THEORY FOR THE EVOLUTION OF DIFFUSIBLE EXTERNAL GOODS

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Organisms from prokaryotes to plants and animals make costly investments in diffusible beneficial external products. While the costs of producing such products are born only by the producer, the benefits may be distributed more widely. How are external goods-producing populations stabilized against invasion by nonproducing variants that receive the benefits without paying the cost? This question parallels the classic question of altruism, but because external goods production need not be altruistic per se, a broader range of conditions may lead to the maintenance of these traits. We start from the physics of diffusion to develop an expression for the conditions that favor the production of diffusible external goods. Important variables in determining the evolutionary outcome include the diffusion coefficient of the good, the distance between individuals, and the uptake rate of the external good. These variables join the coefficient of relatedness and the cost/benefit ratio in an expanded form of Hamilton’s rule that includes both selfish and altruistic paths to the evolution of external goods strategies. This expanded framework can be applied to any external goods trait, and is a useful heuristic even when it is difficult to quantify the fitness consequences of producing the good.

KEYWORDS: Competition, models, population structure, public goods, selection—group/kin, sociality.

Organisms can often benefit from producing costly mobile extra-organisinal products, or external goods. In multicellular organisms, benefits include decreased herbivory (jasmonic acid signaling in plants; Dicke et al. 1999), or strength in numbers in overcoming prey defense (pheromone production in bark beetles; Pureswaran et al. 2006). In addition, diffusible extracellular secondary metabolites are increasingly recognized as playing a central role in microbial evolution and ecology. For example, in bacteria, benefits may arise through decreased intra- or inter-specific competition via bacteriocins (Riley and Gordon 1999) and phenazines (Pierson and Pierson 1996) or through increased access to limiting iron via siderophores (Griffin et al. 2004).

The fact that evolution often favors external goods production may appear counterintuitive, because populations of goods producers could be invaded by a nonproducing (and thus, cost-avoiding) variant that benefits from the investment of others while itself avoiding the cost. This problem closely parallels the classic problem of altruism, in which a trait imposes a fitness cost upon a carrier but benefits others. Indeed, external goods production may sometimes be altruistic; however, an organism excreting a beneficial external product may actually be obtaining a net direct fitness benefit. The evolution of external goods traits is thus a broader phenomenon than the evolution of altruism, and encompasses both altruistic and nonaltruistic traits.

A general theory for evolution of mobile external goods is needed because these traits are not necessarily altruistic, or may be altruistic only under some conditions. There has been an unjustified tendency to equate external goods traits with altruism (e.g., Griffin et al. 2004). In fact, a trait that is not altruistic in nature may become altruistic in a novel (laboratory) environment that increases sharing among individuals. For example, much recent
research has focused on apparently altruistic public goods traits in bacterial populations (Griffith et al. 2004; Harrison and Buckling 2005; Kummerli et al. 2009a). The use of dense, well-mixed liquid cultures in laboratories necessarily prevents the localization of beneficial metabolites that may naturally occur in populations growing in extracellular polymer matrix (Stewart 2003; Stewart and Franklin 2008), which is presumably the environment of adaptation (Costerton et al. 1994). In this case, changing the physical setting could make an individually selected, selfish trait altruistic because the external product is quickly lost from the local microenvironment of the producer. This can lead to a fundamental misunderstanding of the selective forces favoring the trait in question.

Recently, researchers have recognized that the mobility of external goods must be taken into account when interpreting results of experiments in microbial systems (Kummerli et al. 2009b; Le Gac and Doebeli 2009). To explain and predict the evolution of external goods production, a general theory of external goods is needed. Furthermore, a theory based on physically meaningful parameters (e.g., diffusion coefficient, distance between individuals) will facilitate empirical tests of the predictions of social evolution theory, particularly in microbial systems.

A Mathematical Model of Diffusible External Goods

What social and physical conditions positively select for external goods traits? To answer this question, we develop a direct fitness model that predicts the absolute fitness payoffs of two phenotypes, one that produces external goods (X) and one that does not (Y). The average payoff of each variant is a function of the costs and benefits to the production and uptake of a unit of external goods, respectively, as well as the local equilibrium concentration of the external good experienced by each variant on average. While we formulate expressions for the mean neighbor-modulated direct fitness benefits to each strategy, this approach naturally parallels the inclusive fitness approach (Taylor et al. 2007).

The concentration of an external good (G) at a location will change due to external goods production (a) and consumption (u), as well as diffusion. According to Fick’s Law, the total flux due to diffusion is a function of the area for diffusion A, the diffusion coefficient of the external good (D), and the gradient in external goods concentration between that location and a neighboring location, ∇G = (G_{location 1} - G_{location 2})/L where L is the distance between locations. We consider two “types” of microenvironment representing the microenvironments of external goods producers (i), and nonproducers (j). On average, these two types of microenvironments will be either a net source (i), or a net sink (j) of the external good. The gradient in concentration (∇G), and thus the flux between any two microenvironments of the same type, will be 0 and can be ignored. In general, the change in G at a given location is given by

\[
\frac{dG}{dt} = a - uG + AD\nabla G.
\]  

(1)

External goods concentration at any location is in a dynamic equilibrium when production (a), consumption (u), and diffusive flux (AD\nabla G) balance:

\[
0 = a - uG - AD\nabla G.
\]

(2)

Because the producer individual at a location i is both producing (a > 0) and consuming (u > 0) the product, the equilibrium condition here is

\[
a_i = uG_i + AD\nabla G_i.
\]

(3)

However, a nonproducer at j is only consuming (a = 0; u > 0) the product as it diffuses in from its environment, so the equilibrium condition at j is

\[
uG_j = -AD\nabla G_j.
\]

(4)

These two types of locations correspond to those that are net sources (eq. 3), and those that are net sinks (eq. 4). The gain by diffusion to the average sink j is a function of the local frequency (q) of sources i among neighboring microenvironments. From the perspective of a focal nonproducer Y at a location j, the area of diffusion (A) depends on the frequency of producer (X) individuals among the neighbors of the nonproducing (Y) individual:

\[
A = q_X Y.
\]

(5)

(Note that, from the “perspective” of a focal producer individual X at a sink location i, A = q_Y X.) The connection to other social evolution models can be clarified by rewriting the balance equations (3) and (4) such that we express the diffusion area A in terms of phenotypic similarity of a focal individuals to their neighbors. To quantify the phenotypic similarity of a focal individual to their neighbors, we use the relatedness coefficient r, representing the regression coefficient between the trait values of focal individuals and their neighbors (Hamilton 1970, 1972). While the term “relatedness” is often considered to reflect common descent, we stress that it is more generally a measure of similarity among interactants within the population (for recent discussions, see Pepper 2000; Fletcher et al. 2006). When only two trait values exist in a population for a given trait, the regression coefficient for the relatedness between individuals and their spatial neighbors is equivalent to the “subjective difference” formula. This formula represents the difference between type Y and type X individuals in the frequency of type X among their neighbors: r = q_{XY} - q_{YX}, where q_{XY} is the frequency of type X individuals among the neighbors of an
average type $Y$ individual (Wilson 1977; Pepper 2000). Using this formula for $r$, we obtain

$$A = q_X Y = q_X (1 - r).$$

(6)

Where $q_X Y$ is the local frequency of type $X$ among neighbors of type $Y$ individuals, and $q_X$ is the global frequency of $X$. We can now rewrite equation (4) for sink locations by substituting $q_X (1 - r)$ for $A$, yielding

$$uG_j = q_X (1 - r) D \nabla G_j.$$  

(7)

Or, equivalently

$$uG_j = q_X (1 - r) D \left( \frac{G_i - G_j}{L} \right).$$  

(8)

In order to rewrite equation (4) in terms of relatedness, it is convenient to define

$$\chi = \frac{D q_X (1 - r)}{L}.$$  

(9)

With this substitution into equation (8), the equilibrium concentration of the external good at sink locations is

$$G_j = G_i \left( \frac{\chi}{\chi + u} \right).$$  

(10)

The balance condition for $G$ at $i$ can be found by substituting the right-hand side of equation (6) for $A$ into equation (3) to give an expanded form of the balance equation:

$$a_i = uG_i + q_Y (1 - r) D \left( \frac{G_j - G_i}{L} \right).$$  

(11)

Substituting the right-hand side of equation (9) for $G_i$ and rearranging yields the equilibrium value of $G_i$:

$$G_i = \frac{a_i (\chi + u)}{u + b (1 - r) / L}.$$  

(12)

For a given spatial segregation of producers from nonproducers (quantified by $r$), the rate at which the external good will be transferred from source to sink locations is proportional to the diffusion coefficient $D$ divided by the distance between individuals $L$. We label the ratio of these two quantities as the “transfer coefficient” ($D/L$). The equilibrium concentration of the external good at source and sink location is shown graphically in Figure 1.

The source and sink locations depicted in Figure 1 correspond to the microenvironments of producer ($X$) and nonproducer ($Y$) individuals respectively. To calculate the fitness effects of these external good concentrations, we can weight the external goods concentration ($G$) by the uptake rate $u$ and the fitness benefit $b$ per unit taken up. The fitness effect on a nonproducer $Y$ is

$$w_Y = ubG_j.$$  

(13)

When we also include the cost of external goods production $ca_i$, born only by producers, the net fitness effect for producers is

$$w_X = ubG_i - ca_i.$$  

(14)

The fitness payoff for each strategy is shown in Figure 2. For sufficiently low transfer coefficients (see eq. 16 below), the fitness payoff for producers is always greater than for nonproducers, regardless of $r$, although high $r$ increases this difference.

The conditions favoring producers over nonproducers can be found by setting $w_X > w_Y$ using equations (12) and (13). This
EVOLUTION

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moting sharing. To quantify these conditions, we set absolute segregation of producers from nonproducers (spatial structure also increases, approaching the limit of requiring all external goods as “private,” rather than on others, are decisive, such external products are in an important sense “private,” rather than public. In contrast, when the transfer coefficient exceeds the threshold of low relatedness to neighbors (see leftmost region of Fig. 3). Because of diffusion-limited transfer and spatial structure, producers enjoy greater access to the external product than do nonproducers (Fig. 1). This results in higher fitness payoffs for producers than nonproducers when relatedness to neighbors is sufficiently high, and transfer sufficiently low (Fig. 2). When transfer among individuals is too limited for neighbor-modulated fitness benefits to be important (due to high uptake rates and low transfer rates), then production can be favored regardless of low relatedness to neighbors (see leftmost region of Fig. 3 and eq. 16).

Despite common use of the term among biologists, labeling all external goods as “public” is potentially misleading. In game theory models of “public goods,” it is assumed that the goods are shared equally among all interacting individuals potentially capable of producing them. In contrast, the external products called “public goods” in biology are generally not distributed equally. In particular, products that are transferred from producers to nonproducers by diffusion are subject to limited sharing, as limited by diffusion rate (D) and distance (L). Depending on the transfer coefficient (D/L), external goods in biology actually fall on a continuum from private to public. Under low transfer coefficients, external goods are available mostly to their producers only, and thus are relatively “private.” Only under high transfer coefficients do external goods approach the game theoretic assumption of equal sharing. In particular, under the conditions defined by equation (16), neighbor-modulated fitness effects are not required for goods production to be favored. Under these conditions, sharing of goods among neighbors can still increase the fitness advantage of producers over nonproducers, so that relatedness still plays a role. However, because fitness effects of production on producers themselves, rather than on others, are decisive, such external goods are in an important sense “private,” rather than public. In contrast, when the transfer coefficient exceeds the threshold of equation (16), selection for production of external goods requires

\[
D/L \leq u \left( \frac{b}{c} - 1 \right).
\]  

Discussion

Here we present the first general quantitative theory to predict when selection will favor the costly production of beneficial diffusible external products. The key variables determining whether such traits are favored include the cost of producing and benefit of taking up the external product, as well as its uptake rate, the potential for its transfer between individuals, and the coefficient of relatedness, or similarity between neighboring individuals (eq. 15, Fig. 3). Because of diffusion-limited transfer and spatial structure, producers enjoy greater access to the external product than do nonproducers (Fig. 1). This results in higher fitness payoffs for producers than nonproducers when relatedness to neighbors is sufficiently high, and transfer sufficiently low (Fig. 2). When transfer among individuals is too limited for neighbor-modulated fitness benefits to be important (due to high uptake rates and low transfer rates), then production can be favored regardless of low relatedness to neighbors (see leftmost region of Fig. 3 and eq. 16).

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ubG_i - ca_i > ubG_j,
\]

or equivalently,

\[
ub(G_i - G_j) > ca_i.
\]  

(14)

Whether or not a trait for investment in external products is favored depends on the average difference in access enjoyed by producers, weighted by the uptake and benefit of the product. This advantage due to increased access must outweigh the costs of production. Substituting the equations for steady state concentrations of $G$ at $j$ and $i$ from equations (9) and (11) into equation (14), and solving for $r$, we arrive at our goal of a general condition for the evolution of external goods production:

\[
r > 1 - \frac{ul}{D} \left( \frac{b}{c} - 1 \right).
\]  

(15)

Note that the global frequencies of each type are absent in this inequality, so it is frequency-independent. Figure 3 shows equation (15) graphically.

As the transfer coefficient (D/L) increases, the importance of spatial structure also increases, approaching the limit of requiring absolute segregation of producers from nonproducers ($r = 1.0$). For sufficiently low values of the transfer coefficient, positive relatedness is not required to favor the production of costly external goods. In the leftmost region of Figure 3, production is favored through direct fitness effects on producers, because increased access to the external product by producers is beneficial enough to more than offset the cost of production. The region for such “private” external goods production (to the left of the x-intercept of each curve in Fig. 3) shrinks as uptake rate $u$ decreases, promoting sharing. To quantify these conditions, we set $r \leq 0$, and solve equation (15) for $(D/L)$, which yields an expression for the conditions under which external goods production is favored, regardless of spatial structure ($r$):

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(16)
sharing of the good among sufficiently similar neighbors, so that
the external product is truly “public” in an important sense.

Whenever the transfer coefficient is above zero, the evolu-
tion of biological external goods shares with game-theoretical
public goods the potential for a “tragedy of the commons,” where
potential benefits to groups or populations are not obtainable be-
cause natural selection within groups favors nonproducers over
producers, despite the group-level advantage of goods production
(Hardin 1968). This outcome is expected when relatedness is not
high enough to prevent the invasion of free-riding nonproducers.
In the limit of an extremely high transfer coefficient, production
is only favored when similarity to neighbors is absolute ($r = 1$;
see right side of Fig. 3).

Our general model reveals two basic modes for external
goods production to be evolutionarily favored: In one mode, ex-
ternal goods can be more private when transferability is low. Their
production is then favored by fitness benefits due to production by
self only. For example, private external goods production may be
maintained in sparse populations with high $L$ (e.g., in a nonbloom
population of planktonic algae), or by reduced diffusion (e.g.,
in biofilms with extracellular matrix that reduces $D$). In the other
mode, external goods are more public when transferability is high.
Their production is then favored by neighbor-modulated fitness
benefits, which requires high similarity to neighbors (high $r$). Only
in this latter case of truly public goods is there potential for inva-
sion by “free-rider” nonproducers (when $r$ is not high enough).

Fletcher and Doebeli (2009) have emphasized the impor-
tance of the average “interaction environment” experienced by
cooparators and defectors in a classic public goods game. In this
framework, the interaction environment is the same for all mem-
bers of a group, and defectors necessarily have an advantage, as
long as $c > 0$. In our framework, because the interaction envi-
enronment is further partitioned into microenvironments that may
differ between individuals within a group, this is not necessarily
the case. In particular, our equation (14) parallels equation (2.1)
in Fletcher and Doebeli (2009), in that the cost to investing in
an external good must be offset by the increase in environmental
quality experienced by a focal individual. In both models, the con-
ditions favoring investment in the external good may be satisfied
by benefits due to self (low $D/L$ in our model) or by high $r$. In our
equation (14), both of these possibilities can lead to a large value
of $G_i - G_j$; in Fletcher and Doebeli (2009), benefits due to self
and others are split into separate terms.

In practice, some cases of external goods production will
involve intermediate levels of transfer, such that fitness effects
due to self as well as neighbors play a role in their evolution,
and they are neither purely private nor public. As a specific ex-
ample, biofilm extracellular matrix (ECM) may favor the produc-
tion of beneficial external products through both modes discussed
above. By reducing the transfer coefficient, ECM may increase
the benefits to self of production, and stabilize production against
invasion by nonproducers. At the same time, by reducing cell
movement and mixing, ECM also increases relatedness to neigh-
bors, which increases the neighbor-modulated benefits of external
goods production.

Conclusions

The conditions favoring production of beneficial external prod-
ucts cannot be predicted solely on the basis of their fitness effects
on self. At the same time, they do not always meet the criterion for
being biologically altruistic: imposing a net fitness cost on the pro-
ducer. Here we present the first quantitative theory for predicting
their evolution. This model is only precisely suited to the analysis
of diffusible external products, and some external goods are trans-
ferred by mechanisms other than other than diffusion (e.g., the
plant and animal signals mentioned in our Introduction may be
carried by air currents). However, in all cases of beneficial exter-
nal products, many of the same considerations will be germane:
It is important to recognize the continuum from private to public
external goods. Benefits to self can be enhanced by limited trans-
fer and product localization, while neighbor-modulated benefits
are enhanced by high relatedness of producers to recipients.

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