

LIFE HISTORY, HABITAT SATURATION AND THE EVOLUTION OF FECUNDITY AND SURVIVAL ALTRUISM

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Hamilton's rule provides a general description of the conditions for the evolution of altruism. But altruism can take different forms depending on which life-history trait is affected by the helping behavior (fecundity vs. survival helping). In particular, these different forms of helping may have very different demographic consequences, which may feed back on evolution. We examine the interplay between various forms of helping and demography in viscous populations with empty sites. A key component of our analysis is the local density of empty sites experienced by a focal individual, which provides a measure of habitat saturation. Habitat saturation is shown to have contrasting effects depending on (1) whether the physiological costs and benefits of helping affect fecundity, survival or both; and (2) whether the costs of helping are paid in a density-dependent or density-independent manner. For a given level of habitat saturation and with density-dependent reproduction, we find that the conditions for the evolution of helping should be more favorable in the survival altruism life cycle with a cost on fecundity, and more stringent in the fecundity altruism life cycle with a cost on survival. More generally, our analysis stresses the importance of taking into account the feedback between population demography, life history, and kin selection when investigating the selective pressures on altruism.

KEY WORDS: Demography, empty sites, kin selection, life history, population viscosity, spatial moment equations, spatial structure.

Explaining the evolution of cooperative and altruistic behaviors, by which an individual provides a benefit to others at a cost to itself, is essential for our understanding of all levels of biological organization (Maynard Smith and Szathmáry 1995; Frank 1998). Following Hamilton's (1964) suggestion that altruism should evolve more readily in viscous populations than in well-mixed populations, considerable attention has been devoted to understanding how spatial structure and population viscosity affect the

evolution of costly helping behaviors. Hamilton's reasoning was that when dispersal is local, individuals will tend to interact with related individuals, and thus helpers will reap additional indirect fitness benefits. This may allow indiscriminate helping of neighbors to evolve.

Population viscosity, however, is not a sufficient condition for the evolution of indiscriminate helping, because increasing population viscosity may also increase kin competition (Hamilton 1964; Taylor 1992a; Wilson et al. 1992). Using an island model of dispersal with nonoverlapping generations, Taylor (1992a) showed that the inclusive fitness benefits and the competitive

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effects cancel out exactly, so the selective pressure on helping in this scenario is the same as in a well-mixed population. Thus, although population viscosity appears to be a necessary condition for the evolution of indiscriminate helping, other conditions are also required. In this article, we focus on three main factors: (1) population elasticity, (2) the effect of overlapping generations, and (3) the effect of helping on different life-history traits (e.g., fecundity and/or survival).

First, the evolution of altruism has been shown to be strongly dependent on population elasticity (Taylor 1992b; Frank 1998; West et al. 2002; Grafen and Archetti 2008; Lion and van Baalen 2008; Platt and Bever 2009). Population elasticity is the resultant, at the population level, of the feedback between the altruistic trait and population density. In order for altruism to evolve, density-dependence must operate in such a way that the local increase in population density due to altruism is not nullified by population regulation. Thus, population regulation must operate at a more global scale than altruistic interactions (Kelly 1992, 1994a; Taylor 1992b; Queller 1994; Frank 1998; West et al. 2002; Gardner and West 2006; Grafen and Archetti 2008). Factors that may favor population elasticity include empty sites, the form of density-dependence, and fluctuations in population size due to demographic and environmental stochasticity (van Baalen and Rand 1998; Le Galliard et al. 2003, 2005; Lehmann et al. 2006; Alizon and Taylor 2008; Lion and van Baalen 2008; Lion and Gandon 2009). Second, generation overlap may provide another mechanism favoring the evolution of altruism, because increased survival of individuals from one generation to the next increases within-patch relatedness (Taylor and Irwin 2000; Irwin and Taylor 2001; Lehmann et al. 2007; Grafen and Archetti 2008). Third, it has been shown that whether altruism increases the survival or the fecundity of interacting individuals strongly affects the evolution of altruism. For instance, Taylor and Irwin (2000) and Irwin and Taylor (2001) showed that in a population where all patches are always at carrying capacity, increasing the recipient's fecundity (fecundity altruism) will be more favored than increasing the recipient's survival (survival altruism).

Until now, the consequences of those three factors on the evolution of altruism have been studied independently, but one should expect a strong eco-evolutionary feedback between them. At the ecological level, life-history traits affect population dynamics (e.g., population density and the overlapping of generations). For instance, in Taylor and Irwin (2000) and Irwin and Taylor (2001), an increase in mortality has no effect on population density, but one expects an ecological feedback between survival, fecundity, and habitat saturation (e.g., increasing mortality could decrease population density). At the evolutionary level, changes in a trait, such as altruism, will affect population dynamics through its effect on life-history traits, and in turn be affected by changes in population density.

Our aim in this article is to discuss in more detail the interplay of those three different ecological factors, and their impact on the evolution of altruism. Building on previous work (Matsuda et al. 1992; van Baalen and Rand 1998; Le Galliard et al. 2003; Lion and Gandon 2009), we study a spatial birth–death model with empty sites and overlapping generations. We compute the inclusive fitness effect from the spatial ecological dynamics. In contrast to most previous studies, we allow for both fecundity and survival effects of altruism. We derive analytical expressions for the invasion boundaries of altruism under different life cycles. The impact of habitat saturation on the evolution of helping is shown to depend on how the costs and benefits of helping affect the life-history traits, but also on whether the costs are paid in a density-dependent or density-independent manner. We highlight the connections of our results with kin selection theory, and discuss our predictions in the light of earlier models for the evolution of fecundity and survival helping.

Inclusive Fitness

DEMOGRAPHIC MODEL

We consider a spatially structured population in which individuals live on a regular network of sites. Each site is connected to n other sites, and can be either empty (o) or occupied by at most one individual. We assume overlapping generations. Population size fluctuates according to mortality and reproduction events, and these traits are assumed to be age-independent. At rate d , an individual dies, and at rate b it produces an offspring that is sent to a random neighboring site, and settles down only if that site is empty. Reproduction is therefore local and density-dependent.

In a monomorphic population, the dynamics for the expected dynamics of the global density of individuals p_{\times} follows a spatial version of the logistic equation (Matsuda et al. 1992; van Baalen 2000; Lion and Gandon 2009)

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

where $q_{o/\times}$ is the expected local density of empty sites experienced by an individual. From this local density, we can deduce the expected local density of individuals experienced by an individual, $q_{\times/\times} = 1 - q_{o/\times}$. At equilibrium

$$q_{o/\times} = \frac{d}{b}. \quad (2)$$

As expected, when fecundity and survival increase, the local density of empty sites experienced by an individual decreases, and habitat saturation increases. Thus, survival and habitat saturation are positively correlated. Consequently, it is worth noting that it is not possible to keep the habitat saturated while decreasing survival.

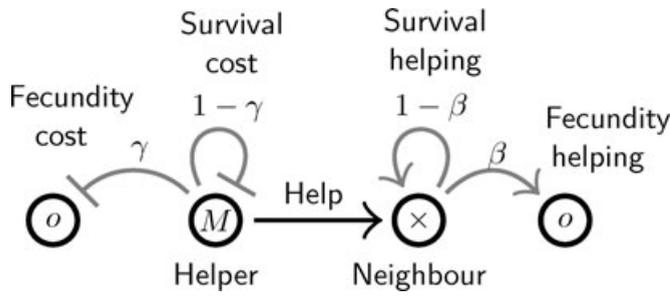


Figure 1. Schematic description of the effects of helping on the life-history traits. An individual bearing the helping trait can either increase its neighbor’s fecundity (with probability β) or its neighbor’s survival (with probability $1 - \beta$), at a cost for itself. The actor’s cost can be paid either in fecundity (with probability γ) or in survival (with probability $1 - \gamma$).

FECUNDITY AND SURVIVAL EFFECTS OF HELPING

We now consider a dimorphic population containing two types R and M , and make the additional assumption that R individuals are selfish, whereas M individuals can help their neighbors. To fully specify the life cycle, we need to describe how the physiological effects of helping affect both survival and fecundity.

We assume that the physiological cost C of helping can be either allocated to the donor’s fecundity rate (with probability γ) or to her mortality rate (with probability $1 - \gamma$) (Fig. 1). Similarly, the physiological benefit B of helping can either be allocated to a recipient’s fecundity rate (with probability β) or to her mortality rate (with probability $1 - \beta$). Under these assumptions, the resulting mortality rates of selfish and helping individuals are

$$\delta_R = d - (1 - \beta)Bq_{M/R} \tag{3}$$

$$\delta_M = d - (1 - \beta)Bq_{M/M} + (1 - \gamma)C. \tag{4}$$

The first term represents the background mortality rate, and the second term is the positive survival effect of interacting with M neighbors, in which $q_{M/i}$ ($i = R, M$) represents the local density of helpers experienced by a i individual. The mortality rate of helpers also has a third term which is the cost of helping.

For the fecundity rates, things are slightly more complicated, because helping will effectively translate into a fecundity gift only if empty sites are available for reproduction. This yields the following expression for the expected fecundity of selfish and helping individuals (van Baalen and Rand 1998; Lion and Gandon 2009)

$$b_R = b + \beta B \bar{\phi} q_{M/Ro} \tag{5}$$

$$b_M = b + \beta B \bar{\phi} q_{M/Mo} - \gamma C. \tag{6}$$

The first term is the background fecundity. The second term is the positive fecundity effect of interacting with M neighbors, in which

Table 1. Under the life cycle assumptions of Figure 1, we can define four limit life cycles if we only allow for pure strategies of helping. Individuals can then engage into fecundity helping with fecundity (FF) or survival (FS) costs, or into survival helping with fecundity (SF) or survival (SS) costs.

	Fecundity cost	Survival cost
Fecundity benefit	FF ($\beta=1, \gamma=1$)	FS ($\beta=1, \gamma=0$)
Survival benefit	SF ($\beta=0, \gamma=1$)	SS ($\beta=0, \gamma=0$)

$q_{M/io}$ represents the expected density of M neighbors experienced by i individuals that are “connected to at least one empty site.” The discounting factor $\bar{\phi} = (n - 1)/n$ takes into account the fact that one neighbor of i is empty. In other words, the expectation is taken over all individuals that effectively reproduce. As before, helpers pay an additional cost.

In the limiting cases when β and γ can only take values 0 or 1, one can identify four different life cycles: FF (fecundity benefit–fecundity cost), FS (fecundity benefit–survival cost), SF (survival benefit–fecundity cost), and SS (survival benefit–survival cost). As indicated in Table 1, FF and FS life cycles can be classified as “fecundity helping” (i.e., helping increases the fecundity of the recipient), whereas SF and SS life cycles represent examples of “survival helping” (i.e., helping increases the survival of the recipient).

INCLUSIVE FITNESS EFFECT

Following a previous analysis (Lion and Gandon 2009), we introduce the frequency of M individuals in the population as $f_M = p_M/(p_R + p_M)$. The expected change in f_M takes the form

$$\frac{df_M}{dt} = f_M(1 - f_M) [(b_M q_{o/M} - b_R q_{o/R}) - (\delta_M - \delta_R)]. \tag{7}$$

Under an assumption of weak selection (B and C small), the direction of selection is given by the inclusive fitness effect (see eq. 6 in Lion and Gandon 2009)

$$\Delta W_{IF} = q_{o/\times} \Delta(b_M - b_R) + b \Delta(q_{o/M} - q_{o/R}) - \Delta(\delta_M - \delta_R), \tag{8}$$

where Δ denotes the partial derivative with respect to investment into helping, evaluated at neutrality. In other words, ΔW_{IF} is the inclusive fitness effect (i.e., the partial derivative of inclusive fitness evaluated at $B = C = 0$), and helpers invade if $\Delta W_{IF} > 0$.

Selective Pressures on Helping

HAMILTON’S RULE

Using equations (3)–(6), we find that the invasion condition $\Delta W_{IF} > 0$ takes the form of Hamilton’s rule

$$\tilde{B}r > \tilde{C}, \tag{9}$$

where \tilde{B} and \tilde{C} are the fitness benefits and costs of helping, and

$$r = \frac{\bar{q}_{M/M} - \bar{q}_{M/R}}{q_{\times/\times}} \quad (10)$$

is a measure of genetic relatedness between neighbors at neutrality. We show elsewhere that r can be put into the traditional form of a covariance over variance ratio of probabilities of identity (Lion and Gandon 2009; Lion 2009). An approximation for r is given in Lion (2009), which gives a good qualitative description of the effect of habitat saturation on genetic relatedness. Relatedness r is an increasing function of the local density of empty sites $q_{o/\times} = d/b$, and varies from $1/(n - 1)$ in a fully saturated habitat to 1 on the verge of population extinction. Note that, in contrast with Taylor and Irwin (2000)’s model, relatedness is a “decreasing” function of survival in our model, due to the feedback between habitat saturation and mortality.¹

Using equations (3) and (4) in (8), we obtain the following expression for the benefit of helping in (9)

$$\tilde{B} = q_{\times/\times} \Delta B_\beta \quad (11)$$

with

$$\Delta B_\beta = \Delta B [\beta \bar{\phi} q_{o/\times\times} + (1 - \beta)]. \quad (12)$$

The benefit of helping depends on the probability of interacting with an individual ($q_{\times/\times}$), on the marginal physiological benefit of helping (ΔB), and on a factor that depends on how helping is allocated to life-history traits. We see that for fecundity helping ($\beta = 1$), the benefits are weighted by $\bar{\phi} q_{o/\times\times}$, which measures the density of empty sites experienced by an individual in an interacting pair. This is a consequence of reproduction being density-dependent. Because $\bar{\phi} q_{o/\times\times} < 1$, the fitness benefits of fecundity helping ($\beta = 1$) are always lower than those of survival helping ($\beta = 0$). In other words, local habitat saturation will decrease the recipient’s net benefits for a fecundity gift, but not for a survival gift (i.e., $d\Delta B_\beta/d\beta < 0$).

Similarly, the cost of helping takes the form

$$\tilde{C} = \Delta C_\gamma + \Delta E \quad (13)$$

with

$$\Delta C_\gamma = \Delta C[\gamma q_{o/\times} + (1 - \gamma)] \quad (14)$$

and

$$\Delta E = -b\Delta(q_{o/M} - q_{o/R}). \quad (15)$$

¹Quantitatively, the approximation underestimates the value of r on a lattice, but performs reasonably well on a regular random network (e.g., a network in which each site has n randomly chosen neighbors) (Lion and Gandon 2009; Lion 2009).

The first term in equation (13) depends on the physiological marginal cost ΔC , weighted by the local density of empty sites $q_{o/\times}$ when the cost is paid in fecundity. Thus, a physiological fecundity cost tends to have a lower fitness effect than a physiological survival cost (i.e., $d\Delta C_\gamma/d\gamma < 0$). This is similar to the effect of fecundity benefits discussed above (compare eqs. 12 and 14) and is also a direct consequence of density-dependence acting on fecundity.

The second-term $\Delta E = -b\Delta(q_{o/M} - q_{o/R})$ measures how a slight increase in helping affects the local density of empty sites available for the reproduction of helpers, relative to selfish individuals. Thus, the term ΔE gives the intensity of competition for space, and can be interpreted as the ecological cost of helping (Lion and van Baalen 2007; Lion and Gandon 2009). It is worth noting the analogy between this ecological cost and the quantity S_{Pr} derived in other kin selection models with demographic stochasticity (Rousset and Ronce 2004; Lehmann et al. 2006). Indeed, both factors quantify the effect of actors, through changes in the demographic states of the population, on the selection gradient. In our model, this ecological cost depends crucially on how helping is allocated to the life-history traits. To determine the direction of selection on helping, we therefore need to carefully calculate ΔE for each life cycle. The following section is dedicated to the derivation of approximations for the value of this ecological cost.

In Table 2, we give the fitness costs and benefits of helping under the four life cycles FF, FS, SF, and SS.

CALCULATING THE ECOLOGICAL COST: MOMENT CLOSURE APPROXIMATIONS

Ultimately, we are interested in how the ecological cost relates to the physiological costs and benefits of helping. In general, computing the ecological cost is a difficult undertaking because it depends on higher-order spatial moments, so the topology of the network will play a critical role, and greatly affect the results. Nonetheless, insightful analytical expressions can be obtained for

Table 2. Fitness costs (\tilde{C}) and benefits (\tilde{B}) of helping under the four demographic scenarios. \tilde{B} and \tilde{C} are shown to depend on the marginal benefit of helping ΔB , the marginal physiological cost of helping ΔC , the marginal ecological cost of helping $\Delta E = -b\Delta(q_{o/M} - q_{o/R})$, on the (neutral) birth rate b and on measures of habitat saturation in the monomorphic process ($q_{o/\times} = 1 - q_{\times/\times}$ and $\bar{\phi} q_{o/\times\times}$).

	Fecundity cost	Survival cost
Fecundity benefit	$\tilde{B} = \bar{\phi} q_{o/\times\times} q_{\times/\times} \Delta B$	$\tilde{B} = \bar{\phi} q_{o/\times\times} q_{\times/\times} \Delta B$
	$\tilde{C} = q_{o/\times} \Delta C + \Delta E_{FF}$	$\tilde{C} = \Delta C + \Delta E_{FS}$
Survival benefit	$\tilde{B} = q_{\times/\times} \Delta B$	$\tilde{B} = q_{\times/\times} \Delta B$
	$\tilde{C} = q_{o/\times} \Delta C + \Delta E_{SF}$	$\tilde{C} = \Delta C + \Delta E_{SS}$

the ecological cost by extending the approach of Lion and Gandon (2009). In short, the idea is to use an argument of separation of time scales to obtain a first-order spatial approximation of the selection gradient. In the Appendix, we show that the inclusive fitness effect can be put in the form

$$\Delta W_{IF} = \left(1 - \frac{q_{\times/\times}}{1 + q_{o/\times}} r\right) \Delta S. \quad (16)$$

The direction of selection on altruism is given by the sign of ΔS (i.e., helping is favored when $\Delta S > 0$). Indeed, the factor in front of ΔS is always positive. This formulation highlights that increasing saturation and/or increasing relatedness both decrease the intensity of selection (see also eq. 13 in Lion and Gandon 2009). In the general case, ΔS takes the form (the Appendix)

$$\Delta S = q_{\times/\times} \Delta B_{\beta} r - \Delta C_{\gamma} - \Delta E_{\beta} \quad (17)$$

with

$$\Delta E_{\beta} = (1 - \beta) q_{\times/\times} \Delta B \phi \left(r + \frac{1 - r}{1 - r + q_{o/\times}(1 + r)} \right) \quad (18)$$

using the notation $\phi = 1/n$. The last term in equation (17) results from the effect of the ecological cost on the inclusive fitness effect. Note that this ecological cost can alter the direction of selection only when helping has an effect on survival ($\beta < 1$). To understand this effect, it is necessary to go back to the definition of the ecological cost. ΔE measures the difference in the available number of empty sites around helping and selfish individuals. If a helper only affects the fecundity of a neighbor ($\beta = 1$), the extra offspring produced will be sent two steps away from the actor, and thus will be less likely to compete with the actor's offspring.² In contrast, increasing a neighbor's survival ($\beta < 1$) will directly feed back on the availability of empty sites experienced by helpers, and therefore leads to an increase of the competition between the donor's offspring and neighboring adults (Fig. 1). Hence, the term ΔE_{β} measures the erosion of the fitness benefit associated with helping neighbors to survive.

The fact that the ecological cost of survival helping is higher than that of fecundity helping illustrates the fact that survival and fecundity helping operate at different regulation scales: competition is more local for survival than for fecundity helping (Grafen and Archetti 2008). A particularly enlightening way of dealing with this is to incorporate the ecological cost into a net coefficient of relatedness measured with respect to the scale of population regulation (Queller 1994; Kelly 1994a; Frank 1998; Gardner and West 2006; Platt and Bever 2009). Using expression (18) to rearrange equation (17), we obtain

²In fact, on some networks, such as random regular networks, the competitive effect of increasing a neighbor's reproduction will be exactly zero.

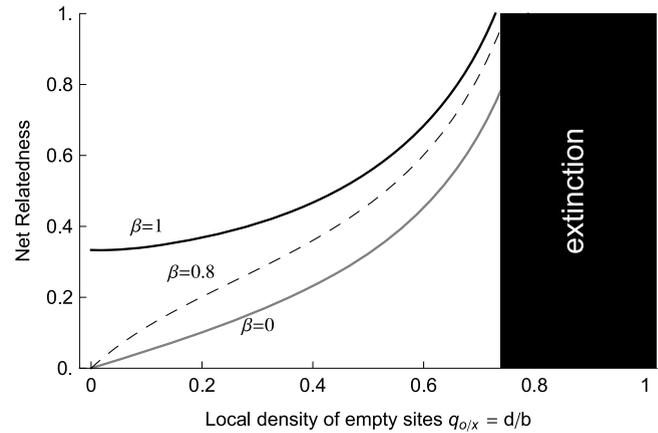


Figure 2. Net relatedness \hat{r} (eq. 20) for increasing values of β and as a function of habitat saturation. Parameters: $\phi = 1/4$. The black region corresponds to the region of population extinction predicted by the ordinary pair approximation (Lion and Gandon 2009; Lion 2009).

$$\Delta S = \tilde{B} \hat{r} - \Delta C_{\gamma}, \quad (19)$$

where \hat{r} is a net coefficient of relatedness given by

$$\hat{r} = r - \phi \frac{1 - \beta}{1 - \beta + \beta \bar{\phi} q_{o/\times}} \left(r + \frac{1 - r}{1 - r + q_{o/\times}(1 + r)} \right). \quad (20)$$

For fecundity helping ($\beta = 1$), $\hat{r} = r$, but when helping also has an effect on recipients' survival, we see that the net relatedness \hat{r} is always lower than the genetic relatedness r (Fig. 2). In the limit of high habitat saturation ($q_{o/\times} \rightarrow 0$), we find that $\hat{r} = 0$ for survival helping (the Appendix), which implies that the positive effect of viscosity on relatedness and its negative competitive effect cancel each other. As habitat saturation decreases, both r and \hat{r} increase (Fig. 2).

Conditions (17) and (19) are equivalent but represent different ways of conceptualizing this issue (Queller 1994; Frank 1998; West et al. 2002; Gardner and West 2006). In contrast with previous studies, we provide an ecological underpinning for the interplay between net relatedness and competition through the effect of helping on life-history traits (see also Gardner and West 2006). In particular, equation (19) provides a synthetic condition for the direction of selection on helping, which can be used to investigate the effects of habitat saturation and life history on the evolution of helping. Note that equation (19) can be used to show that costly harming behaviors ($\Delta C > 0$, $\Delta B < 0$) never evolve in our ecological model.

Finally, it is important to note that any costly helping behavior in our model always has positive fitness benefits and costs (Section Habitat Saturation and Density-Dependence) and therefore strictly qualifies as altruistic (Hamilton 1964; Frank 1998; Rousset 2004; West et al. 2007). We will therefore indifferently use the terms helping and altruism in the next section,

in which we discuss the effect on habitat saturation, density-dependence and life-history assumptions on the evolution of altruism.

Evolution of Fecundity and Survival Altruism

LIFE HISTORY AND THE EVOLUTION OF ALTRUISM

Which life cycle should we expect to be more conducive to the evolution of altruism? To answer this question, we will use equation (19) and analyze the effects of γ and β on the benefits and costs of helping. First, as discussed above (Section Hamilton's Rule), the cost of helping is a decreasing function of γ (i.e., $d\Delta C_\gamma/d\gamma < 0$). In other words, because our model assumes density-dependent reproduction, helping is always favored when the physiological cost affects fecundity. Second, we have seen that the benefit of helping \tilde{B} decreases with β (i.e., $d\tilde{B}/d\beta < 0$),

whereas relatedness with the social neighborhood \hat{r} increases with β (i.e., $d\hat{r}/d\beta > 0$). However, it can be shown that $d(\tilde{B}\hat{r})/d\beta < 0$. In other words, allocating helping to survival should be more conducive to the evolution of altruism. Consequently, in spite of the higher ecological cost associated with survival helping, and all other things being equal, survival altruism is expected to evolve more readily than fecundity altruism. Hence, for a given level of habitat saturation, the conditions for the evolution of helping should be most favorable in the SF life cycle (survival altruism with a cost on fecundity), and most stringent in the FS life cycle (fecundity altruism with a cost on survival), whereas FF and SS life cycles should lie somewhere in between. Figure 3 confirms this general prediction.

Whether helping evolves or not, however, will depend on the details of the life history and on the saturation of the habitat. We will now investigate the impact of density-dependence and habitat saturation on the invasion of helping.

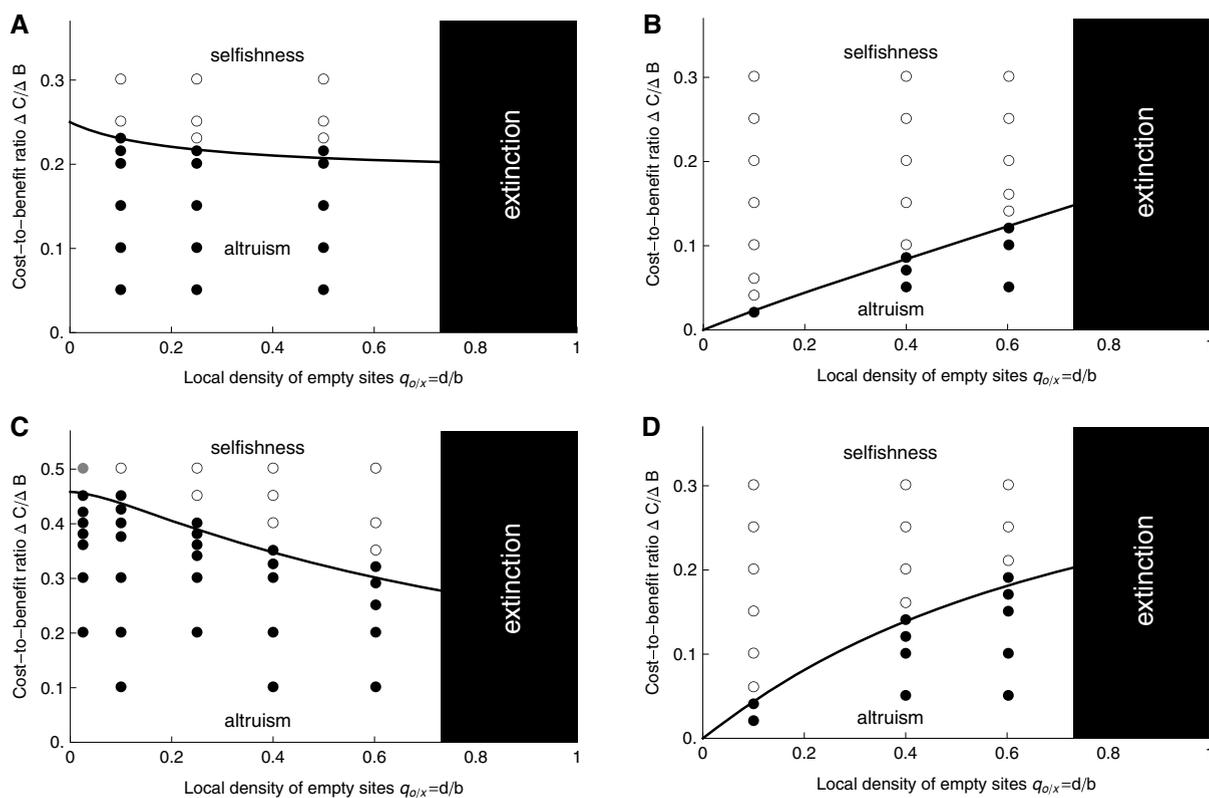


Figure 3. Boundary for the invasion of helping for constitutive costs, as a function of the local density of empty sites $q_{o/x} = d/b$. Inclusive fitness is positive below the invasion boundary (black line). The black region represents population extinction. Top: fecundity helping (left: FF; right: FS). Bottom: survival helping (left: SF; right: SS). 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 different levels of habitat saturation and increasing cost of altruism (between 0.05 and 0.5), 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 colored 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 $1/(Np_x)$. See Lion and Gandon (2009) for more details.

HABITAT SATURATION AND DENSITY-DEPENDENCE

From equation (19), we obtain the following conditions for the invasion of fecundity helping

$$(FF) \quad \bar{\phi} q_{o/\times} q_{\times/\times} \Delta B r > q_{o/\times} \Delta C \quad (21)$$

$$(FS) \quad \bar{\phi} q_{o/\times} q_{\times/\times} \Delta B r > \Delta C \quad (22)$$

which are two simplified versions of Hamilton's rule in which only the impact of habitat saturation on the costs differ between the two scenarios.

For survival helping, the selection coefficient has a more involved expression, and we obtain the following invasion conditions

$$(SF) \quad q_{\times/\times} \Delta B \hat{r} > q_{o/\times} \Delta C \quad (23)$$

$$(SS) \quad q_{\times/\times} \Delta B \hat{r} > \Delta C, \quad (24)$$

where \hat{r} is given by equation (20) in the limit $\beta = 0$. Again, only the impact of habitat saturation on the costs is different in the two conditions. Note that, because reproduction is density-dependent in our model, habitat saturation acts by decreasing the fecundity benefits and fecundity costs of helping. This accounts for the factors $q_{o/\times}$ and $\bar{\phi} q_{o/\times}$ in equations (21)–(24).

From equations (21) to (24), we derive the critical cost-to-benefit ratios $\Delta C/\Delta B$ above which altruism cannot invade a selfish resident population. Figure 3 shows the results for each life cycle, and compares the predictions to the results of stochastic simulations on a regular random network, on which the approximation we use is known to be accurate (Lion and Gandon 2009).

Conditions (21)–(24) can be used to understand the effect of habitat saturation on the evolution of altruism under the corresponding four life cycles. Two main patterns emerge. First, under FF and SF life cycles, habitat saturation is more favorable to the evolution of altruism. This is mainly due to the modulation of the cost of helping with the local density of empty sites (the cost of altruism is only paid when there are empty sites around the focal individual). Second, under the FS and SS life cycles, habitat saturation has the opposite effect and tends to prevent the evolution of altruism. This effect can be explained by the increase in relatedness (both r and \hat{r}) with the local density of empty sites (Fig. 2).

It might seem counterintuitive that the boundary is relatively flat in the FF life cycle, whereas it is rather steep in the SS life cycle, given that only fecundity is density-dependent in our model. This effect can be understood by taking into account the fact that density-dependence has a similar effect on both sides of equation (21) ($q_{o/\times} \approx q_{o/\times}$ on a random network), so the difference between the FF and SS life cycles can be fully understood by studying how habitat saturation affects the relatedness measures

r (in the FF life cycle) and \hat{r} (in the SS life cycle). In other words, the explanation lies in the interplay between genetic relatedness and local competition, but the details of this interaction cannot be deduced from the density-dependence of fecundity and survival rates alone.

The detailed effects of habitat saturation on the components of inclusive fitness are further illustrated in Fig. 4, which shows fitness profiles for a fixed value of the cost-to-benefit ratio (here, we chose $\Delta C/\Delta B = 0.05$, so that helping is under the most favorable conditions). Figure 4 illustrates three important aspects. First, the magnitude of the ecological cost $-b\Delta(q_{o/M} - q_{o/R})$ (dashed line) is higher for survival helping (Fig. 4C,D) than for fecundity helping (Fig. 4A,B), reflecting the difference in the scale of competition. Second, a higher density of empty sites leads to a lower ecological cost for survival helping because it reduces local competition, but has an opposite effect for fecundity helping, because the ecological cost for fecundity helping ($\beta = 1$) is proportional to relatedness (Lion and Gandon 2009), which is a decreasing function of habitat saturation. Third, the total inclusive fitness effect ΔW_{IF} (gray line) is a decreasing function of habitat saturation. Thus, if helping evolves, it will always evolve more readily when the local density of empty sites is high. Note that, although the ecological cost for survival helping is always positive, it can be negative for fecundity helping in the regions of parameter space where the behavior is counter-selected. For instance, Fig. 4(B) shows that, when habitat saturation is too high, helping in the FS scenario can lead to a negative ecological cost. This happens when the higher mortality of the actor can actually increase the likelihood that related individuals have an open site in their neighborhood. However, in this case, inclusive fitness is negative, and the behavior is counter-selected.

CONSTITUTIVE VERSUS CONDITIONAL COST OF HELPING

Until now, we have assumed that helping bears a constitutive physiological cost. When habitat saturation is maximal, and all sites are occupied, each individual is surrounded by n other individuals, so it makes no difference whether the cost of helping is constitutive or conditional on interacting with other individuals. When habitat saturation decreases, however, those two biological assumptions will have very different ecological consequences because a conditional cost is density-dependent.

The effect of a density-dependent cost of helping can be investigated by slightly altering our previous model (the Appendix), resulting in the invasion boundaries presented in Figure 5. A clear pattern emerging in all four life cycles is that empty sites always have a positive effect on the evolution of helping. In contrast with constitutive costs, conditional costs therefore allow to recover the predictions of existing theory (Taylor 1992b; Alizon and Taylor 2008; Lion and Gandon 2009) for all life cycles assumptions.

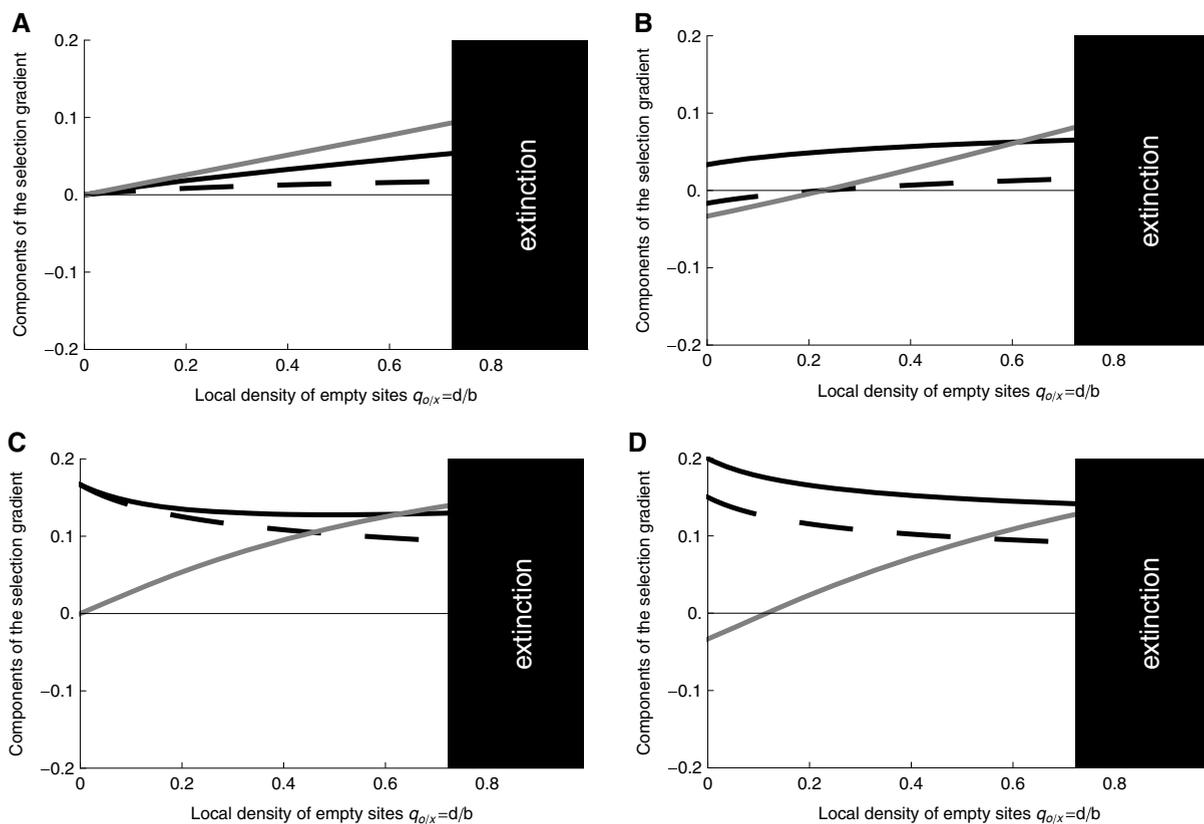


Figure 4. Inclusive fitness effect (ΔW_{IF} , gray line), ecological cost ($-b\Delta(q_{o/M} - q_{o/R})$, dashed line) and fitness cost of helping (\bar{C} , blackline) as a function of habitat saturation, for constitutive helping. The black region represents population extinction. Top: fecundity helping (left: FF; right: FS). Bottom: survival helping (left: SF; right: SS). Parameters: $\Delta B = 1$, $\Delta C = 0.05$, $n = 4$.

Discussion

This article provides a synthetic framework in which to investigate the joint effect of population demography on the evolution of social traits under different assumptions regarding the life-history consequences of helping. We derive clarifying analytical expressions for the selective pressures on costly helping in a spatially structured population in which the density of empty sites is determined by the balance between fecundity and survival. Allowing for this demographic feedback contrasts with previous studies and in particular with Taylor and Irwin (2000).

COMPARISON WITH PREVIOUS PREDICTIONS

Taylor and Irwin (2000), Irwin and Taylor (2001) have studied the FF and SS life cycles in a deme-structured model under the assumptions that fecundity and survival have no impact on the density of the population. Hence, their model assumes that habitat saturation is always maximal. In the limit of high habitat saturation, we recover their main prediction that helping can evolve when helping affects fecundity (FF) but not when it affects survival (SS) (Figs. 3 and 5).

A second prediction of Taylor and Irwin's (2000) analysis was that the evolutionary success of helping should be unaffected by whether the actor pays a fecundity or a survival cost. Our results show that this does not hold true when the life-history traits affect population density. Indeed, Figure 3 and, to a lesser extent, Figure 5 clearly indicate that the demographic impact of the costs of helping is a determinant factor. When the habitat is saturated, altruism can only evolve if the costs of helping affect fecundity, irrespective of whether the benefits increase the recipient's fecundity or survival. Note that these results depend critically on the assumptions that reproduction is a density-dependent process, but mortality is density-independent. Other assumptions on the density-dependence of life-history traits (e.g., density-dependent survival, nonlinear density-dependent effects) may yield different predictions.

Third, the effect of increasing survival is markedly different in our model and in Taylor and Irwin's (2000) analysis. In contrast with their predictions that increasing survival should favor the evolution of altruism, we find that increasing survival has a detrimental effect except when the costs of helping affect

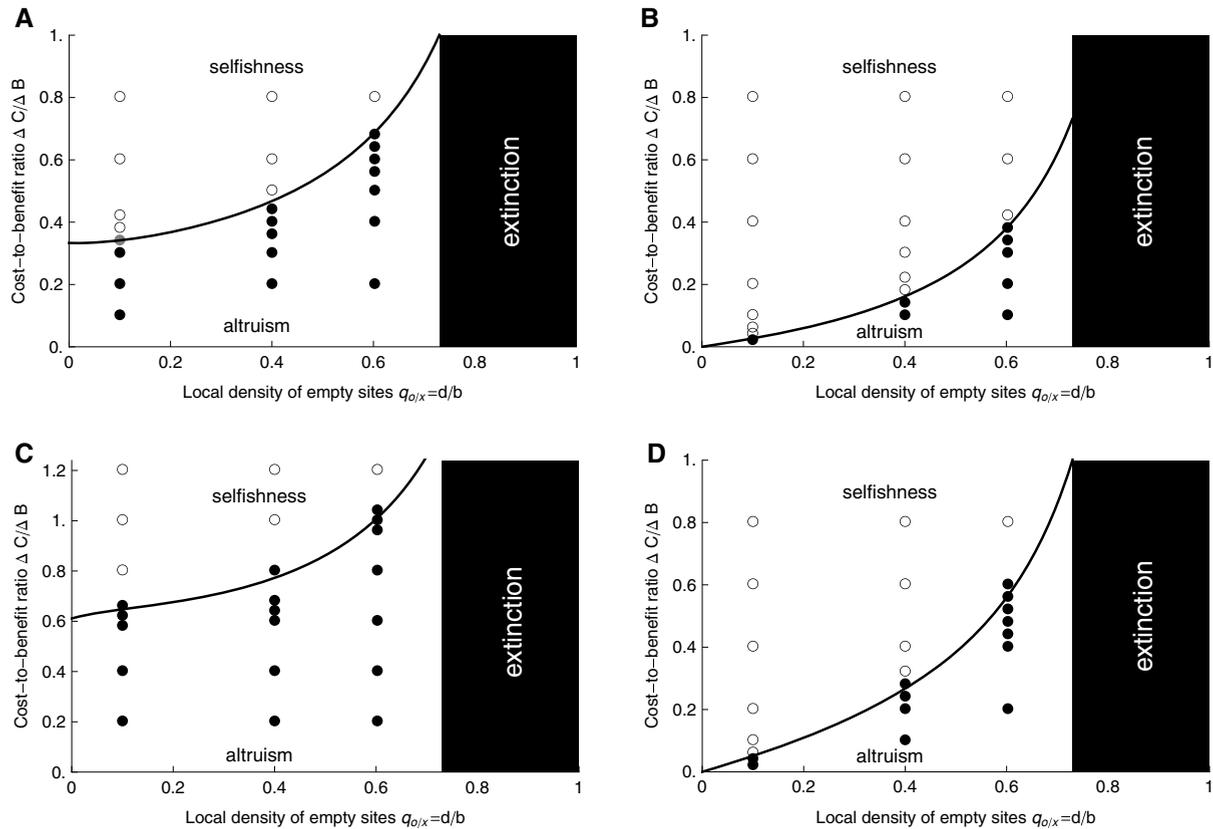


Figure 5. Boundary for the invasion of helping for conditional costs as a function of the local density of empty sites $q_{o/x} = d/b$. Inclusive fitness is positive below the invasion boundary (plain line) and the circles indicate the results of stochastic simulations (see Fig. 3 for more details). The black region represents population extinction. Top: fecundity helping (left: FF; right: FS). Bottom: survival helping (left: SF; right: SS).

fecundity and are constitutive. This can be explained by the fact that, in our model, there is a positive correlation between survival and habitat saturation.

It is important to note, however, that other differences exist between the life cycles used in Taylor and Irwin (2000) and in our model. For instance, an increase in survival in Taylor and Irwin (2000) has an effect on the age structure of the population (overlapping generations) and on the timing of demographic events (i.e., whether individuals have synchronous or asynchronous clocks), but not on population density. In contrast, in our model survival affects both age structure and habitat saturation, but has no effect on the synchronization of individuals' demographic events. This strongly suggests that predictions regarding the impact of life-history traits on the evolution of helping will largely depend on the underlying population dynamics model, and calls for caution when trying to generalize the results obtained with specific models. In particular, it is not necessarily possible to make general predictions on the effect of a given parameter on the basis of simple models, although, as we show here, the con-

ceptual toolbox generated by these models may come in handy when trying to interpret the results.

DEMOGRAPHY MATTERS

Our analysis shows that taking into account the feedback between population dynamics and evolution is crucial to the understanding of the evolution of social traits. Analyses assuming constant population size might be valid when habitat saturation is high, or when the feedback with population dynamics is weak; but in general one should expect that the selective pressures on a given social trait will depend on how it affects the various life-history traits and on how life history in turn affects population dynamics.

A crucial component of our analysis is the ecological cost, which measures the net effect of competition for empty sites on a focal individual's inclusive fitness. We show that competition for empty sites takes very different forms depending on whether helping affects survival or fecundity. Importantly, in our theoretical approach, we do not incorporate local competition

as a model parameter, as in previous approaches (Frank 1998; Gardner and West 2004; Griffin et al. 2004). Rather, we derive the competitive term from basic ecological principles (see also Gardner and West 2006), under the assumption of local reproduction (i.e., no migration of adults and offspring). This allows us to recover the concept of relatedness with the social neighborhood as an emergent property of the spatial ecological dynamics.

It is important to keep in mind that the impact of habitat saturation in our model crucially relies on the population dynamical model on which the evolutionary analysis is based. For instance, our model assumes that density-dependence affects reproduction in a linear way. Other population dynamics can be envisioned, such as nonlinear effects, or density-dependent survival. The latter effect could be investigated by making the mortality rate proportional to the local density of neighbors, or by using a model in which individuals can reproduce with the same probability into an empty site and an occupied site, as in the Birth–Death direct competition model described in Lion and Gandon (2009), which effectively transfers density-dependence from fecundity to survival.

More generally, fecundity and survival rates may be affected by the environment, for instance through the dynamics of resources, interspecific competition or density regulation via predators or parasites. This, in turn, is likely to have significant implications for the evolution of helping behaviors. For instance, the presence of a heterospecific competitor has been shown to have a double effect on the evolutionarily level of communal foraging, through the reduction in available resources and through a change in the scale of population regulation (Kelly 1994b). In our framework, the role of interspecific competition and its interplay with habitat saturation could be investigated by adding a second species that competes for empty sites at a certain rate, either globally (through a removal rate) or locally (in which case the spatial dynamics of the competitor will need to be analyzed explicitly). Although the general method we describe here can still be applied to these alternative ecological scenarios, the relationship between the evolution of helping and the local density of empty sites $q_{o/x}$ will strongly depend on the details of the population dynamics.

BIOLOGICAL IMPLICATIONS

Is the increased complexity of our model biologically justified compared to models that do not consider the feedback between altruism, life-history traits, and habitat saturation? We think cooperative breeding is a good illustration of the need for detailed ecological models for the evolution of helping. In species with cooperative breeding, some individuals (helpers) do not reproduce and help breeders to raise juveniles, or to reproduce, thereby increasing the fecundity of breeders at a fecundity cost for them-

selves. Numerous examples are documented in birds, mammals, and insects (for reviews, see Brown 1987; Clutton-Brock 2002; Koenig and Dickinson 2004).

Two main explanations have been invoked to explain the evolution of cooperative breeding (Brown 1987; Hatchwell and Komdeur 2000). Under the ecological constraint hypothesis, helping evolves more readily when habitat saturation is high (shortage of breeding vacancies). Under the life-history hypothesis, low adult mortality should favor cooperative breeding. It has been noted previously, however, that the two hypotheses are not mutually exclusive, in particular because a low population turnover leads to higher levels of habitat saturation (Hatchwell and Komdeur 2000). Our model gives a theoretical underpinning to the life history and ecological constraint hypotheses, and provides a natural framework in which to explore the impact of the feedback between life history and ecology on the evolution of cooperative breeding.

At first sight, it may seem that cooperative breeding falls into the FF category we define in this article. However, the reality is more complex, as it has recently been shown that helpers may also have an effect on breeder survival, through a reduction of breeder workload (Khan and Walters 2002) or by allowing breeders to invest less in eggs (Russell et al. 2007). Moreover, from the point of view of the helper, cooperative breeding induces costs than may affect both fecundity and survival, but it can also have direct benefits through increased personal survival for the helper (McGowan et al. 2003).

More generally, the contrasting theoretical predictions between our model and previous studies suggest that different ecological and life cycle assumptions may lead to different predictions for the correlations between the presence of a helping behavior and life history (survival, reproductive effort) or ecological traits (habitat saturation). Caution should therefore be taken when interpreting across-species data. Because the details of the life history and ecological context in each population are averaged out, the conclusions drawn from these studies may be misleading. In particular, an across-species positive correlation between, say, survival and helping, does not imply that, within a species, a negative correlation could not be observed.

PERSPECTIVES

There are a number of future directions of research that may be worth investigating in detail. First, as discussed in Section Demography Matters, we expect that the details of density dependence are likely to strongly affect the selective pressures on altruism. It would be particularly interesting to extend our analysis to allow density dependence to affect both survival and fecundity. The direct competition model studied by Lion and Gandon (2009) could be a way to formalize these effects. Alternatively, the life cycle used in this study could be modified to include density-dependent

survival or nonlinear density-dependent effects. Second, a natural extension of our work would be to allow the helping trait to evolve. Our analysis indicates when a helping behavior is favored in a selfish population (the problem of the origin of altruism), but tells us nothing about the evolutionarily stable investment into the cooperative behavior. The adaptive dynamics of helping in the FF life cycle has already been analyzed in great detail (Le Galliard et al. 2003), revealing interesting phenomenon such as evolutionary suicide. A similar analysis could be applied to the FS, SF, and SS life cycles. This ESS analysis is needed to make precise predictions on the correlations between helping, habitat saturation and survival that can be expected to be found in the field.

Another, particularly interesting avenue of research would be to study the joint evolution of helping and of other traits, such as mobility (studied by Le Galliard et al. (2005) for the FF life cycle), reproductive effort (the mortality and fecundity rates), or the allocation of helping to fecundity and survival (the β and γ traits in our model). In particular, the joint evolution of helping and demographic parameters such as survival or mobility would yield testable predictions about correlations between helping and survival or between helping and habitat saturation under different ecological scenarios (e.g., fecundity vs. survival altruism).

Other extensions of the modeling framework are possible to investigate the interplay between helping and other life-history traits. Indeed, although our simple ecological model allowed us to summarize the life history in two traits (fecundity and survival), it would be interesting to use the approach presented here to account for interactions between different age classes, extending previous studies of between-class helping (Ronce et al. 2000; Lion and van Baalen 2007). Although mathematically more challenging, this framework would allow us to investigate the impact of age-dependent life-history traits, such as senescence or maturation, on the evolution of helping, as well as the joint evolution between helping and these life-history traits. Finally, as discussed above, it is also possible to extend our approach to investigate the role of interspecific interactions on the evolution of intraspecific helping behaviors.

More broadly, our study shows the importance of investigating the evolution of cooperative behaviors in an explicit ecological context. Most kin selection models, however, neglect the richness of the feedback between cooperative traits (or other behavioral or life-history traits) and population dynamics (but see Rousset and Ronce 2004; Gardner and West 2006; Lehmann et al. 2006; Lehmann 2007; Alizon and Taylor 2008). Further advances in the study of the evolution of social behaviors require theoretical studies that take into account the interplay between demography and evolution.

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Appendix: Deriving the Selection Gradient

The last equation of appendix D2 in Lion and Gandon (2009) gives the general expression of the selection gradient on helping

in a selfish population, when helping can affect both fecundity and survival. In the limit where mobility is zero, this equation reduces to

$$(b + d)\Delta W_{IF} = d\bar{\phi}[2q_{o/o\times} + q_{M/oR} + q_{R/oM}]\Delta(b_M - b_R) - 2d\Delta(\delta_{Mo} - \delta_{Ro}) - \bar{\phi}b(q_{M/oR} + q_{R/oM})\Delta(\delta_{MR} - \delta_{RM}) + 2\bar{\phi}bd\Delta(q_{o/oM} - q_{o/oR}),$$

where δ_{ij} is the death rate of a i individual in a ij pair.

We can simplify things further by noting that $q_{M/oR} + q_{R/oM} = 1 - q_{o/o\times} - (q_{M/oM} - q_{M/oR})$. It is shown in Lion and Gandon (2009) that $q_{M/oM} - q_{M/oR} = (q_{\times/\times}r - \phi)/\bar{\phi}$ and $q_{o/o\times} = d/(\bar{\phi}b) = q_{o/\times}/\bar{\phi}$, so we can rewrite the expression for the selection gradient as

$$(1 + q_{o/\times})\Delta W_{IF} = q_{o/\times}[1 + q_{o/\times} - q_{\times/\times}r]\Delta(b_M - b_R) - 2q_{o/\times}\Delta(\delta_{Mo} - \delta_{Ro}) - [1 - q_{o/\times} - q_{\times/\times}r]\Delta(\delta_{MR} - \delta_{RM}), \quad (A1)$$

where we have neglected, as in Lion and Gandon (2009) the selective pressure due to empty sites two steps away from a focal individual $\Delta(q_{o/oM} - q_{o/oR})$.

Until now, the derivation of equation (A1) has not depended upon whether helping affects survival of fecundity, or whether costs are conditional or constitutive. We shall now show how we can incorporate the ecological and life-history assumptions of our model in equation (A1).

CONSTITUTIVE COSTS

For the fecundity rates, we can use expressions (5) and (6) in the main text, and we obtain

$$\Delta(b_M - b_R) = \beta\Delta B\bar{\phi}(q_{M/Mo} - q_{M/Ro}) - \gamma\Delta C. \quad (A2)$$

For the death rates, we need to compute the rates at which different pairs are destroyed because of the death of one individual. A selfish individual connected to an empty site will die at rate

$$\delta_{Ro} = d - (1 - \beta)B\bar{\phi}q_{M/Ro}$$

and a helping individual at rate

$$\delta_{Mo} = d - (1 - \beta)B\bar{\phi}q_{M/Mo} + (1 - \gamma)C.$$

This yields

$$\Delta(\delta_{Mo} - \delta_{Ro}) = -(1 - \beta)\Delta B\bar{\phi}(q_{M/Mo} - q_{M/Ro}) + (1 - \gamma)\Delta C. \quad (A3)$$

Similarly, the death rate of the helping individual in a MR pair is

$$\delta_{MR} = d - (1 - \beta)B\bar{\phi}q_{M/MR} + (1 - \gamma)C$$

but for a selfish individual in a *RM* pair we must take into account the fact that the selfish individual has an increased survival probability because it can be helped by its neighbor. Therefore, we have

$$\delta_{RM} = d - (1 - \beta)B(\phi + \bar{\phi}q_{M/RM}).$$

This yields

$$\Delta(\delta_{MR} - \delta_{RM}) = -(1 - \beta)\Delta B(\bar{\phi}(q_{M/MR} - q_{M/RM}) - \phi) + (1 - \gamma)\Delta C. \tag{A4}$$

In equations (A2) and (A3), the quantity $q_{M/Mo} - q_{M/Ro}$ can be rewritten as $(q_{o/\times}/q_{o/\times}) q_{\times/\times}r$. In the following, we shall use the approximation $q_{o/\times} \approx q_{o/\times}$ to simplify the equations. Moreover, we use the ordinary pair approximation to approximate $q_{M/MR} - q_{M/RM}$ as $q_{M/M} - q_{M/R} = q_{\times/\times}r$. Those approximations are very good on a random regular network, but will introduce some quantitative errors on a lattice.

Putting everything together into equation (A1), we obtain after simplifications

$$\begin{aligned} (1 + q_{o/\times})\Delta W_{IF} = & (1 + q_{o/\times} - q_{\times/\times}r) [q_{o/\times}(\beta\Delta B\bar{\phi}q_{\times/\times}r - \gamma\Delta C) \\ & + ((1 - \beta)\Delta B\bar{\phi}q_{\times/\times}r - (1 - \gamma)\Delta C)] \\ & - (1 - q_{o/\times} - q_{\times/\times}r)(1 - \beta)\phi\Delta B. \end{aligned}$$

Using the fact that $\bar{B} \approx (\beta\bar{\phi}q_{o/\times} + (1 - \beta))\Delta Bq_{\times/\times}$ and $\Delta C_\gamma = (\gamma q_{o/\times} + (1 - \gamma))\Delta C$, we obtain the equation

$$\Delta W_{IF} = \bar{B}r - \Delta C_\gamma - r \underbrace{\frac{q_{\times/\times}}{1 + q_{o/\times}}(\bar{B}r - \Delta C_\gamma) - (1 - \beta)\phi\Delta B}_{\Delta E} \left(\frac{1 + q_{o/\times} - q_{\times/\times}r}{1 + q_{o/\times}} q_{\times/\times}r + \frac{1 - q_{o/\times} - q_{\times/\times}r}{1 + q_{o/\times}} \right).$$

Comparison with equations (9) and (13) allow us to identify the underbraced expression with the ecological cost $\Delta E = -b\Delta(q_{o/M} - q_{o/R})$. We can simplify things further and rearrange that equation into

$$\Delta W_{IF} = \frac{1 + q_{o/\times} - q_{\times/\times}r}{1 + q_{o/\times}} \Delta S,$$

where

$$\Delta S = \bar{B}r - \Delta C_\gamma - \Delta E_\beta$$

with

$$\begin{aligned} \Delta E_\beta = (1 - \beta)\phi\Delta B \left(q_{\times/\times}r + \frac{1 - q_{o/\times} - q_{\times/\times}r}{1 + q_{o/\times} - q_{\times/\times}r} \right) \\ = (1 - \beta)\phi q_{\times/\times} \Delta B \left(r + \frac{1 - r}{1 - r + q_{o/\times}(1 + r)} \right) \end{aligned}$$

using the fact that $1 - q_{o/\times} - q_{\times/\times}r = q_{\times/\times}(1 - r)$. We can further simplify the expression for ΔS as

$$\Delta S = \bar{B}\hat{r} - \Delta C_\gamma,$$

where the net relatedness \hat{r} takes the form

$$\hat{r} = r - \phi \frac{1 - \beta}{1 - \beta + \beta\bar{\phi}q_{o/\times}} \left(r + \frac{1 - r}{1 - r + q_{o/\times}(1 + r)} \right)$$

which is equation (20) in the main text.

In the limit of high habitat saturation ($q_{o/\times} = 0$), we find that $\hat{r} = \bar{\phi}r - \phi$. Because $r = 1/(n - 1)$ in the limit of high habitat saturation (Lion and Gandon 2009; Lion 2009), this implies that $\hat{r} = 0$.

On the verge of extinction, we know that $r \rightarrow 1$, so that $\hat{r} = 1 - \phi(1 - \beta)/(1 - \beta + \beta\bar{\phi}q_{o/\times})$. Hence, \hat{r} takes values between $\bar{\phi} = (n - 1)/n$ (when $\beta = 0$, that is, for survival helping) and 1 (when $\beta = 1$, that is, for fecundity helping) on the verge of extinction.

CONDITIONAL COSTS

The previous result is derived for constitutive costs. For conditional costs, we need to take into account density-dependence, and assume that the fecundity rate of helpers takes the form

$$b_M = b + \beta B\bar{\phi}q_{M/Mo} - \gamma\bar{\phi}q_{\times/Mo}C,$$

that is, the costs are proportional to the number of neighbors of a helper connected to an empty site. In the neutral model, $q_{\times/Mo}$ can be approximated by $q_{\times/o} = 1 - q_{o/\times}$ (Lion 2009), so equation (A2) becomes

$$\Delta(b_M - b_R) = \beta\Delta B\bar{\phi}(q_{M/Mo} - q_{M/Ro}) - \gamma\bar{\phi}(1 - q_{o/\times})\Delta C, \tag{A5}$$

Similarly, equation (A3) becomes

$$\begin{aligned} \Delta(\delta_{Mo} - \delta_{Ro}) = -(1 - \beta)\Delta B\bar{\phi}(q_{M/Mo} - q_{M/Ro}) \\ + (1 - \gamma)\bar{\phi}(1 - q_{o/\times})\Delta C. \end{aligned} \tag{A6}$$

For equation (A4), there is an additional subtlety because the cost of the helping individual in a *MR* is due to the $(n - 1) q_{\times/MR}$ other neighbors and to the *R* individual in the pair. This yields

$$\begin{aligned} \Delta(\delta_{MR} - \delta_{RM}) = -(1 - \beta)\Delta B(\bar{\phi}(q_{M/MR} - q_{M/RM}) - \phi) \\ + (1 - \gamma)(\phi + \bar{\phi}(1 - q_{o/\times}))\Delta C \end{aligned} \tag{A7}$$

using $q_{o/MR} \approx q_{o/\times}$ in the neutral model (Lion 2009). Putting everything together, and using the approximation $q_{o/\times i} \approx q_{o/\times}$, we find eventually a closed expression for the selection gradient when costs are conditional.