the evolution of a cooperative trait. In each, the black line demarks the population while the blue and red lines indicate the scale of cooperation and density dependence, respectively. Gray dots represent non-cooperative individuals while open dots represent cooperative individuals. In all cases, the green group has a higher initial ($T = 0$) frequency of cooperative individuals than does the yellow group. For each ecological scenario we then show the composition of both groups after cooperation and reproduction, but before the progeny disperse ($T = 1$).

Figure 1a. Cooperative traits are unlikely to spread when local density dependence occurs at the same scale as cooperative benefits if the cooperative behavior does not increase the locally carrying capacity. In this example, the local carrying capacity is fixed at seven individuals for each group and for simplicity each group is assumed to stay at this carrying capacity. After cooperation and reproduction, the frequency of cooperative individuals decreases within both groups due to the cost associated with the cooperative behavior. Under these ecological conditions, local density dependence constrains group productivity such that cooperative groups do not contribute more to the next generation, preventing the spread of cooperative individuals in the global population.

Figure 1b Global density dependence facilitates the spread of cooperative traits by allowing cooperative groups to contribute more to the next generation. In this example, the scale of

density dependence is more global than the scale of cooperation. For simplicity, the global carrying capacity is fixed in this example. Under these conditions, cooperative individuals once again decline in frequency within both interaction groups; however their frequency increases globally because the group with more cooperative individuals contributes more to the next generation. The more cooperative group is shown larger at $T = 1$ than $T = 0$. It might not remain this way as the additional individuals can subsequently disperse away. Conditions that facilitate the potential of a cooperative interaction group exporting the benefits of cooperation (e.g. empty sites³³ and kin-structured dispersal⁵⁵) help facilitate the evolution of cooperation.

Figure 1c. Cooperative traits that increase local carrying capacity are able to spread under local density dependence. When a cooperative trait increases the local carrying capacity, cooperative groups contribute more to the next generation thereby facilitating the spread of cooperative traits. As before, the frequency of cooperators declines within both groups due to the costs of cooperation. Though differing in the scale of density dependence, this case is similar to that of Figure 1b in that both depend on elasticity of group productivity resulting from cooperation. Likewise, increased local population size in response to the cooperative behavior also facilitates the evolution of cooperation under global density dependence (Figure 1b and 1c).

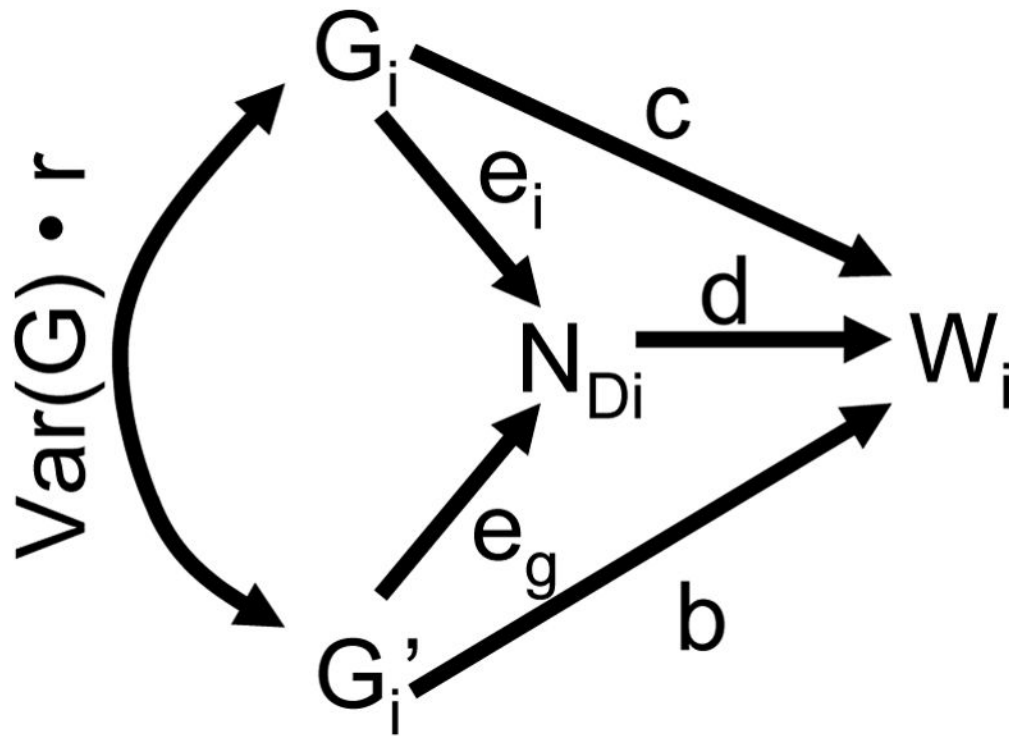


Figure 2. Path diagram of factors influencing individual fitness for a cooperative trait that influences population growth or decline. This yields a modified version of Hamilton's rule that includes the direct and indirect fitness consequences of the cooperative trait (c and $b \cdot r$, respectively) as well as the direct and indirect effects of the trait's impact on pre-dispersal population size ($d \cdot e_i$ and $d \cdot e_g \cdot r$, respectively).

Table 1

Some factors promoting the evolution of cooperation in viscous populations

Factor	Increases cooperative benefits	Restricts relative scale of competition	Increases relatedness	Examples
Population elasticity ^{34, 35, 77}	✓	✓		Social insects ⁷⁸ Cooperatively breeding beetles ⁷⁹ Beaver dam construction ⁸⁰ AM Fungi ⁵³ <i>Myxococcus</i> cooperative predation ⁴⁵ <i>Agrobacterium</i> opine catabolism ⁴⁷ <i>Rhizobium</i> rhizopine catabolism ⁴⁸ <i>Pseudomonas</i> siderophore production ²⁹
Empty sites ³³	✓	✓		
Global density dependence ^{7, 29}	✓	✓		
Kin recognition ³⁰		✓	✓	<i>Agrobacterium</i> opine catabolism ⁴⁷ <i>Rhizobium</i> rhizopine catabolism ⁴⁸ Social insect colony discrimination ⁴
Kin-structured dispersal ^{55, 56}			✓	Colony fission or budding of social insects ⁶⁰ Bacterial biofilm dispersal ⁶²