Habitat saturation and the spatial evolutionary ecology of altruism

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Abstract

Under which ecological conditions should individuals help their neighbours? We investigate the effect of habitat saturation on the evolution of helping behaviours in a spatially structured population. We combine the formalisms of population genetics and spatial moment equations to tease out the effects of various physiological (direct benefits and costs of helping) and ecological parameters (such as the density of empty sites) on the selection gradient on helping. Our analysis highlights the crucial importance of demography for the evolution of helping behaviours. It shows that habitat saturation can have contrasting effects, depending on the form of competition (direct vs. indirect competition) and on the conditionality of helping. In our attempt to bridge the gap between spatial ecology and population genetics, we derive an expression for relatedness that takes into account both habitat saturation and the spatial structure of genetic variation. This analysis helps clarify discrepancies in the results obtained by previous theoretical studies. It also provides a theoretical framework taking into account the interplay between demography and kin selection, in which new biological questions can be explored.

Introduction

The evolutionary puzzle of the origin and maintenance of costly helping behaviours has attracted much interest over the years. In well-mixed populations, in which individuals disperse at long distances or at high rates, helping should be counter-selected because individuals that exploit helpers without paying the cost would always be better off. However, in populations with limited dispersal (viscous populations), clustering leads to a high degree of interactions between helping individuals, so that helping may be favoured because of the additional benefits reaped by helpers. As Hamilton (1964) realized early on, this mechanism falls under the scope of kin selection theory as population viscosity will lead to high values of relatedness between interacting individuals. If reproduction is local, a focal individual will tend to bear the same trait as its neighbours, and thus indiscriminate helping may evolve as individuals helping neighbours will tend to help related individuals, thereby increasing the fixation probability of the helping trait.

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However, Hamilton (1964) also realized that population viscosity may have a double-edged effect on the selective pressures on helping, because population viscosity increases competition between relatives at the same time that it increases relatedness (West *et al.*, 2002). In some circumstances, those two forces may cancel each other (Taylor, 1992a; Wilson *et al.*, 1992), and the resulting selective pressure on helping takes the same form as in a well-mixed population.

Yet, the fate of helping individuals may not be as bleak as predicted by Taylor's (1992a) island model, and it is now well understood that indiscriminate helping can still evolve in a viscous population through a variety of ecological mechanisms (Lehmann & Keller, 2006; Lehmann, 2007; Lion & van Baalen, 2008). In particular, population elasticity (Grafen, 1984; Taylor, 1992b; West *et al.*, 2002) has attracted much attention, as it can allow helping individuals to export the overproduction of offspring to nearby locations, thereby decreasing the negative impact of local competition. In order to predict accurately the direction of selection on helping, we need a modelling approach accounting for the impact of population structure and demography on the selective pressures on helping behaviours.

A striking feature of most models for the evolution of helping in spatially structured populations is that they

tend to rely on simplifying assumptions regarding demography, so that population size remains constant. For example, most population genetics models of kin selection assume, in the wake of Wright's (1931) island model, that space consists in a large number of demes with fixed and equal numbers of individuals (Hamilton, 1975; Taylor, 1988; Frank, 1998; Rousset, 2004). More recently, models in evolutionary graph theory (Lieberman *et al.*, 2005; Ohtsuki *et al.*, 2006) have been introduced. These models are a limiting case of the deme-structured models in which deme size is fixed to one individual (Lehmann *et al.*, 2007; Taylor *et al.*, 2007a). Although the assumption of constant population size is usually made for mathematical convenience, it has important biological consequences. The main consequence of the assumption of constant population size is that population elasticity is zero, which may preclude the evolution of helping (Taylor, 1992a; West *et al.*, 2002; Taylor *et al.*, 2007a; Lion & van Baalen, 2008). Relaxing these simplifying assumptions is feasible (Metz & Gyllenberg, 2001; Rousset & Ronce, 2004; Lehmann *et al.*, 2006; Alizon & Taylor, 2008) but complexifies the analysis and requires numerical simulations.

An alternative approach has been followed by several authors to explore the impact of demography on the evolution of helping (Matsuda *et al.*, 1992; van Baalen & Rand, 1998; Le Galliard *et al.*, 2003, 2005; Lion & van Baalen, 2007). In those spatial demographic models, reproduction is density dependent and depends on the availability of empty sites in the neighbourhood of an individual. An unfortunate consequence of making reproduction conditional to the availability of empty sites is that most of the symmetry properties of models with constant population size are lost. The increased complexity makes it more difficult to obtain closed analytical results, so that these models typically yield an infinite hierarchy of spatial moments for which no exact solution is known. In other words, the cost of taking into account both spatial and evolutionary ecology in the same model is the use of some approximate descriptions of the spatial structure in order to close the system (Matsuda *et al.*, 1992; van Baalen & Rand, 1998; van Baalen, 2000). Yet, we think this approximate treatment may be worth pursuing as it helps to reveal qualitative processes which may be overlooked under simplified demographic scenarios.

We extend the analysis of spatial demographic models in two novel directions. First, we provide a link with population genetics models. We extend previous analyses of demographic models (van Baalen & Rand, 1998) by relaxing the assumption of mutant rarity, and deriving an expression for the change in frequency of helping individuals. We show that the expression for inclusive fitness takes the form of Hamilton's rule, and that the expression for relatedness is similar to classical measures of relatedness based on identity in state (Rousset & Billiard, 2000). We then demonstrate that additional assumptions on spatial structure can be made to obtain a closed expression for inclusive fitness. We show that, when the costs and benefits of helping both affect fecundity, the threshold for the evolution of helping depends on nearest-neighbour relatedness and network connectivity. Second, we develop a more general demographic model in which reproduction can be competitive (i.e. individuals can be replaced by the offspring of their neighbours). We show that, in the limiting case of high habitat saturation, the selective pressures on helping collapse to those analysed in two recent models with constant population size (Ohtsuki *et al.*, 2006; Taylor *et al.*, 2007a), but that the effects of habitat saturation on the evolution of helping are strongly dependent on the form of competition. Our analysis stresses the importance of taking into account population demography when investigating the selective pressures on helping behaviours.

Demographic model

We consider a model introduced by van Baalen & Rand (1998) in which individuals can reproduce, die or move at rates depending on their environment. Space is represented as an (infinite) network of sites. Each site can be empty (*o*) or occupied by one individual. Each site is connected to *n* other sites (the network is thus regular). An inverse measure of network connectivity is given by $\phi = 1/n$. We shall also use the notation $\bar{\phi} = 1 - \phi = (n-1)/n$ for the sake of simplicity (see Table 1 for notations).

We start with the simplest case of a monomorphic population. We assume that an individual at site *x* can either die at rate d_x, move to an empty neighbouring site at rate m_x or reproduce into an empty neighbouring site at rate b_x. Reproduction (and mobility) is therefore density dependent. These rates need not be constant but may depend upon the structure of the neighbourhood, hence the dependence on *x*.

The expected dynamics of the global density $p_\times$ of occupied sites ($\times$) is (Appendix A)

$$\frac{dp_\times}{dt} = (bq_{o/\times} - d)p_\times \qquad (1)$$

where $q_{o/\times}$ is the local density of empty sites experienced by an average individual, and *b* and *d* are the expected birth and death rates respectively. Note that the mobility rate *m* does not appear in this equation, because mobility events do not change the number of individuals. Equation 1 is a spatial version of the classical logistic dynamics. The birth–death–mobility process we define is a variant of the well-known contact process (Harris, 1974), in which individuals can move, and the birth and death rates depend on the local environment. Note that there is a critical birth–death ratio below which the population goes to extinction (Appendix A).

Importantly, eqn 1 depends on the expected dynamics of higher-order spatial moments, such as $q_{o/\times}$. In turn, the dynamics of $q_{o/\times}$ will depend on triple local densities

Table 1 Notations and description of the model.

Type	Symbol	Expression	Description
Space	n		Number of nearest neighbours
	ϕ	$1/n$	
	$\bar{\phi}$	$1 - \phi$	
Demography	o		Empty site
	$\times$		Occupied site
	b		Background birth rate
	d		Background death rate
	m		Mobility rate
Helping	ϵ		Investment into helping
	$B(\epsilon)$		Fecundity benefit of helping
	$C(\epsilon)$		Fecundity cost of helping
Densities	p_i		Global density of type i
	p_{ij}		Global density of pairs of connected sites ij
	p_{ijk}		Global density of triples of connected sites ijk
	$q_{i/j}$		Local density of type i experienced by type j
	$q_{i/jk}$		Local density of type i experienced by a j individual in a jk pair
Frequencies	f_i	$p_i/p_{\times}$	Frequency of individuals of type i
	f_{ij}	$p_{ij}/p_{\times\times}$	Frequency of ij pairs of occupied sites
Pair dynamics	α_i	$\bar{\phi}\,(b_i + m_i)$	
	β_i	$\phi b_i + \alpha_i q_{i/oi}$	Rate of transition $io \rightarrow ii$
	δ_{io}	$\delta_i + \bar{\phi} m_i q_{o/io}$	Rate of transition $io \rightarrow oo$
	δ_{ij}	$\delta_i + \bar{\phi} m_i q_{o/ij}$	Rate of transition $ji \rightarrow jo$

$q_{i/jk}$, that give the expected density of sites in state i experienced by a site in state j connected to a site in state k, and likewise, the dynamics of $q_{i/jk}$ will depend on higher order moments.

Evolution of helping under competition for empty sites

Change in phenotypic frequency

We now assume that the population may be polymorphic, and consists of two types of individuals: R (selfish phenotype) and M (helper phenotype). Let $f_M = p_M/(p_R + p_M)$ be the frequency of the helper phenotype in the population. The change in phenotypic frequency is given by

$$\frac{\mathrm{d}f_M}{\mathrm{d}t} = f_M(1 - f_M)(\lambda_M - \lambda_R) \qquad (2)$$

where λ_M (respectively λ_R) is the per capita growth rate of M (respectively R) individuals. From eqn 1, we know that $\lambda_i = b_i q_{o/i} - d_i$.

In order to incorporate the demographic effects of helping in our model, we consider that M individuals can increase a neighbour's fecundity but have to pay a fecundity cost. On the other hand, R individuals are selfish, and can receive a fecundity benefit from a helping neighbour without paying any cost. This is the life cycle

used by van Baalen & Rand (1998). Note that in this model, the survival of individuals is unaffected by the helping trait and, therefore, using the fact that $d_M = d_R = d$, eqn 2 can be rewritten as

$$\frac{\mathrm{d}f_M}{\mathrm{d}t} = f_M(1 - f_M)[b_M q_{o/M} - b_R q_{o/R}]. \qquad (3)$$

Let ϵ be the investment into helping of M individuals, $B(\epsilon)$ be the fecundity benefit of helping and $C(\epsilon)$ be the fecundity cost of helping. Having a helping neighbour will only increase the recipient's birth rate if the recipient has an empty site in its neighbourhood. This leads to the following expression for the average birth rate of a helping individual (van Baalen & Rand, 1998)

$$b_M = b + B(\epsilon)\bar{\phi}q_{M/Mo} - C(\epsilon) \qquad (4)$$

where b is the background birth rate and $\bar{\phi}q_{M/Mo}$ is the proportion of M individuals in the neighbourhood of an M individual that has an empty site in its neighbourhood. A selfish individual, on the other hand, does not pay the physiological cost of helping, and therefore

$$b_R = b + B(\epsilon)\bar{\phi}q_{M/Ro} \qquad (5)$$

Note that, in eqn 4, the physiological cost is paid in a density-independent manner, which means that helping is expressed even when there is no one to help (constitutive cost of helping). The consequences of making helping conditional will be addressed in the discussion.

Weak selection approximation

The above description of the change in frequency of helpers is exact but does not shed light on the conditions promoting the evolution of helping behaviours. In the following, we use a weak selection approximation to disentangle the different selective pressures on helping in our model. This approximation is classically used in population genetics model of kin selection (Rousset & Billiard, 2000; Rousset, 2004; Taylor *et al.*, 2007b) and amounts to assuming that mutations have small phenotypic effects.

Inclusive fitness effect
Assuming that selection is weak (ϵ is small), we can Taylor-expand eqn 3 around $\epsilon = 0$. Using the short-hand notation $\Delta \equiv (\partial/\partial\epsilon)|_{\epsilon=0}$ to simplify the writing, we obtain

$$\frac{\mathrm{d}f_M}{\mathrm{d}t} = f_M(1 - f_M)[q_{o/\times}\Delta(b_M - b_R) + b\Delta(q_{o/M} - q_{o/R})]\epsilon + o(\epsilon) \qquad (6)$$

This expression follows from the fact that $B(0) = C(0) = 0$ and that in the neutral model, individuals experience the same local density of empty sites than in the monomorphic population ($q_{o/M} = q_{o/R} = q_{o/\times}$ when $\epsilon = 0$). This equation is of the form

$$\frac{\mathrm{d}f_M}{\mathrm{d}t} = f_M(1 - f_M)\Delta W_{\mathrm{IF}}(f_M)\epsilon + o(\epsilon)$$

where, by definition, $\Delta W_{\mathrm{IF}}(f_M)$ refers to the inclusive fitness effect (Hamilton, 1964; Taylor & Frank, 1996; Rousset & Billiard, 2000; Rousset, 2004). In Appendix B, we show that the expression for the inclusive fitness effect in our model can be written as

$$\Delta W_{\mathrm{IF}} = \tilde{B}\tilde{r} - \tilde{C}, \qquad (7)$$

where

$$\tilde{B} = \bar{\phi}q_{o/\times\times}\Delta B \qquad (8)$$

$$\tilde{r} = \bar{q}_{M/M} - \bar{q}_{M/R} \qquad (9)$$

$$\tilde{C} = q_{o/\times}\Delta C - b\Delta(q_{o/M} - q_{o/R}) \qquad (10)$$

In these equations, $\bar{q}_{i/j}$ denotes the (equilibrium) value of $q_{i/j}$ in the neutral model, i.e. the model where R and M have the same trait value and $q_{o/\times}$ and $q_{o/\times\times}$ are the equilibrium densities for a monomorphic population. We thus recover a variant of Hamilton's rule,

$$\tilde{B}\tilde{r} > \tilde{C}, \qquad (11)$$

as the condition for the evolution of helping. In the following, we emphasize the validity of this formulation by showing that: (1) $\tilde{r}$ is indeed a measure of relatedness between nearest neighbours and (2) $\tilde{B}$ and $\tilde{C}$ have a clear biological meaning in terms of fitness benefits and costs of helping. Thus, we can use these quantities to characterize whether the helping behaviour can be referred to as altruism (Rousset, 2004, p. 114), that is a trait which carries fitness costs for the actor (i.e. $\tilde{C} > 0$) and fitness benefits for the recipient ($\tilde{B} > 0$).

Relatedness
The variable $\tilde{r} \equiv \bar{q}_{M/M} - \bar{q}_{M/R}$ measures the difference between the average local density of helping individuals experienced by a helping individual and the average local density of helping individuals experienced by a selfish individual. $\tilde{r}$ therefore measures the assortment of helping individuals, and is actually equal to what Wilson (1977) called the 'difference in subjective frequencies' (see also Kelly, 1992b), and what Wilson *et al.* (1992) interpreted as a measure of population viscosity (the V in their eqn 5).

A more enlightening interpretation of $\tilde{r}$ is obtained by decoupling the ecological variables (the *densities* of pairs and singlets) from the genetical variables (the *frequencies* of pairs and singlets). Let $f_{MM} = p_{MM}/p_{\times\times}$ be the frequency of MM pairs among all pairs $\times\times$ of occupied sites. Then, f_{MM} is a measure of identity in state between neighbouring individuals. Following the algebra in Appendix C, we show that $\tilde{r}$ can be rewritten as

$$\tilde{r} = q_{\times/\times}r = q_{\times/\times}\left(\frac{f_{MM} - f_M^2}{f_M - f_M^2}\right)$$

where $q_{\times/\times}$ is the local density of individuals experienced by an average individual.

In this form, we have effectively decoupled population demography (the $q_{\times/\times}$ factor) from a genetical measure (the bracketed term) that can be readily recognized as a measure of relatedness between neighbours (Rousset & Billiard, 2000). Indeed, the ratio $r = (f_{MM} - f_M^2)/(f_M - f_M^2)$ is a ratio between the covariance between donor and recipient states ($f_{MM} - f_M^2$) and the variance in the state of the actor ($f_M - f_M^2$) (Michod & Hamilton, 1980; Day & Taylor, 1998; Rousset & Billiard, 2000). The discounting factor $q_{\times/\times}$ accounts for the fact that individuals can be surrounded by empty sites at demographic equilibrium, and measures the probability of interacting with an other individual. In the remainder of this article, we will often use $\tilde{r}$ as a measure of relatedness and define it as the *effective relatedness*, but the reader should bear in mind that habitat saturation has opposite effects on r and $\tilde{r}$. In fact, $\tilde{r}$ is a decreasing function of the local density of empty sites, but genetic relatedness r is an increasing function (Lion, in press).

Note that if helping individuals are rare, $q_{M/R} \approx 0$ and relatedness is given by $q_{M/M}$ as found in invasion analyses (van Baalen & Rand, 1998; Le Galliard *et al.*, 2003; Lion & van Baalen, 2007). We recover the fact that for a *rare* mutant, relatedness is the probability that the recipient of helping is a mutant, given that the donor is a mutant (Day & Taylor, 1998).

As in population genetics models of subdivided populations, the assumption of weak selection (eqn 9) implies that relatedness needs to be computed in the neutral process. However, the usual method of deriving a recursion for probabilities of identity at different distances (Rousset, 2004) cannot be applied in a straightforward manner when reproduction takes place into empty sites, because relatedness between nearest neighbours depends on measures of identity in state that are function not only of the distance between individuals but also of the state (occupied or empty) of the sites between them (see Appendix C for the initial equation of such a recursion). An exact computation of relatedness is therefore currently beyond our reach, and its intricacies are discussed elsewhere (Lion, in preparation).

Fitness costs and benefits of helping
Having identified $\tilde{r}$ with a measure of relatedness between neighbours, we turn to the marginal benefits of helping $\tilde{B}$ (eqn 8). We see that the marginal increase in fecundity due to helping is weighted by a measure of habitat saturation. Indeed, $\bar{\phi}q_{o/\times\times}$ measures the density of empty sites around an individual who has at least one other individual in its neighbourhood. If the availability of empty space decreases (for instance, as a result of an increased background reproduction rate), so does the overall benefit of helping.

The marginal costs of helping $\tilde{C}$ have a more complicated form (eqn 10). The first term represents the marginal physiological cost of helping, weighted by a measure of habitat saturation $q_{o/\times}$. The second term $-$

$b\Delta(q_{o/M} - q_{o/R})$ measures the relative intensity of competition for space for helping and selfish individuals. We expect this quantity to be positive because, on average, individuals that help a neighbour to reproduce will have a lower number of empty sites in their neighbourhood than selfish individuals. Therefore, the positive term $-b\Delta(q_{o/M} - q_{o/R})$ can really be interpreted as the ecological cost of helping Lion & van Baalen, 2007, 2008).

Thus, if the physiological costs and benefits of altruism are both positive, the fitness benefits and costs of helping are also positive in our model. Any helping behaviour selected in our model can then be classified as altruistic, following a strict definition of altruism (Hamilton, 1964; Rousset, 2004; West *et al.*, 2007).

Moment closure approximations

Equation 7 is informative about the selective pressures that affect helping but allows little exploration. Indeed, we lack a closed expression for both relatedness and the ecological cost of helping because they depend on the local environments of helping and selfish individuals. In this section, we use spatial moment equations to derive the dynamics of pairs and triples of sites, and close the resulting system of equations using moment closure approximations (Matsuda *et al.*, 1992; Sato *et al.*, 1994; Rand, 1999; van Baalen, 2000).

Computing relatedness
In a first attempt to compute relatedness in the neutral model, we follow van Baalen & Rand (1998) and Le Galliard *et al.* (2003) and use ordinary pair approximation (PA). We show in Appendix C that

$$\tilde{r} \underset{\text{PA}}{=} \phi \frac{b}{b + \bar{\phi}m}$$

where $\underset{\text{PA}}{=}$ denotes a result valid only for PA, so that for low mobility $(m = 0)$ of individuals, we obtain

$$\tilde{r} \underset{\text{PA}}{=} \phi = \frac{1}{n} \qquad (12)$$

In our model, *under PA*, and in the limit of low mobility and low investment in helping, $r = 1$ over the connectivity of the network, i.e. a measure of population viscosity, as previously found by van Baalen & Rand (1998) and Le Galliard *et al.* (2003). This expression is expected to work well on random regular networks (regular networks in which sites are connected randomly; Hauert & Szabó, 2005; Szabó & Fáth, 2007) but not on two-dimensional lattice structures (e.g. square and triangular lattices). Indeed, the existence of short loops in those lattice structures is known to cause ordinary PA to break down (Sato *et al.*, 1994; Rand, 1999; van Baalen, 2000).
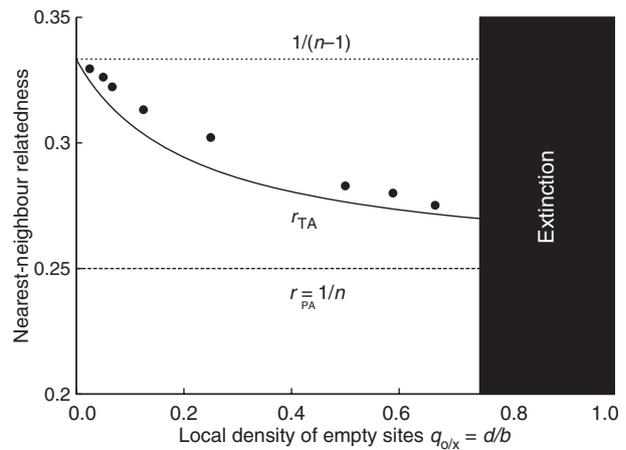

Fig. 1 Effective relatedness $\tilde{r} = q_{M/M} - q_{M/R}$ as a function of habitat saturation, computed from stochastic simulations of the neutral model on a random regular network (dots). The predictions of the pair approximation (PA) and of the triple approximation (TA) are shown. The dotted line indicates the maximal value $1/(n-1)$. The black region corresponds to population extinction (Appendix A). Network size: 10 000 sites. Parameters: $n = 4$, $d = 1$, $m = 0$.

Simulations of the neutral model on a regular random network revealed, however, that effective relatedness $\tilde{r}$ is an increasing function of habitat saturation (Fig. 1), in contrast to the prediction of PA. In particular, in the limit of high habitat saturation and low mobility, $\tilde{r}$ tends towards $1/(n-1)$ instead of $1/n$ as predicted by eqn 12. Thus, PA only yields a lower bound to the value of relatedness, even on a random regular network.

A better approximation for relatedness can be obtained by closing the system at the higher level of triples, which is discussed elsewhere (Lion, in press). The triple approximation of $\tilde{r}$, which is plotted in Fig. 1, closely matches the results of simulations. In particular, this higher order approximation of $\tilde{r}$ is an increasing function of habitat saturation (Appendix C; Lion, in press). Moreover, in the limit of high habitat saturation ($q_{o/x} = 0$), this expression tends towards $1/(n-1)$, which is the exact value in the neutral process on an infinite tree with no empty sites (L. Lehmann, personal communication; Lion, in press.)

Computing the ecological cost
In order to derive an expression for the ecological cost of altruism, $b\Delta(q_{o/M} - q_{o/R})$, we extend a method introduced by van Baalen & Rand (1998) (Appendix D). This method relies on an argument of separation of timescales: under weak selection, we show in Appendix D that the local densities are fast variables. This allows us to compute the per capita growth rates λ_R and λ_M as the dominant eigenvalues of two matrices, and yields a second expression for inclusive fitness.

In the limit of low mobility ($m = 0$), we obtain the following expression for the ecological cost of altruism (Appendix D)

$$b\Delta(q_{o/M} - q_{o/R}) = -\frac{\tilde{r}q_{o/\times}}{1 + q_{o/\times}}\Delta(b_M - b_R)$$
$$+ 2\bar{\phi}b\frac{q_{o/\times}}{1 + q_{o/\times}}\Delta(q_{o/oM} - q_{o/oR}).$$

We observe that the ecological cost can be split into two terms. The first term depends on the difference in fecundities of helping and selfish individuals, weighted by the effective relatedness with neighbours and the local density of empty sites. Hence, the ecological cost can also be interpreted as a form of kin competition.

The second term depends on $\Delta(q_{o/oM} - q_{o/oR})$ and measures the impact of altruism on the local density of empty sites at distance 2 from a reproducing individual, and thus may be interpreted as a second-order ecological cost. In order to close the system, we will neglect this second term in the following derivation. The rationale behind this simplification is that the impact of empty sites at distance 2 should be weaker than the effect of empty neighbouring sites. Using that approximation, the ecological cost becomes proportional to $\Delta(b_M - b_R)$. Together with eqn 6, this gives

$$\Delta W_{IF} = \frac{1 + q_{o/\times} - \tilde{r}}{1 + q_{o/\times}}q_{o/\times}\Delta(b_M - b_R) \quad (13)$$

which entails, following Appendix D, that inclusive fitness has the same sign as

$$\Delta(b_M - b_R) = \bar{\phi}\Delta B\tilde{r} - \Delta C$$

This yields a simpler Hamilton's rule than eqn 11

$$\bar{\phi}\Delta B\tilde{r} > \Delta C, \quad (14)$$

which depends only on the physiological costs and benefits of altruism. In order for altruism to evolve, the benefit-to-cost ratio $\Delta C/\Delta B$ must be below the threshold $1/(\bar{\phi}rq_{\times/\times})$ where r is the genetic relatedness between nearest neighbours in the neutral model and $q_{\times/\times}$ measures the probability of interacting with another individual. Figure 2a presents simulation results obtained by comparing the fixation probability U of a single altruistic mutant with the fixation probability U_0 of a single neutral mutant (Taylor *et al.*, 2007a). This figure shows that the condition $\bar{\phi}\Delta B\tilde{r} > \Delta C$ accurately predicts the invasion boundary of altruism for different levels of habitat saturation.

Equation 13 can also be used to understand the effects of several ecological factors on the *speed* of evolution (i.e. the intensity of selection). In particular, the factor $q_{o/\times}$
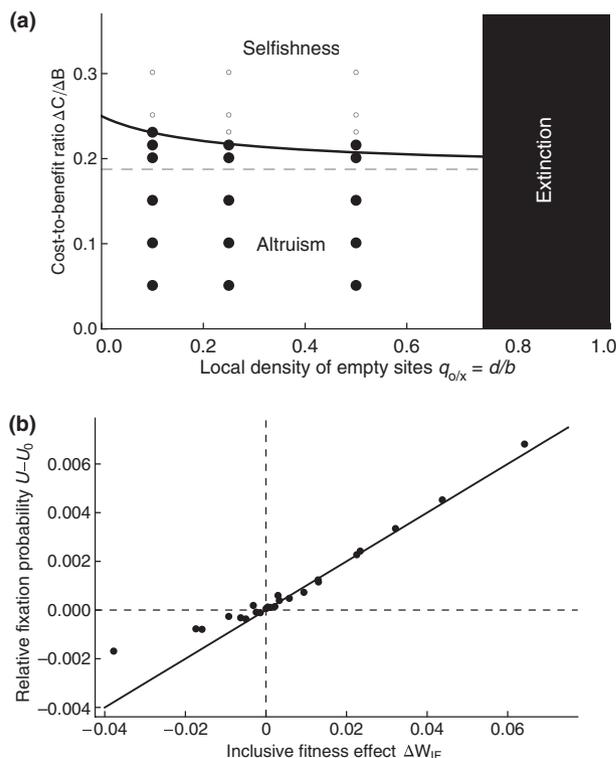

Fig. 2 Evolution of altruism under competition for empty sites. (a) Boundary for the evolution of altruism as predicted by the triple approximation, as a function of the local density of empty sites $q_{o/\times} = d/b$. When the cost-to-benefit ratio $\Delta C/\Delta B$ is below the curve, altruism is convergence stable ($\Delta W_{IF} > 0$). The black region corresponds to population extinction (Appendix A). In order to check the analytical predictions against the results of stochastic simulations (circles), we estimated the fixation probability U of a single altruistic mutant ($\epsilon = 0.1$) from $n_{run} = 10^6$ runs, for three levels of habitat saturation ($b = 10$, $b = 4$, $b = 2$) and increasing cost of altruism (between 0.05 and 0.3), on a random regular network with 900 sites. The 95% confidence interval for U was then computed as $U \pm \sqrt{U(1 - U)/n_{run}}$. The circle was coloured black if the neutral fixation probability U_0 was above the confidence interval (invasion), white if U_0 was below the confidence interval (no invasion). The neutral fixation probability U_0 was estimated from simulations, and is well approximated by $1/(Np_\times)$. (b) Relationship between the analytical expression of inclusive fitness ΔW_{IF} (eqn 13) and the difference $U - U_0$ between the fixation probability of a single altruistic mutant U and the neutral fixation probability estimated from stochastic simulations. The bold line is $\epsilon\Delta W_{IF}$ and accurately predicts the first-order effect of selection on the fixation probability of altruists (the slope of the relationship between ΔW_{IF} and $U - U_0$, when selection is weak). Parameters: $n = 4$, $d = 1$, $m = 0$, $\Delta B = 1$.

indicates that the intensity of selection vanishes in the limit of high habitat saturation ($b \to \infty$ or $d \to 0$). Because inclusive fitness gives the first-order effect of selection on the fixation probability (Rousset & Billiard, 2000; Taylor *et al.*, 2007b), we further expect that $U - U_0 = \epsilon\Delta W_{IF} + o(\epsilon)$. In Fig. 2b, we show that this simple

relationship holds true. Thus, eqn 13 yields an accurate prediction of both the invasion boundary and the intensity of selection on altruism.

Until now, we have assumed that mobility was negligible, but this raises the question of how mobility affects the selective pressures on altruism. For nonvanishing mobility rates, it is necessary to use PA (Matsuda *et al.*, 1992; van Baalen & Rand, 1998; van Baalen, 2000) to make progress. Under PA, we simply assume that $q_{i/jk} \approx q_{i/j}$. This allows us to show in Appendix D that the direction of selection on altruism is also given by $\bar{\phi}\Delta B\tilde{r} > \Delta C$. The only effect of mobility on the inclusive fitness effect is therefore to decrease relatedness.

Biological conclusions

The analysis of the evolution of helping when individuals compete for empty sites yields another version of Hamilton's rule (eqn 11). This condition can be used to understand why habitat saturation has a weak effect on the evolutionary outcome (Fig. 2). Although genetic relatedness (i.e. r) increases with the number of empty sites, the effective relatedness (i.e. $\tilde{r}$) decreases weakly with $q_{o/\times}$ (Fig. 1). This is because the positive effect of empty sites on genetic relatedness is overridden by the decrease in the number of neighbours.

Evolution of helping under direct competition between individuals

Until now we have assumed that individuals can reproduce into empty sites only (indirect competition). Let us now consider that reproducing individuals can also replace an individual in their neighbourhood (direct competition), where the competitive ability of juveniles to take over an occupied site (relative to an empty site) is measured by c. When $c = 0$, we recover the model we have just analysed, in which reproduction only occurs into empty sites. When $c = 1$, individuals do not make any difference between empty and occupied sites as far as reproduction is concerned. The resulting dynamics of the density of helping individuals then becomes

$$\frac{dp_M}{dt} = p_M[b_M q_{o/M} - d_M + cq_{R/M}(b_{MR} - b_{RM})] \quad (15)$$

where the additional term represents the change due to the replacement of a selfish neighbour by a helping individual (at rate b_{MR}), and to the replacement of a helping neighbour by a selfish individual (at rate b_{RM}). The rates of replacement b_{MR} and b_{RM} are spatial averages that depend on life cycle assumptions, and in particular on the type of competition. Different types of competition have been considered previously, and we shall focus on two processes introduced by Ohtsuki *et al.* (2006) that have

recently received some attention (Lehmann *et al.*, 2007; Taylor *et al.*, 2007a; Grafen & Archetti, 2008). In the 'death–birth' (DB) process, a random individual dies at a rate independent of investment into helping and the vacancy is immediately filled by an offspring whose mother is chosen randomly among the neighbours according to their relative fecundities (competition occurs *locally* between the neighbours of the empty site). In the 'birth–death' (BD) process, an individual is selected to reproduce according to its fecundity (competition occurs *globally*), and its offspring replaces a randomly chosen neighbour. Because the local rates at which those replacement events occur enter the equations in a nonlinear fashion, we will use a combination of weak selection and PA to get some qualitative insight about the evolution of helping in our direct competition model.

Invasion condition

It is feasible to derive an expression for the inclusive fitness effect when direct competition occurs ($c > 0$), but the resulting expression is very messy, and not particularly enlightening. For the sake of simplicity, we will therefore restrict our attention to the limiting case where the mutant is rare, and compute the invasion condition of rare helping individuals in a selfish population. The selection gradient (the first-order effect of selection on λ_M) takes the form

$$\Delta \lambda_M = q_{o/\times}\Delta b_M + b\Delta q_{o/M} + c\bar{q}_{R/M}\Delta(b_{MR} - b_{RM}) \quad (16)$$

In Appendix E, we derive an expression for $\Delta q_{o/M}$ using PA and show that the selection gradient can be put into the form

$$\Delta \lambda_M = (1 - T)q_{o/\times}\Delta b_M + (1 - q_{o/\times}T)c\bar{q}_{R/M}\Delta(b_{MR} - b_{RM}) \quad (17)$$

where $T = \phi/(1 + q_{o/\times} + \bar{\phi}cq_{R/M})$. In the limit $c = 0$, we recover the results of the previous section, and invasion fitness has the same sign as Δb_M. In the limit of high habitat saturation ($b \to \infty$ or $d \to 0$), $q_{o/\times} = 0$, and invasion fitness has the same sign as $\Delta(b_{MR} - b_{RM})$. Therefore, when habitat saturation is high, the selective pressures due to reproduction into empty sites vanish, and only the fitness effects of direct competition remain. The intensity of selection is then given by the factor $c\bar{q}_{R/M}$; thus under direct competition ($c > 0$), selection does not vanish in the limit of high habitat saturation, in contrast to the indirect competition model ($c = 0$).

The role of empty sites for DB and BD competition

In Appendix E (see online Supporting Information), we derive an expression for $b_{MR} - b_{RM}$ for both the DB and

BD processes using a combination of weak selection and PA. Interestingly, in the DB process, the selective pressure due to direct competition is the same as the selective pressure due to indirect competition; so, $\Delta(b_{MR} - b_{RM}) = \Delta b_M = \bar{\phi}\Delta B\tilde{r} - \Delta C$. In the BD process, however, there is an additional cost of helping when competition is direct, and $\Delta(b_{MR} - b_{RM}) = \bar{\phi}\Delta B\tilde{r} - \Delta C - \phi\Delta B$. Putting everything together, we find the following invasion conditions

$$(\text{DB}) \quad \bar{\phi}\,\Delta B\,\tilde{r} > \Delta C \tag{18}$$

$$(\text{BD}) \quad \bar{\phi}\,\Delta B\,\tilde{r} > \Delta C + \phi\,\Delta B\gamma \tag{19}$$

where γ is an increasing function of habitat saturation, that depends on c, $\tilde{r}$ and $q_{o/\times}$ (Appendix E). Note again
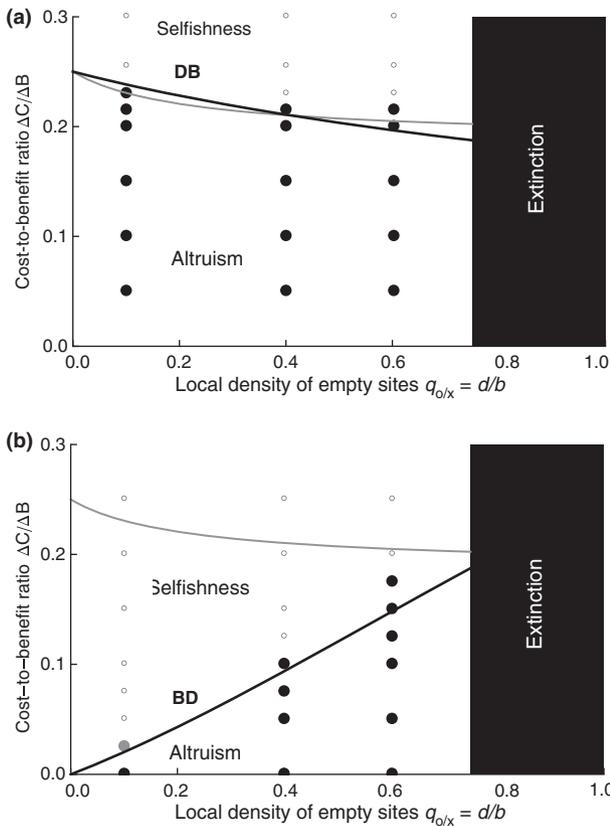

(a)

(b)

Fig. 3 Boundary for the evolution of altruism for death–birth competition (a) and birth–death competition (b) as a function of the local density of empty sites $q_{o/\times} = d/b$. When the cost-to-benefit ratio $\Delta C/\Delta B$ is below the black curves, altruism is convergence stable. The black region corresponds to population extinction. The grey line recalls the prediction of the triple approximation under indirect competition ($c = 0$). Circles indicate the results of stochastic simulations, obtained as in Fig. 2 for three levels of habitat saturation ($b = 10$, $b = 2.5$, $b = 1.66$) and values of the cost of helping ranging from 0 to 0.25. Parameters: $n = 4$, $d = 1$, $m = 0$, $\Delta B = 1$, $c = 1$.

that the fitness costs and benefits of helping are positive in both scenarios; hence, the selected behaviour classifies as altruism (Hamilton, 1964; Rousset, 2004; West et al., 2007).

Because there is an additional cost $\phi\Delta B\gamma$ under BD competition, altruism always evolves more readily under DB competition than under BD competition, as shown by previous studies in the limiting case of habitat saturation (Ohtsuki et al., 2006; Taylor et al., 2007a). In the latter case, we have $q_{o/\times} = 0$ and $\gamma = 1$ and we show in Appendix E that $\tilde{r}$ tends towards $1/(n - 1)$, which, because $\bar{\phi} = (n - 1)/n$, yields the following invasion conditions

$$(\text{DB}) \quad \Delta B > \Delta C\,n \tag{20}$$

$$(\text{BD}) \quad 0 > \Delta C \tag{21}$$

We therefore recover the exact conditions found by Ohtsuki et al. (2006) and Taylor et al. (2007a). As shown by Grafen & Archetti (2008), the key point is that the fecundity effects of helping affect global competition in the BD process but local competition in the DB process. This is made explicit in Appendix E.3, where we show that the two different invasion conditions come solely from different assumptions on how individuals are selected and replaced.

Using the expression of r calculated in Appendix E, we obtain the expression of the cost-to-benefit threshold $\Delta C/\Delta B$ as a function of the local density of empty sites (Fig. 3). We see that decreasing habitat saturation is slightly detrimental to altruism in DB but that it is actually beneficial in BD. Equations 18 and 19 allow to get some insight into these contrasting predictions. Under the DB process, the only effect of increasing the density of empty sites is to decrease the effective relatedness $\tilde{r}$, thereby decreasing the threshold $\Delta C/\Delta B$ below which altruists can invade. On the other hand, under the BD process, habitat saturation also decreases the cost $\phi\Delta B\gamma$ on the right-hand side of eqn 19. In this case, the overall effect of habitat saturation is to increase the threshold $\Delta C/\Delta B$ below which altruists can invade.

Note that condition 18 is identical to condition 14 found under indirect competition. Moreover, simulations show that increasing the intensity c of indirect competition has a weak impact on relatedness: although relatedness tends to be higher when direct competition increases, the qualitative trend remains unchanged (Fig. E1 in Appendix E). Thus, the conditions for evolution of altruism are similar when individuals compete only for empty sites and when they can also compete for occupied sites in the DB life cycle but strikingly different when the BD life cycle is considered. These qualitative predictions are borne out by the results of stochastic simulations (Fig. 3).

Biological conclusions

When individuals can compete for both empty and occupied sites, unconditional altruism can evolve under both BD and DB competitions when habitat saturation is not maximal, but only in the DB process in a saturated habitat. The impact of empty sites is mildly negative under indirect competition and DB competition but actually positive under BD competition. This is because helping individuals bear an additional ecological cost under BD competition, which is reduced when habitat saturation decreases.

Discussion

In this article, we study the evolution of helping in a spatial model where population demography is allowed to feed back on the evolutionary process. We extend previous ecological models incorporating density-dependent reproduction to empty sites in two ways. First, we derive conditions for the evolution of helping that do not depend on the assumption of mutant rarity. This leads us to point out an explicit connection with population genetics models. In particular, we establish a relationship between local densities and coefficients of relatedness based on measures of identity in state. Second, we develop a model taking into account direct competition between individuals as well as indirect competition for empty sites. By doing so, we can explore the impact of habitat saturation under two different competition schemes (BD and DB) that have been previously analysed in the literature under an assumption of complete habitat saturation. This allows us to shed some light on different 'rules' for the evolution of altruism that have been previously proposed. Our analysis relies on several technical approximations that we will discuss before turning our attention to the biological results and potential extensions of our analysis.

Approximations

Throughout our analysis, we used a sequence of approximations, starting with the classical assumption of weak selection. Assuming weak selection allowed us to obtain an expression for the first-order effect of selection on the change in the frequency of mutants in the populations, and readily gave an expression of inclusive fitness that takes the form of Hamilton's rule. Yet, this expression depends on the local environments of individuals. Using a separation of timescales argument and moment closure approximations, we obtain a closed invasion condition that depends only on relatedness and on the physiological costs and benefits of helping. As we increased the ecological complexity of the model, including direct competition, algebraic difficulty increased and we had to use an additional assumption (mutant rarity) to obtain interpretable results.

It is worth noting that we use moment closure approximation at two different levels to: (1) obtain an approximate expression of the selection gradient and (2) compute relatedness in the neutral model. In this study, we observed that the prediction of the inclusive fitness effect on random regular networks is much improved when a higher order moment approximation is used to derive relatedness. Hence, we use a PA to compute the costs and benefits in the selection gradient, but move to a triple approximation to compute relatedness in the neutral model. Therefore, even on a random regular network, PA may not be sufficient to describe the direction of selection. The situation would be even worse on more realistic descriptions of physical space (e.g. two-dimensional square or triangular lattices). In this case, it is well known that short loops such as squares and triangles arise, so that lower order moment closure approximations break down (van Baalen, 2000).

Kin selection

We use spatial moment equations to derive an expression of inclusive fitness that takes the form of Hamilton's rule. As in models of spatial population genetics, relatedness must be computed in a neutral model and the marginal benefits and costs depend on spatial self-structuring. In particular, there is an emergent ecological cost of altruism that represents the reduction in the number of empty sites available for reproduction in the vicinity of an altruist, as a result of increased fecundity of neighbours. This result extends previous analyses of viscous populations with demography (van Baalen & Rand, 1998; Lion & van Baalen, 2007, 2008) to a population genetics setting, and deepens the connection between these studies and works in spatial evolutionary genetics that usually assume that the population is of constant size. Note that eqn 7 is valid for any regular graph provided the weak selection assumption holds true. Although the relative magnitude of the different components of this equation will depend on graph structure, the direction of selection on altruism is positive provided nearest-neighbour relatedness is above a threshold. Concepts such as graph selection or network reciprocity (Nowak, 2006) are ambiguous in this context. By contrast, interpreting the results in terms of kin selection presents both a conceptual and biological advantage, as emphasized by Lehmann *et al.* (2007) and Grafen (2007b).

Ohtsuki *et al.* (2006) showed that altruism could evolve in a spatially structured population if $\Delta B > \Delta C\, n$ (a result later extended to finite populations by Taylor *et al.*, 2007a). They contrasted their results with a slightly different condition ($\Delta B > \Delta C\, n^2/(n-1)$) obtained by van Baalen & Rand (1998) and argued that the discrepancy was due to the fact that the analysis of van Baalen & Rand (1998) relied on the computation of invasion fitness of a rare mutant, instead of fixation probability. Our analysis shows that this interpretation does not hold

true and demonstrates that the discrepancy is due to differences in the underlying ecological assumptions of the two models. The two conditions for the evolution of altruism are actually two limit cases of the same 'rule' $[(n-1)/n]\Delta B\,\tilde{r} > \Delta C$, which is a variant of Hamilton's rule. Ultimately, the discrepancy follows from applying the same mathematical technique (PA) to compute relatedness under two very different ecological scenarios (direct competition and indirect competition). Indeed, although Ohtsuki *et al.* (2006) argue that relatedness is $1/n$ in their model, they implicitly find using PA in their SOM that $\tilde{r} = q_{M/M} - q_{M/R} = 1/(n-1)$, which yields their condition. van Baalen & Rand (1998) also used PA, but because they considered the indirect competition model instead of the direct competition model used by Ohtsuki *et al.* (2006), they found that $\tilde{r} = 1/n$ (which is a lower bound for the 'true' value of $\tilde{r}$). Although this is a very subtle point, it has important biological implications because it shows that kin selection analysis provides an unifying conceptual framework to understand evolution of altruism in viscous populations. Arguably, keeping an eye on relatedness is useful when one tries to put some order in the numerous and often confusing results that have been published to explain the evolution of cooperation on networks. By contrast, the simplicity of the condition $\Delta B > \Delta C\, n$ tends to obscure some of the underlying biological processes (e.g. the importance of direct vs. indirect competition).

The role of habitat saturation and density dependence

The distinction between direct and indirect competitions is a novel feature of our model, and our analysis allowed us to shed some light on the impact of habitat saturation on the selective pressures on altruism. When individuals compete only for empty sites ($c = 0$), an important conclusion of our analysis is that habitat saturation should have only a weak effect on the conditions under which altruism can spread when the physiological benefits and costs of altruism both affect fecundity. Habitat saturation, however, is expected to have a strong effect on the intensity of selection on altruism: eqn 13 predicts selection to become weaker when habitat saturation increases.

When individuals are allowed to compete for occupied sites ($c > 0$), the impact of habitat saturation depends on the form of direct competition. Habitat saturation has a strong positive effect on the evolution of helping in the BD process, because altruists pay an extra cost which decreases when the local density of empty sites increases. In the DB process, however, habitat saturation has only a slightly negative impact on the evolution of altruism, mediated through relatedness. Note that the negative effect of empty sites under DB competition is at odds with the common conception that adding empty sites should increase population elasticity and thus promote altruism (Taylor, 1992b; West *et al.*, 2002; Grafen, 2007a).
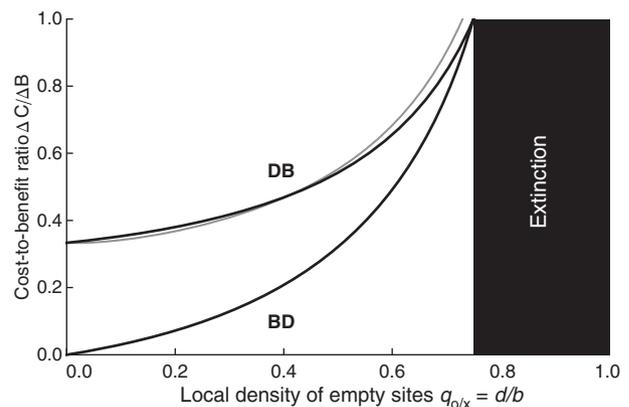

Fig. 4 Boundary for the evolution of altruism for birth–death competition and death–birth competition as a function of the local density of empty sites $q_{o/x} = d/b$. The only difference from that of Fig. 3 is that the physiological cost of altruism is only paid if an interaction takes place, and is thus density dependent.

However, different life cycle assumptions can change the picture. In this paper, we have assumed that the cost of altruism depends only on the magnitude of the trait. This is a reasonable assumption when helping is mediated through the constitutive production of a resource or signal. In this case, helpers release a costly 'common good' product in a density-independent manner which benefits the focal individual and all its neighbours. This can occur, for instance, in bacteria that produce siderophores (Griffin *et al.*, 2004) or antibiotic (e.g. β-lactam) degradation compounds (Dugatkin *et al.*, 2005), when density-dependent regulatory mechanisms are absent or weak.

Many social traits, however, are density dependent to some extent (e.g. public good production mediated through quorum sensing in micro-organisms, trophallaxis in social insects or grooming in primates). In our model, the scenario in which the cost of altruism depends on how many individuals you interact with can be simply investigated by replacing ΔC with $\Delta C\,\bar{\phi}q_{\times/\times o} \approx \Delta C\bar{\phi}(1 - q_{o/\times})$ in eqns 14, 18 and 19. We find that increasing the local density of empty sites has a positive effect on altruism not only for both BD and DB competitions but also in the absence of direct competition. In the limit of low habitat saturation (near the extinction boundary), altruism can even be favoured for values of the benefit-to-cost ratio as high as 1 (Fig. 4). This is consistent with the conclusions of previous studies that also assumed the cost of helping to be paid conditional to interacting with other individuals (Alizon & Taylor, 2008) and allows to recover the common expectation that empty sites should promote altruism. This makes sense in the end, because altruists should be better off if they can avoid paying the cost of helping when there is nobody to help. However, the physiological details really matter here. Indeed, helping can be

conditional because of the nature of the act (as in trophallaxis or grooming) or because of active density-dependent regulatory mechanisms (as in quorum-sensing mediated secretion). In the latter case, simply assuming that the cost of helping is conditional leaves open the crucial problem of how those regulatory mechanisms arise in the first place. Crucially, regulatory mechanisms such as quorum sensing are often a social trait as well (Diggle *et al.*, 2007); so, there is scope for a careful ecological analysis of the evolution of conditional altruism that explicitly takes into account population demography. This may come not only from further theoretical developments but also from empirical testing of the predictions of spatial ecological models, in the wake of recent studies (Boots & Mealor, 2007; Kümmerli *et al.*, 2009).

DB or not DB? How should we model direct competition?

There is a close analogy between the demographic model with direct competition and host–parasite interactions with superinfection (Nowak & May, 1994; Gandon *et al.*, 2001) and constant population size (empty sites being susceptible individuals, reproduction being transmission and mortality being recovery). The parameter c measures the strength of the superinfection process compared with single infections of susceptible hosts. This analogy raises the question of the biological underpinning of DB competition: although BD competition seems to follow naturally from reasonable assumptions on the super-infection process, DB competition appears more loosely connected to realistic life cycle assumptions and represents a more *ad hoc* model of population elasticity.

Moreover, the conditions for altruism to evolve are actually very close under indirect competition and under DB direct competition, as shown by the similarity of conditions 14 and 18, and it is unclear whether using the DB process adds any biological insight compared with the model with indirect competition. In the context of the evolution of altruism, DB competition therefore seems to only serve the purpose of allowing altruism to evolve when habitat saturation is high. As we show, this necessity is alleviated as soon as one considers indirect competition for empty sites.

Perspectives

Building on the analogy between direct competition and superinfection, an interesting prospect for future work would be to use the direct competition model to study the evolution of other life-history traits. For instance, we may use our model to investigate whether individuals are likely to evolve strategies that lead to direct competition (i.e. $c > 0$). Should an individual compete directly with its neighbours, or wait for a neighbouring site to become empty?

Biologically, this question is particularly relevant in the context of superparasitism behaviour in parasitoid species that can either avoid or accept to lay their eggs in already parasitized hosts. Superparasitism leads to intra-host competition between different parasitoid larvae and often results in the death of all but one larvae. Crucially, in solitary parasitoid species, the second larva is most likely to be outcompeted when two eggs have been laid in the same host (Van Alphen & Visser, 1990). For this reason, one would expect superparasitism to be strongly counterselected. Superparasitism is, however, a common occurrence both in the laboratory and in the field (Janssen, 1989; Van Alphen & Visser, 1990). The question of the adaptive nature of parasitoid superparasitism has been addressed by several theoretical studies but always in nonspatial models (Van Alphen & Visser, 1990; Gandon *et al.*, 2006). It would thus be particularly interesting to investigate the importance of spatial structure and habitat saturation on the evolution of super-parasitism. Although the mathematical analysis will be more intricate, we expect that most of the difficulties can be solved using an improved PA (Lion, in press).

The evolution of other important life-history traits could also be investigated, such as the evolution of reproduction effort under a fecundity–survival trade-off (Pen, 2000) or the evolution of costly mobility (Frank, 1986; Taylor, 1988; Gandon & Rousset, 1999). Although several studies have looked at those questions in detail, they usually rely on simplified metapopulation models where all demes have a fixed and constant density (but see Rousset & Ronce (2004). We argue that a more satisfying description of the ecological context is needed, that considers both genetic and demographic spatial self-structuring. By explicitly taking into account the feedback between demography and evolution, our approach provides a method to deepen our understanding of the evolution of important life-history traits. This may come at the expense of additional approximations but could prove to be biologically enlightening.

Acknowledgments

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Appendix A: Monomorphic Model

A.1 Deriving the expected dynamics of global densities

The state of site x is given by the indicator variables

$$\sigma_x(i) = \begin{cases} 1, & \text{if site } x \text{ is in state i,} \\ 0, & \text{otherwise.} \end{cases}$$

Information about the neighbourhood of site x is given by the variable $q_x(j) = (1/n)\Sigma_{y \in \mathcal{N}_x}\sigma_y(j)$ where the sum is taken over all sites y in the neighbourhood of x. $q_x(j)$ gives the proportion of sites in state j in the neighbourhood of site x. Average spatial statistics can be computed from these variables as across-network expectations, such as the global density of sites in state i, $p_i = \langle\sigma_x(i)\rangle$ and the local density $q_{j/i} = \langle q_x(j)|\sigma_x(i) = 1\rangle$. Likewise, we will be interested in local densities of the form $q_{i/jk}$, which measure the average density of sites in state i in the neighbourhood of a site in state j connected to a site in state k.

An individual at site x dies at rate d_x and will send an offspring to an empty neighbouring site at rate $b_x q_x(o)$. The rates b_x and d_x may depend on the local environment experienced by the individual at site x. Therefore, the expected dynamics of the global density $p_\times$ of individuals is

$$\frac{dp_\times}{dt} = \langle b_x q_x(o) - d_x | \sigma_x(\times) = 1\rangle p_\times = (bq_{o/\times} - d)p_\times$$

We now turn to the expected dynamics of pair densities. Following van Baalen & Rand (1998), we have

$$\frac{dp_{o\times}}{dt} = (\alpha q_{o/o\times} - \beta - \delta_{\times o})p_{o\times} + \delta_{\times\times}p_{\times\times}$$
$$\frac{dp_{\times\times}}{dt} = 2\beta p_{o\times} - 2\delta_{\times\times}p_{\times\times} \tag{A1}$$

along with the conservation relationship $p_{oo} = 1 - 2p_{o\times} - p_{\times\times}$. The rates α, β and δ are defined in van Baalen & Rand (1998) and summarized in Table 1. See van Baalen & Rand (1998) and van Baalen (2000) for the detailed derivation of this set of equations.

A.2 Equilibrium densities

From eqn 1, we see that at equilibrium

$$q_{o/\times} = \frac{d}{b}.$$

Using the conservation equation $q_{o/\times} + q_{\times/\times} = 1$, this yields $q_{\times/\times} = 1 - d/b$. Likewise, from eqns A1, it is easy to find that

$$q_{o/o\times} = \frac{\delta_{\times o}}{\alpha}$$

which yields $q_{\times/o\times} = 1 - \delta_{\times o}/\alpha$. Other densities, such as $p_\times$, $q_{\times/o}$ or $q_{o/\times\times}$, are not independent of the geometry of the network (van Baalen, 2000). Approximate values can be computed using moment closure approximations (Matsuda *et al.*, 1992; Sato *et al.*, 1994; van Baalen, 2000).

A.3 Extinction boundary

Using PA, we can obtain an approximation (actually a lower bound) for the critical birth–death ratio of the stochastic process. Under PA, $q_{\times/o\times} \approx q_{\times/o}$. Then $q_{\times/o} = 1 - \delta_{\times o}/\alpha$, and the extinction threshold can be obtained from $q_{\times/o} > 0$. Some algebra then leads to

$$\frac{b}{d} > \frac{1 + \bar{\phi}w}{\bar{\phi}(1 + w)}$$

where $w = m/b$. In the limit of low mobility, we find that the birth–death ratio must be greater than $1/\bar{\phi}$. In the limit of high mobility, the condition collapses to $b > d$.

Appendix B: Computing the inclusive fitness effect from singlet dynamics

We start with the expression

$$\Delta W_{IF} = \Delta(b_M q_{o/M} - b_R q_{o/R})$$

where $\Delta \equiv (\partial/\partial\epsilon)|_{\epsilon=0}$. Using the expressions for the birth rates (eqns 4 and 5), we obtain

$$\Delta W_{IF} = q_{o/\times}[\Delta B \bar{\phi}(\bar{q}_{M/Mo} - \bar{q}_{M/Ro}) - \Delta C] + b\Delta(q_{o/M} - q_{o/R})$$

where we have used the fact that, in the neutral model, $\bar{q}_{o/M} = \bar{q}_{o/R} = q_{o/\times}$. Then, for $i = R$ or M,

$$q_{M/io} = \frac{q_{o/iM}p_{iM}}{p_{oM}} = \frac{q_{o/iM}q_{i/M}}{q_{o/M}},$$

which leads to

$$q_{M/Mo} - q_{M/Ro} = q_{o/MM}\frac{q_{M/M}}{q_{o/M}} - q_{o/RM}\frac{q_{M/R}}{q_{o/R}}.$$

In the neutral model, $\bar{q}_{o/M} = \bar{q}_{o/R} = q_{o/\times}$, and, using the mild assumption $\bar{q}_{o/RM} = \bar{q}_{o/MM} = q_{o/\times\times}$ (Lion, in press), we obtain finally

$$\Delta W_{IF} = \bar{\phi}q_{o/\times\times}\Delta B(\bar{q}_{M/M} - \bar{q}_{M/R}) - q_{o/\times}\Delta C \\ + b\Delta(q_{o/M} - q_{o/R}).$$

Appendix C: Relatedness

In this appendix, all calculations are performed in the neutral model ($\epsilon = 0$). For the sake of simplicity, we have dropped the bars over the symbols.

C.1 Decoupling densities and frequencies of pairs

Using the fact that

$$\frac{q_{M/R}}{q_{R/M}} = \frac{p_M}{p_R} = \frac{f_M}{1 - f_M}$$

we can write

$$\tilde{r} = q_{M/M} - q_{R/M}\frac{f_M}{1 - f_M}.$$

Using the conservation relationship $q_{o/M} + q_{R/M} + q_{M/M} = 1$, this leads to

$$\tilde{r} = \frac{q_{M/M} - (1 - q_{o/M})f_M}{1 - f_M}.$$

In the neutral model, we have $q_{o/M} = q_{o/\times} = 1 - q_{\times/\times}$, and therefore

$$\tilde{r} = \frac{q_{M/M} - q_{\times/\times}f_M}{1 - f_M}.$$

Now, we use the definition of f_{MM} to write

$$q_{M/M} = \frac{p_{MM}}{p_M} = \frac{f_{MM}p_{\times\times}}{f_M p_\times} = q_{\times/\times}\frac{f_{MM}}{f_M}$$

which yields directly

$$\tilde{r} = q_{\times/\times}\frac{f_{MM} - f_M^2}{f_M - f_M^2}.$$

C.2 Relatedness in terms of higher moments

The dynamics of the pair densities p_{MM} and p_{RM} are

$$\frac{dp_{RM}}{dt} = (\alpha_R + \alpha_M)q_{R/oM}p_{oM} - (\delta_{RM} + \delta_{MR})p_{RM}$$

$$\frac{dp_{MM}}{dt} = 2\beta_M p_{oM} - 2\delta_{MM}p_{MM}$$

where, for convenience, we use the following notations introduced by van Baalen & Rand (1998) $\alpha_i = \bar{\phi}(b_i + m_i)$, $\beta_i = \phi b_i + \alpha_i q_{i/oi}$, $\delta_{ij} = d_i + \bar{\phi}m_i q_{o/ij}$ (see Table 1).

In a neutral model, these equations can be simplified, because $\alpha_R = \alpha_M = \alpha$, $b_M = b_R = b$ and $\delta_{RM} = \delta_{MR} = \delta_{MM} = \delta_{\times\times}$. This leads to

$$\frac{dp_{RM}}{dt} = 2\alpha\bar{q}_{R/oM}p_{oM} - 2\delta_{\times\times}p_{RM} \qquad (C1)$$

$$\frac{dp_{MM}}{dt} = 2\beta_{\bar{M}}p_{oM} - 2\delta_{\times\times}p_{MM}. \qquad (C2)$$

Using the fact that $q_{R/oM}p_{oM} = q_{M/oR}p_{oR} = q_{M/oR}q_{o/R}p_R$, we can divide the first equation by p_R, set the time derivatives to zero and subtract the two resulting equations. After rearrangement, and using the fact that in the neutral model $q_{o/M} = q_{o/R} = q_{o/\times}$, we find

$$q_{M/M} - q_{M/R} = \frac{q_{o/\times}}{\delta_{\times\times}}[\beta_M - \alpha\bar{q}_{M/oR}]$$

which, because $\beta_{\bar{M}} = \phi b + \alpha\bar{q}_{M/oM}$, leads finally to

$$\tilde{r} = q_{M/M} - q_{M/R} = \frac{q_{o/\times}}{\delta_{\times\times}}[\phi b + \alpha(q_{M/oM} - q_{M/oR})].$$

Again, $q_{M/oM} - q_{M/oR}$ can be rewritten as

$$q_{\times/o\times}\left(\frac{f_{MoM} - f_M^2}{f_M - f_M^2}\right) \qquad (C3)$$

where $f_{MoM} = p_{MoM}/p_{\times o\times}$. Hence, $\tilde{r}_o = q_{M/oM} - q_{M/oR}$ is a measure of identity in state between individuals *connected by an empty site*. Note that eqn C3 follows from the assumption that at neutrality $\bar{q}_{o/oM} = \bar{q}_{o/oR} = q_{o/o\times}$, but this is a very mild assumption, as simulations suggest that this approximation is very accurate (Lion, in press for a discussion).

Using PA (Matsuda *et al.*, 1992; van Baalen, 2000), $q_{M/oM} \approx q_{M/oR} \approx q_{M/o}$; so,

$$\tilde{r} \underset{PA}{=} \phi\frac{bq_{o/\times}}{\delta_{\times\times}}$$

where $\underset{PA}{=}$ denotes a result valid only using PA. Some algebra then leads to the following expression for R

$$\tilde{r} \underset{PA}{=} \phi\frac{b}{b + \bar{\phi}m}$$

so that for low mobility of individuals, we obtain

$$\tilde{r} \underset{\text{PA}}{=} \phi = \frac{1}{n}.$$

A more accurate approximation of $\tilde{r}$ can be obtained using a triple approximation, the derivation of which is done elsewhere (Lion, in press). The first-order effect of habitat saturation on $\tilde{r}$ is given by

$$\tilde{r} \underset{\text{TA}}{=} \frac{1}{n-1} + \frac{1-2n}{(n-2)(n-1)^2} q_{o/\times} + o(q_{o/\times})$$

which shows that in the limit of high habitat saturation $\tilde{r}$ tends towards $1/(n-1)$.

Appendix D: Computing inclusive fitness from pair dynamics

D.1 Separation of timescales

Let us introduce the vector $\mathbf{q}_M$ of local densities

$$\mathbf{q}_M = (\, q_{o/M} \quad q_{R/M} \quad q_{M/M} \,)^{\text{T}}.$$

The dynamics of $\mathbf{q}_M$ can be written in matrix form as

$$\frac{\mathrm{d}\mathbf{q}_M}{\mathrm{d}t} = \mathbf{A}_M \mathbf{q}_M - \lambda_M \mathbf{q}_M$$

where $\mathbf{A}_M$ is a square matrix of dimension 3 that depends on local densities $q_{i/j}$, $q_{i/jk}$ and so on (Ferrière & Le Galliard, 2001). Under weak selection, we have

$$\frac{\mathrm{d}p_M}{\mathrm{d}t} = \epsilon \frac{\partial \lambda_M}{\partial \epsilon} p_M + o(\epsilon)$$

and

$$\frac{\mathrm{d}\mathbf{q}_M}{\mathrm{d}t} = \mathbf{A}_M \mathbf{q}_M - \epsilon \frac{\partial \lambda_M}{\partial \epsilon} \mathbf{q}_M + o(\epsilon).$$

Because $\mathbf{A}_M$ is not of order ϵ, when ϵ is small, p_M is a slow variable, whereas $\mathbf{q}_M$ is a fast variable. Therefore, under weak selection, the local densities $\mathbf{q}_M$ reach a quasi-equilibrium on a fast timescale, and using the fact that $\mathrm{d}\mathbf{q}_M/\mathrm{d}t = 0$

$$\mathbf{A}_M \mathbf{q}_M = \lambda_M \mathbf{q}_M.$$

This means that λ_M and $\mathbf{q}_M$ form an eigenvalue–eigenvector pair. We can then use standard eigenvalue perturbation analysis to derive the value of $\partial \lambda_M / \partial \epsilon$. The same reasoning applies to p_R and

$$\mathbf{q}_R = (\, q_{o/R} \quad q_{M/R} \quad q_{R/R} \,)^{\text{T}}.$$

D.2 Inclusive fitness effect

The inclusive fitness effect is given by

$$\Delta W_{\text{IF}} = \Delta \lambda_M - \Delta \lambda_R$$

where Δ is a short-hand notation for $\partial/\partial\epsilon$ evaluated at neutrality. Using eigenvalue perturbation analysis, we can write

$$\Delta W_{\text{IF}} = \frac{\bar{\mathbf{v}}_M \Delta \mathbf{A}_M \bar{\mathbf{u}}_M}{\bar{\mathbf{v}}_M \bar{\mathbf{u}}_M} - \frac{\bar{\mathbf{v}}_R \Delta \mathbf{A}_R \bar{\mathbf{u}}_R}{\bar{\mathbf{v}}_R \bar{\mathbf{u}}_R}$$

where $\bar{\mathbf{u}}_M$ and $\bar{\mathbf{v}}_M$ are the left and right eigenvectors of the matrix $\mathbf{A}_M$ evaluated in the neutral process, and $\Delta \mathbf{A}_M$ is the perturbed matrix (similar notations are used for R). This extends the method of van Baalen & Rand (1998) beyond the limit of mutant rarity.

The invasion matrix given in van Baalen & Rand (1998) is implicitly derived using a triple approximation, and this gives some limitations for the validity of the results we are about to derive. Under this approximation, the matrix $\mathbf{A}_M$ reads

$$\mathbf{A}_M = \begin{pmatrix} \alpha_M q_{o/oM} - \alpha_R q_{R/oM} - \beta_M - \delta_{Mo} & \delta_{RM} & \delta_{MM} \\ (\alpha_M + \alpha_R) q_{R/oM} & -\delta_{MR} - \delta_{RM} & 0 \\ 2\beta_M & 0 & -2\delta_{MM} \end{pmatrix}.$$

At neutrality, this simplifies to

$$\bar{\mathbf{A}}_M = \begin{pmatrix} \alpha q_{o/o\times} - \alpha \bar{q}_{R/oM} - \beta_{\bar{M}} - \delta_{\times o} & \delta_{\times\times} & \delta_{\times\times} \\ 2\alpha \bar{q}_{R/oM} & -2\delta_{\times\times} & 0 \\ 2\beta_{\bar{M}} & 0 & -2\delta_{\times\times} \end{pmatrix}.$$

This yields

$$\bar{\mathbf{u}}_M = \begin{pmatrix} \delta_{\times\times} \\ \alpha \bar{q}_{R/oM} \\ \beta_{\bar{M}} \end{pmatrix}$$

and

$$\bar{\mathbf{v}}_M = (\, 2 \quad 1 \quad 1 \,)$$

The matrix $\Delta \mathbf{A}_M$ takes the form

$$\Delta \mathbf{A}_M = \begin{pmatrix} \Delta\alpha_M \bar{q}_{o/oM} + \alpha\Delta\bar{q}_{o/oM} - \Delta\alpha_R \bar{q}_{R/oM} - \alpha\Delta q_{R/oM} - \Delta\beta_M - \Delta\delta_{Mo} & \Delta\delta_{RM} & \Delta\delta_{MM} \\ (\Delta\alpha_M + \Delta\alpha_R)\bar{q}_{R/oM} + 2\alpha\Delta q_{R/oM} & -\Delta\delta_{MR} - \Delta\delta_{RM} & 0 \\ 2\Delta\beta_M & 0 & -2\Delta\delta_{MM} \end{pmatrix}$$

Similar expressions can be obtained for $\Delta \mathbf{A}_R, \bar{\mathbf{u}}_R$ and $\bar{\mathbf{v}}_R$ by permuting R and M. A useful result is that

$$\bar{\mathbf{v}}_M \bar{\mathbf{u}}_M = \bar{\mathbf{v}}_R \bar{\mathbf{u}}_R = 2\delta_{\times\times} + \phi b + \alpha(1 - q_{o/o\times}) \equiv \kappa$$

Some algebra yields, after rearrangement

$$\begin{aligned} \kappa \Delta W_{\text{IF}} = {} & 2\alpha\delta_{\times\times}\Delta(q_{o/oM} - q_{o/oR}) + \delta_{\times\times}[2q_{o/o\times} + q_{M/oR} \\ & + q_{R/oM}]\Delta(\alpha_M - \alpha_R) - 2\delta_{\times\times}\Delta(\delta_{Mo} - \delta_{Ro}) \\ & - \alpha(q_{M/oR} + q_{R/oM})\Delta(\delta_{MR} - \delta_{RM}) \end{aligned}$$

D.3 Low mobility limit

In the limit of low mobility $(m = 0)$, $\delta_{ij} = d$, and inclusive fitness simplifies to

$$\kappa\Delta W_{IF} = 2\alpha d\Delta(q_{o/oM} - q_{o/oR}) + d[2q_{o/o\times} + q_{M/oR} + q_{R/oM}]\Delta(\alpha_M - \alpha_R).$$

Using the definition of $\tilde{r}_o$ introduced in Appendix C and the fact that $\kappa = b + d$ when $m = 0$, and neglecting $\Delta(q_{o/oM} - q_{o/oR})$, one obtains eqn 13. Moreover, from Appendix B, we know that

$$\Delta W_{IF} = q_{o/\times}\Delta(b_M - b_R) + b\Delta(q_{o/M} - q_{o/R}).$$

Eliminating ΔW_{IF}, we obtain the following expression for the ecological cost

$$\Delta(q_{o/M} - q_{o/R}) = -\frac{\tilde{r}q_{o/\times}}{1 + q_{o/\times}}\Delta(b_M - b_R)$$
$$+ 2\frac{\bar{\phi}bd}{b+d}\Delta(q_{o/oM} - q_{o/oR}).$$

D.4 Pair approximation

When mobility is nonzero, the algebra is more difficult, because

$$\Delta\delta_{ij} = \bar{\phi}m\Delta q_{o/ij}$$

Using PA, the expression for inclusive fitness becomes

$$\kappa\Delta W_{IF} \underset{PA}{=} \delta_{\times\times}[2q_{o/o} + q_{M/o} + q_{R/o}]\bar{\phi}\Delta(b_M - b_R)$$
$$- 2\bar{\phi}m[\delta_{\times\times} + \alpha(q_{M/o} + q_{R/o})]\Delta(q_{o/M} - q_{o/R})$$

However, as we know from Appendix B that

$$\Delta W_{IF} = q_{o/\times}\Delta(b_M - b_R) + b\Delta(q_{o/M} - q_{o/R})$$

it is easy to show, by equating both expressions, that

$$\Delta(q_{o/M} - q_{o/R}) \propto \Delta(b_M - b_R)$$

Plugging the expression for $\Delta(q_{o/M} - q_{o/R})$ into one of the expressions for ΔW_{IF}, we obtain an expression for ΔW_{IF}. The main result is that ΔW_{IF} has the same sign as

$$\Delta(b_M - b_R)$$

where $b_M = b + \bar{\phi}Bq_{M/Mo} - C$ and $b_R = b + \bar{\phi}Bq_{M/Ro}$. In summary, following Appendix B, the direction of selection is given by

$$\bar{\phi}\frac{q_{o/\times\times}}{q_{o/\times}}\Delta B(\bar{q}_{M/M} - \bar{q}_{M/R}) - \Delta C$$

which finally yields, using PA $(q_{o/\times\times} \approx q_{o/\times})$

$$\bar{\phi}\ \Delta B\ \tilde{r} - \Delta C.$$

Supporting information

Additional supporting information may be found in the online version of this article:

Appendix E Direct competition model.

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