

EMPTY SITES CAN PROMOTE ALTRUISTIC BEHAVIOR

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Spatial structure has been shown to promote altruistic behavior, however, it also increases the intensity of competition among relatives. Our purpose here is to develop a model in which this competition is minimized, more precisely a local increase in fecundity has a minimal competitive effect on the fitness of nearby individuals. We work with an island model in which sites are allowed to be empty, choosing our demographic rules so that in patches with higher fecundity, empty sites are filled at a higher rate. We also allow dispersal rates to evolve in response to the proportion of empty sites in the patch. Patches with different numbers of empty sites differ in frequency, in within-patch consanguinity, and in reproductive value. Using an inclusive fitness argument, we show that our model does promote altruism; indeed Hamilton's Rule is shown to hold. The only negative effect on an actor of a gift of fecundity to a patchmate turns out to be a slight decrease in reproductive value due to an increased probability of an empty site being occupied. We show that altruists are most favored in islands with an intermediate number of empty sites.

KEY WORDS: Altruism, dispersal, empty sites, inclusive fitness, kin selection, spatial structure.

Indiscriminate altruism is a fascinating phenomenon from an evolutionary point of view because it seems extraordinarily fragile. If an altruist provides a benefit b to a neighbor at a cost c , it is difficult to see how such an individual could survive among cheaters who accept the gift without cooperating. Hamilton (1964) provided an elegant solution to this dilemma by showing that when two individuals are related, it can be in the interest of an altruist to help its kin.

An easy way to introduce systematic variation in relatedness is to work with spatially structured populations. The idea is that if reproduction is mostly local, a focal individual is more likely to be related to individuals that are next to him. Local interactions and local reproduction increase the relatedness among interacting individuals and thereby increase the chance for an altruist to interact with another altruist (if the trait is heritable). Altruists can thus survive in a population of cheaters by creating clusters in which most interactions are between altruists, a fundamental idea that arguably dates from Wilson (1975).

However, local interactions and reproduction can also inhibit altruism because helping a neighbor can increase the strength of local competition. Hamilton (1964) already noticed that the negative effect of increased competition could decrease, and even cancel, the advantage of altruism. It is now well understood that this is a standard feature of spatially structured models (Taylor 1992a; West et al. 2002).

Our objective in this article is to attempt to understand better what aspects of population structure or demography can minimize or even eliminate these local competitive effects and thereby promote altruistic behavior. In a sense, we are interested in the question of what needs hold so that the simple classic condition $Rb > c$, where R is the relatedness between the two interacting individuals, completely describes the selective effects of the altruistic act. As a first cut, this question is tackled as follows. We need a tendency for offspring to stay localized (to keep local relatedness high) without creating increased local mortality. We can imagine two ways this might be arranged. The first is to allow

local expansion or elasticity (Hamilton 1971), and the second is to impose regulation at the global level. In a population of constant size these must in fact be two sides of the same coin, as a local expansion in numbers must be paid for by increased mortality somewhere else. The only way around this might be to have fluctuating resources or selection pressures so that periods of population increase and decrease might alternate. In this case altruism might well be selected during periods of increase, although the opposite might hold during decrease (but the first might win over the second: Uyenoyama 1979). In any event, in a population of constant size, we would need reproduction to be local and population regulation to be global, or more precisely, we need the first to be more local than the second.

Ours is not the first study that introduces empty sites to reduce local competition and favor altruism. Grafen (2007) and Killingback et al. (2006) work with a model that allows patch sizes to increase according to average patch fecundity with global regulation of patch size. Lehmann et al. (2006) developed an analytical model with spatial structure to study the evolution of helping behavior. Finally, in ecology, several models have studied the effect of the elasticity of the population on altruism (for a review, see Lion and van Baalen 2007b). In the Model section, we highlight the difference between this model and these previous models. We also do a more general discussion in the last section.

We work here with a patch-structured model that allows empty sites. The basic idea is that the empty sites should provide “free space” so that a breeder with increased fecundity will have space for her offspring without disadvantaging a neighbor. But care must be taken here; different assumptions on the effect of empty sites on the fecundity of breeders will have different effects, and some of these will reduce local competition and some will not. We look at this question more closely in the Discussion.

Our model uses an inclusive fitness argument to study the fitness of an altruist emerging in a population of cheaters. For the sake of simplicity, individuals are assumed to reproduce asexually and the population is assumed to be infinite. The originality of our study lies in the combination of three points: (1) the strong

analytical basis that allows us to obtain a simple expression for the inclusive fitness of an altruist, (2) the identification of the underlying processes, particularly the fact that we keep track of the number of empty sites, and (3) the fact that we allow dispersal rates to depend on the patch type.

Model and Results

We develop an infinite island model similar to that of Cadet et al. (2003) (Fig. 1). The population is structured into patches with n sites, each site occupied by a single breeder or empty. A patch of type i ($0 \leq i \leq n$) has i sites occupied and we let p_i be the proportion of type i patches in the population and denote by $x_i = i/n$ the proportion of full sites in the patch (all the notations used are summarized in Table 1).

We use a Moran model (Moran 1962) to provide a continuous-time population dynamic. We suppose that each breeder in a type- i patch produces offspring at rate 1, sending each offspring to a random patch with probability m_i and keeping it to compete at home with probability $h_i = 1 - m_i$. We assume that at each patch, native and immigrant offspring compete for the empty sites on an equal basis and each empty site is filled at a rate proportional to the total “pressure” exerted by both kinds of offspring. More precisely, we assume that each offspring, native or immigrant, fills each empty site in the patch (at which it is competing for a site) at rate $1/n$. It is important to note the significance of this assumption—it implies that the more offspring there are in competition at a particular patch, the higher will be the patch growth rate, that is, the rate at which any empty site is filled. In addition, each breeder dies at rate k . Note that contrary to Cadet et al. (2003) we do not follow explicitly the density variations in the pool of offspring competing at each patch; those who do not obtain a breeding site are simply assumed to die.

Recent Moran models have been classified into a number of types, two of which are BD and DB (Lieberman et al. 2005; Taylor et al. 2007). Both of these are fecundity-based models in that relative fecundity determines competitive success in offspring

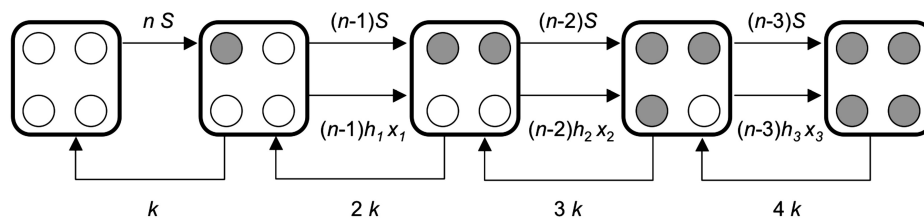


Figure 1. Transitions between types of patches. Each patch has the same number of sites (here $n = 4$) that can be full (in gray) or empty (in white). Bottom arrows indicate that a site becomes vacant following the death of a breeder (which occurs with probability k). Middle arrows indicate that a site gets filled through local reproduction of one of the individuals in the patch (the birth rate is density dependent). Top arrows indicate that a site gets filled by an immigrant offspring, coming from another patch (at a rate that depends on the immigrant pressure S defined in equation A.2). For further details, see the Appendix.

Table 1. Symbols and notation used. The second column indicates the default value of constant parameters.

| Notation | Value | Description |
|----------|-------|--|
| R | — | Relatedness |
| b | — | Fecundity benefit conferred by an altruist |
| c | — | Cost of conferring benefit b |
| i | — | Number of full sites in a patch |
| n | 10 | Total number of sites per patch |
| x_i | — | $= i/n$, Proportion of full sites in a type- i patch |
| m_i | — | Fraction of the offspring that disperse in a type- i patch |
| h_i | — | $= 1 - m_i$, Fraction of the offspring that stay in a type- i patch |
| S | — | Rate at which an empty site is filled by an immigrant |
| k | 0.5 | Uniform death rate of breeders |
| p_i | — | Equilibrium proportion of type- i patches in the population |
| v_i | — | Reproductive value of an individual in a type- i patch |
| G_i | — | Consanguinity between patchmates in a patch of type i |

recruitment. In BD models, patch birth rates (effectively, offspring occupancy rates) increase with average patch fecundity and also, therefore, do death rates. In DB models, death rates, and therefore patch-wide birth rates, are constant, and individual birth rate depends on relative fecundity within the patch. By this classification, our model incorporates features of both kinds—our patch birth rate increases with average patch fecundity, and our death rate is constant.

DISPERSAL

One other notable feature of our model needs emphasis. Contrary to previous patch-structured models (Lehman et al. 2006; Grafen 2007), we do not fix patch dispersal rate m_i at an arbitrary value, but assume that it is determined by evolutionary dynamics, that is, we set the m_i at their ESS values (see the Appendix for further details). Our intuition predicts that patches with many empty sites (small i) should have low dispersal rates, as there are good reproductive opportunities at home, and patches with few empty sites (large i) should have high dispersal rates. This turns out to be the case (Fig. 2D); indeed we find a “bang-bang” strategy—there is a transitional value i_0 below which m_i is 0 and above which m_i is 1. In the cases we have made calculations for, i_0 turns out to be close to $n/2$. Note that this differs from the assumptions of Cadet et al. (2003) where m_n is taken to be 1 and all other m_i are set at a common smaller value that is allowed to evolve to a stable value.

We remark that in standard island models in which there are no empty sites, all offspring will be selected to disperse un-

less there is a cost to dispersal (Hamilton and May 1977; Taylor 1988). In our model we assume no physiological, proximate cost of dispersal (although other costs may emerge); nevertheless dispersal is favored for high-density patches precisely because of the variation in patch density.

Figure 2A shows the distribution of patch type proportions p_i , when values of m_i are at equilibrium (see below) for the case in which there are $n = 10$ sites per patch. With the demographic settings described above, we find that patches with high or low local densities are rare and that most patches have intermediate densities.

REPRODUCTIVE VALUE

In our model, breeders in patches with different density have different reproductive value and this must be taken into account both in the calculation of the ESS dispersal rate and, more significantly, in the calculation of the inclusive fitness effect of any interaction between breeders (Taylor 1990). For example, an interaction that changes the fecundity of one breeder will affect the rate at which the patch moves to a higher i value and will therefore affect the reproductive value of all breeders in the patch. We let v_i be the reproductive value of a patch i breeder. These values are shown in Figure 2B for the case where $n = 10$. Note that reproductive value decreases rapidly when within-patch density increases.

RELATEDNESS

Because we work with an infinite population, the relatedness between two breeders from different patches is zero. We let G_i denote the coefficient of consanguinity between two (different) random breeders in the same i -patch, and these are plotted against i in Figure 2C for $n = 10$. These are seen to decrease with patch density, although it is interesting to note that if the dispersal rates m_i are set to be the same in all patches, independent of i , then the G_i are also independent of i . An interesting feature of Figure 2C is the relatively slow linear decline of relatedness until $i = 6$ followed by a relatively large drop from $i = 6$ to $i = 7$. The reason is that because patches of size $i \leq 5$ keep all their offspring at home (and also receive immigrants, they have a high growth rate and patches of size $i \leq 6$ are often formed from those with one less breeder. Suddenly at $i = 7$ this ceases to be the case, as patches of size $i \geq 6$ disperse all their offspring. Another consequence of this is the sudden drop in patch type frequency from $i = 6$ to $i = 7$ illustrated in Figure 2A, as a 6-patch can become a 7-patch only when an immigrant offspring colonizes an empty site.

Equations and calculations for the p_i , G_i , and v_i are given in the Appendix.

INCLUSIVE FITNESS

We suppose a rare altruist confers a benefit b on one of its patchmates at a cost c , and we use an inclusive fitness argument to find

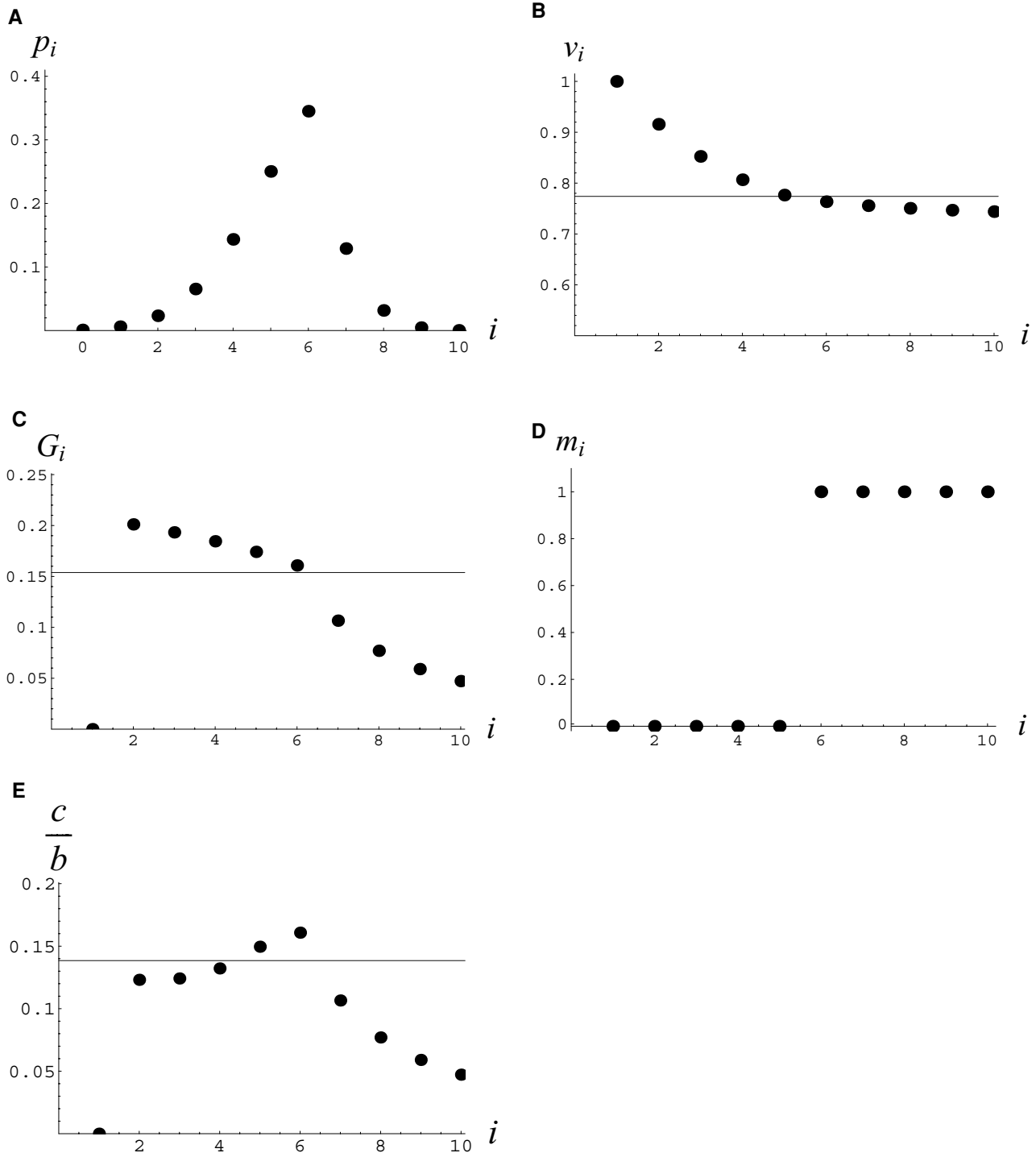


Figure 2. Equilibrium values of patch type frequency (A), reproductive rate (B), consanguinity (C), dispersal rate (D) and inclusive fitness (E). Figures A, B and C are obtained following the calculations described in Appendix A. Figure D shows the evolutionary stable dispersal rate for each patch type. Figure E shows the c/b ratio that allows an altruistic mutant to invade. The horizontal lines indicate the average value in the whole population. Parameter values are: $n = 10$ and $k = 0.5$.

the condition for this behavior to invade the population. We expect the condition to depend on the patch type i .

Note that we implicitly assume that the evolution of dispersal strategies takes place on a faster time scale than the evolution of

cooperation, and we thereby set the m_i at their evolutionary equilibrium before studying the inclusive fitness. This makes sense considering the fact that dispersal behavior is often a plastic response to changes in local densities, as shown from unicellulars

to Vertebrates (Bernstein 1984; Fonseca and Hart 1996; Lambin et al. 2001; Matthysen 2005; Hauzy et al. 2007). In the case there are $n = 10$ sites per patch, we find that $m_i = 0$ for $i \leq 5$ and $m_i = 1$ for $i > 5$.

An extra offspring produced in an i -patch translates into an extra breeder at home at rate $h_i(1 - x_i)$, and in a foreign patch at rate $m_i \sum_{j=0}^{n-1} (1 - x_j)p_j$. The total fitness effect through this offspring is then:

$$h_i(1 - x_i)v_{i+1} + m_i \sum_{j=0}^{n-1} (1 - x_j)p_j v_{j+1} \quad (1)$$

Now suppose a focal individual in patch type i gives b to a patchmate at cost c . The change W_i in her inclusive fitness is the sum of two terms—the RV of the extra offspring resulting from the interaction, and the change in RV of other breeders in the patch due to the extra rate of increase in patch type from i to $i + 1$ (Taylor 1988; Rousset and Ronce 2004):

$$W_i = (bG_i - c) \left[h_i(1 - x_i)v_{i+1} + m_i \sum_{j=0}^{n-1} (1 - x_j)p_j v_{j+1} \right] + (b - c)(1 + (i - 1)G_i)h_i(1 - x_i)(v_{i+1} - v_i) \quad (2)$$

Here, $bG_i - c$ is the sum of the extra offspring produced, weighted by their relatedness to the focal, and these are multiplied by the rate at which they will obtain breeding sites (eq. 1). The second term is the product of the total number of offspring $b - c$, the relatedness of the focal individual to the patch as a whole, the rate at which each of these extra offspring obtains a local breeding site, and the resulting change in RV. Note that this second term is the only effect on others in the patch (other than donor and recipient) and this shows that the model has effectively removed the local competitive effects of benefits given to patchmates.

For small b and c , the invasion condition for the altruistic behavior is $W_i > 0$, that the inclusive fitness be positive (Taylor 1988). Note that when $h_i = 0$ (all offspring disperse), as is the case for $i \geq 6$, the second term of equation (2) is zero, and the invasion condition is simply $bG_i - c > 0$. Note how this is reflected in a comparison of Figure 2C and 2E—the last five points in the two graphs coincide.

Figure 2E shows that the highest critical c/b ratio is obtained in a patch of type $i = 6$, the first patch in which m_i shifts from 0 to 1. A couple of factors contribute to this. First there is the sharp drop in relatedness from $i = 6$ to $i = 7$ (Fig. 2C) discussed above, and second because any new offspring in a 6-patch will disperse, the altruist does not pay the cost of a decreased RV due to an increase in the rate of growth from $i = 6$ to $i = 7$.

Discussion

William Hamilton's groundbreaking (1964) paper gave the world the classic formula

$$Rb > c \quad (3)$$

for the selective advantage of altruism in a population. Here, b is the benefit given to a neighbor with relatedness R at cost c to the altruist. Hamilton was clear that for this formula to apply, both b and c must measure ultimate fitness effects, for example, the number of adult offspring of an individual. Of course this is rarely the case—it has been understood for a long time that such an exchange of fitness, from donor to recipient, will generally have fitness effects on others in the population, for example, those provided by the competitive effects created or removed by changes in local density. For example, in an island model such as the one studied here, an extra unit of fecundity given to a patchmate will compete with the donor's offspring and indeed with the recipient's offspring, whenever there are constraints on the total reproductive output of the patch. In such cases, Hamilton's Rule requires a more general "inclusive fitness" formulation

$$\sum_i R_i B_i > C_0, \quad (4)$$

where C_0 is the ultimate fitness cost to the focal individual, B_i is the ultimate fitness benefit to individual i , and R_i is the relatedness of the focal to individual i . These ultimate fitness effects can often be hard to measure and require precise knowledge of the population structure and the interaction of its components. Since the time of Hamilton's original paper, a large literature has established that, under simple general conditions, mainly weak selection and additive gene action, condition (4) is the precise condition for the altruistic allele to increase in frequency.

However it is of interest to ask under what circumstances the more direct formulation (3) might provide the correct condition. Suppose that b and c are measured in immediate terms such as fecundity or survival—when will (3) give us an accurate measure of the ultimate effects? If you like, when is condition (3) equivalent to condition (4)? For example, this can be the case in a panmictic population, with interactions between "neighbors" when b and c measure immediate fecundity effects and population regulation (mortality) is global. But what other general demographics will provide this equivalence? This is one of the questions we are interested in here.

In terms of the selective effects of an altruistic act, Hamilton realized already in 1964 that the negative effects of competition can work against the positive effects of genetic similarity. For populations that are subdivided into "standard-sized batches," each of which is allotted a "standard-sized pool of reproductive potential," the progress of an altruistic gene will be slowed. He credited the

original observation of this phenomenon to an earlier study of Haldane (1922) on sib competition. Hamilton returns to this idea in 1971 with the observation that “the most ‘system-like’ version of an ‘isolation-by-distance’ model, which is supposed to preclude long-range migration and elastic expansion from vigorous areas, is rather hostile to altruism.” Here Hamilton is describing island-like models of various kinds and he identifies two factors that ought to reduce the competitive effects of a gift of fitness: the first is that the resulting extra offspring will disperse so that they have little chance of meeting a relative, and the second is that there is some opportunity for the patch to “expand” thus moderating the competitive effects. These two factors can be distinguished by describing one as global, sending extra offspring away, and the other as local, an “elasticity” of the island itself.

With respect to Hamilton’s rule, these two factors work in very different ways. Analyses of Wilson et al. (1992) and Taylor (1992a,b) show that in the simplest cases the global effect plays no role in promoting altruism and the dispersal rate does not even appear in the condition for altruism to be favored. Increased dispersal, which exports the benefits of altruism, also reduces within-patch relatedness that makes altruism less profitable, and in simple models with nonoverlapping generations, these two effects exactly cancel.

Thus, if we want to construct a structured population that can promote altruistic interactions in the sense that condition (3) will track allele frequency change, we need to find a mechanism for local expansion. If empty sites come available to be filled at a fixed rate and all occupants of the patch compete for these sites according to their fecundity, then extra fecundity of one breeder will in fact decrease the chances of all others. To eliminate this competitive effect, we must arrange for a patch with increased average fecundity to have an increased average reproductive rate, or more precisely, a patch with increased average fecundity must have an increased average reproductive rate at home. In a nonoverlapping generation model, this is awkward to do, but in a continuous time Moran model, such as we use here, this is easily done by making the rate at which empty sites are filled increase with average patch fecundity. This is what we assume here. To emphasize this point, we remark that it is a common idea (West et al. 2002) that inserting a dispersal stage between the phases of interaction and competition will alleviate the competitive effects of the altruism, reducing condition (4) to condition (3). (An exception is found when dispersal is in groups (buds)—[Gardner and West 2006].) There is much truth in this, but it is a pyrrhic victory for condition (3) as it is restored with a small or a zero relatedness coefficient. For example, in Taylor’s simple (1992a) model, dispersal separates interaction and competition, but the conditions for altruism to be selected are independent of the dispersal rate and are the same as if the population were randomly mixed.

The effect of our model on within-patch competition can be clearly seen in our calculation of the fitness effects of incremental fecundity to a focal individual. There is, of course, the direct effect of more offspring for the focal individual, both local and global, but there is no direct “competitive” effect on others. Indeed the only effect on patchmates is found in the second term of equation (2) and depends on the fact that individuals in patches of different types have different reproductive value. That is, if all individuals had the same RV, equation (2) would be zero.

Indeed, the variation in individual reproductive value among patch types is an interesting feature of our model. As Figure 2B shows, the expected contribution of a breeder to the future of the population depends on and decreases with patch density, the reproductive value of an individual in a full patch being 75% of that of an individual who finds itself alone in the patch.

A number of previous works have studied patch elasticity. A two-dimensional lattice model of Mitteldorf and Wilson (2000) allows empty sites and gives them a “fitness” as if they were a special third type of occupant (the others being altruist and selfish). To get a stable internal equilibrium they also need a small fitness-independent death rate, but given this, they find selection for altruism for large benefit:cost ratios. Killingback et al. (2006) discuss a public-goods game in an island model in which regulation is global and keeps the average island size constant, while allowing islands to fluctuate in size. If we convert the interaction to a direct fecundity benefit and cost, the game can be regarded as a model of altruism, and in this case, for an average group size of five and a dispersal rate of 0.1, they find that altruism is selected for a c/b ratio of close to 0.4 (taking the parameter values of their Fig. 2A as a critical set for the selection of altruism, where b is the fecundity benefit given to others in the group). Grafen (2007) shows that their model lies squarely within the domain of inclusive fitness and shows how the relatedness can be calculated (which for fluctuating group size is nontrivial). His calculations give an average relatedness (to other members of the group) of R close to 0.4, so that the classic condition (3) appears to hold. Lehmann et al. (2006) develop a rich spatial model to test both the effects of demographic stochasticity and environmental stochasticity on helping behaviors. As Killingback et al. (2006) and Grafen (2007) they assume a constant dispersal rate, which means they only have access to an average inclusive fitness value. They study several processes by which the altruist may confer a benefit to his patchmates. The process they use which is the closest to ours (‘density-dependent survival of juveniles’ and ‘helping increases the fitness of all individuals in the deme excluding the actor’) leads to threshold values ranging from 0.25 to 0 depending on the fecundity value (which in our model is set to 1).

Our model has similarities and differences from those described above. It has a fixed island size in the sense of a fixed number of sites, but allows empty sites, so that the effective group

size fluctuates. A stable average group size is maintained by having a constant death rate but making group productivity density dependent in a natural way. The most original feature of the model is perhaps that the dispersal rate d is also determined by the condition that dispersal behavior be at evolutionary equilibrium, and we find (as expected) extreme dispersal rates of $d = 0$ in low density patches and $d = 1$ at high density (Fig. 2D). Because of this feature, our model is perhaps more related to models on the evolution of dispersal. It corroborates classical results, that is, optimal dispersal decreases when density increases (Frank 1986; Taylor 1988). Interestingly, our solution also fits with the approximation Cadet et al. (2003) derive from their simulations: they show the same “bang-bang” distribution when they plot dispersal as a function of mortality, or fecundity, or carrying capacity. They also argue in the discussion that kin selection is likely to operate but that its consequences are difficult to assess. Here, we manage to estimate inclusive fitness values that depend on the type of patch the altruist is in. If we take patch size to be $n = 10$, we get an average patch relatedness of 0.15 and that is very close to our average c/b ratio (Fig. 2E). So again condition (3) appears equivalent to condition (4).

Let us emphasize the significance of condition (3). We suppose that a focal individual gives a fecundity benefit b to a neighbor with relatedness R at fecundity cost c . It is not hard to argue (from a Taylor expansion) that for small b and c , the fitness effects C_0 and B_i in condition (4) will be linear expressions in b and c and therefore condition (4) depends only on the ratio c/b . Let the threshold value of this ratio be R_H . Think of this as the value that relatedness would have to take for condition (3) to completely describe the action of selection. Then condition (4) that the altruistic act be selected can be written in the form

$$R_H b > c. \quad (5)$$

The difference between this condition and condition (3) is that condition (5) accounts for all the competitive effects on the focal individual of the extra offspring. Thus we generally expect that $R_H < R$. That is, because of competitive effects, for the behavior to be selected, a fixed benefit b would have to come at a smaller cost than condition (3) would predict. Our interest here is to find conditions under which $R_H = R$ as these represent models in which there are no local competitive effects of the altruistic behavior; in a sense, the set of such examples provide a natural boundary for models of altruism. We have pointed above to two examples for which R_{AH} appears to be close to R —Grafen’s (2007) model of variable-size patches and our own model of empty sites. This emphasis on the validity of equation (3) was already made by Lehmann and Keller (2006) in a review that led to an interesting discussion.

It is also interesting to compare our model with certain ecological models with spatial self-structuring (van Baalen and Rand

1998; Le Galliard et al. 2003a, 2005; Lion and van Baalen 2007a). In these models, space is usually defined as a network of sites. In their review, Lion and van Baalen (2007b) show that the invasibility condition of a rare altruistic mutant in these populations when the physiological benefit of altruism affects survival, and the physiological cost affects fecundity can be summarized by the condition

$$\Delta B q_{M/M} > -\Delta(b_M q_{o/M}), \quad (6)$$

where ΔB is the marginal benefit obtained by a recipient and $b_M q_{o/M}$ is the fecundity of an altruist in the group of altruists that is invading. The term $q_{o/M}$ is the average density of empty sites seen by a mutant (it decreases when neighbors reproduce): it comes from the fact that these models are analyzed using spatial correlation equations. As Lion and van Baalen note, this equation is very similar to condition (4) (i.e., R_H is close to R) because the mean number of mutants seen by a mutant ($q_{M/M}$) can be seen as a measure of relatedness.

There are three specificities of our model that make it interesting to test experimentally. The first one is that we work with measurable quantities (number of empty sites). The second specificity is that dispersal rates are not constant but vary across patch types. Finally, we make testable predictions regarding the effect of the number of empty sites on the fitness of an altruist. Our study could provide an analytical framework for laboratory and field studies that follow both the relatedness and the dispersal. For instance, it has been showed that both local female density and kinship affect dispersal in the lizard *Lacerta vivipera* (Lena et al. 1998; Le Galliard et al. 2003b). Recently, Moore et al. (2006) also showed that kin competition avoidance favors dispersal in fig wasps. However, as stressed by Lambin et al. (2001), the evidence for links between dispersal and kinship is very scarce. The few existing studies are done with Vertebrates and focus on the importance of sexual disparities in dispersal rates. A possibility to test these ideas experimentally could be to work with microorganisms that have specialized dispersal forms. It might also be interesting to use a simple bacterial system in which cooperative behavior occurs (see West et al. 2006 for a review) to recreate the spatial structure and the dispersal behaviors of this model. In this setup, a patch would be a set of tubes (the ‘sites’) that can be empty or filled with bacteria. The main limitation is that our model rests upon the assumption of infinite population, or more precisely here an infinite number of patches. This assumption is important because it allows us to assume that relatedness between individuals from different patches is zero. Precise application of our model to biological systems might require lifting the infinite patch assumption, which would require a numerical approach.

In many evolutionary studies of behavior, the equilibrium attained represents a balance between reproduction and local

competition. Our empty sites model is of potential interest in exploring the effect of population “elasticity” on such behavior. An interesting development of our model could be to study diploid individuals because dispersal often involves asymmetric behavior between the sexes. For example, a number of studies have investigated the coevolution of sex-ratio and sex-specific dispersal (e.g., Leturque and Rousset 2003; Wild and Taylor 2004) and sex-ratio bias can be interpreted as an altruistic trait (Colwell 1981). It would be of interest to understand the effect of variation in patch density found in our model on these traits.

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Appendix

Because p_i is the proportion of type i patches in the population, the overall proportion of full sites is given by

$$\bar{x} = \sum p_i x_i \tag{A1}$$

Each breeder reproduces at rate 1, the offspring staying to compete home with probability h_i and arriving to compete at a random patch with probability $m_i = 1 - h_i$. Thus an i -patch produces native offspring at rate $i h_i$ and exports migrants at rate $i m_i$. Immigrant offspring arrive to compete at a random patch at rate $\sum_{j=1}^n j m_j p_j$ so that the total rate at which offspring arrive to compete at an i -patch is $i h_i + \sum_{j=1}^n j m_j p_j$. However, for the parameter set we use here, not all of these offspring find a breeding site, and those who do not are presumed to die. Indeed, under our assumption that each competing offspring fills each empty breeding site at rate $1/n$, each empty site in an i -patch is filled by a native at rate $i h_i/n = x_i h_i$ and by an immigrant at rate

$$S = \sum_{j=1}^n x_j m_j p_j \tag{A2}$$

so that an i -patch is occupied by an offspring at rate $(n - i)(x_i h_i + S)$. This is the rate at which an i -patch becomes an $i + 1$ patch. In addition, because each breeder dies at rate k , the i -patch becomes $i - 1$ at rate $i k = n x_i k$.

Note that each i -individual places a native offspring at rate $h_i (n - i)/n = (1 - x_i) h_i$ and places a migrant offspring in a j patch at rate $m_i p_j (n - j)/n = m_i p_j (1 - x_j)$.

With these elementary birth and death processes, we first derive the stable distribution of type frequencies (p_i). Then, we derive the relatedness (G_i) and the reproductive value (v_i) of each type of patch. This allows us to find the evolutionary equilibrium value of the dispersal rate (m_i). Finally, we derive the inclusive fitness (W_i) for each type of patch.

Calculation of patch type frequencies. The rate at which the frequency of type i patches changes has four components:

$$\begin{aligned} i\text{-patch birth:} & \quad - (n - i) (S + x_i h_i) p_i \quad (i < n) \\ i\text{-patch death:} & \quad - i k p_i \quad (i > 0) \\ (i - 1)\text{-patch birth:} & \quad (n - i + 1) (S + x_{i-1} h_{i-1}) p_{i-1} \quad (i > 0) \\ (i + 1)\text{-patch death:} & \quad (i + 1) k p_{i+1} \quad (i < n) \end{aligned}$$

Thus, for $0 < i < n$:

$$\begin{aligned} \Delta p_i &= -[(n - i)(S + x_i h_i) + i k] p_i \\ &\quad + (n - i + 1)(S + x_{i-1} h_{i-1}) p_{i-1} + (i + 1) k p_{i+1} \\ \Delta p_0 &= -n S p_0 + k p_1 \\ \Delta p_n &= -n k p_n + (S + x_{n-1} h_{n-1}) p_{n-1} \end{aligned} \tag{A3}$$

Solving this $n + 1$ equation system allows us to find the values of the p_i when the stable distribution is reached. However, the solution is intractable and we use a numerical approach.

Reproductive value calculations. Let v_i be the RV of an individual in a type- i patch. Look at the probabilities of the different events in time dt that could affect the RV of a focal class i individual.

Table A1. Changes in reproductive value.

| Event | rate | New RV | Change in RV |
|---|-------------------------|-----------------|------------------|
| Focal dies | k | 0 | $-v_i$ |
| Another in patch dies | $(i - 1) k$ | v_{i-1} | $v_{i-1} - v_i$ |
| Focal offspring occupies native site | $h_i (1 - x_i)$ | $2v_{i+1}$ | $2v_{i+1} - v_i$ |
| An offspring of a patchmate occupies native site | $(i - 1) h_i (1 - x_i)$ | v_{i+1} | $v_{i+1} - v_i$ |
| Focal offspring occupies site in foreign j -patch ($0 \leq j \leq n - 1$) | $m_i (1 - x_j) p_j$ | $v_{j+1} + v_i$ | v_{j+1} |
| Empty site in focal patch is occupied by foreign offspring | $(n - i) S$ | v_{i+1} | $v_{i+1} - v_i$ |

The expected change in RV for type i is the average of the rows in Table A1:

$$\begin{aligned} \Delta v_i &= v_{i-1}(i - 1)k - v_i[ik + (1 - x_i)(ih_i + nS)] \\ &\quad + v_{i+1}(1 - x_i)(ih_i + h_i + nS) + m_i \sum_{j=0}^{n-1} (1 - x_j) p_j v_{j+1} \end{aligned} \tag{A4}$$

If we set all these to zero, for $1 \leq i \leq n$, we get a set of n equations in v_1, v_2, \dots, v_n , which can be solved to give the v_i . However, note that the system has rank $n - 1$. Indeed we expect the average change in RV to be zero. Because a type i breeder has frequency $x_i p_i / \bar{x}$, the average change in RV is $\sum_{i=1}^n \frac{x_i p_i}{\bar{x}} \Delta v_i$ and it can be shown that this is zero. We solve the system by setting $v_1 = 1$ (for example), and solving any $n - 1$ of the equations.

Calculation of the coefficients of consanguinity. Because we work with an infinite population, the average relatedness between two breeders on different patches is zero. If the dispersal rates vary among sites, then the relatedness between two individuals on the same patch depends on the type of patch they are in. Let G_i be the coefficient of consanguinity between two random individuals on an i -patch.

Consider the set of all i -patches. This gets new members in a number of ways.

- (1) an $(i - 1)$ -patch becomes an i -patch through internal birth at rate $\alpha_i = (n - i + 1) h_{i-1} x_{i-1} p_{i-1}$
- (2) an $(i - 1)$ -patch becomes an i -patch through migrant birth at rate $\beta_i = (n - i + 1) S p_{i-1}$

(3) an $(i + 1)$ -patch becomes an i -patch through death at rate $\gamma_i = (i + 1) k p_{i+1}$

where S is given by equation (A2).

Now we take two (different) focal individuals in an i -patch ($i \geq 2$) and ask where they came from. What was the most recent event?

In Table A2, for $i = n$, the second-last row is missing and the total is $\alpha_i + \beta_i$. For $i = 2$, the G_{i-1} rows are absent but they have zero weight so the total is still $\alpha_i + \beta_i + \gamma_i$.

Table A2. Changes in consanguinity.

| Event that created i -patch ($2 < i < n$) | rate | Former G |
|--|------------------------------------|------------|
| Internal birth in $i - 1$ patch — one focal gives birth to the other | $2\alpha_i / i(i-1)$ | 1 |
| Internal birth in $i - 1$ patch — otherwise | $\alpha_i(i^2 - i - 2) / (i(i-1))$ | G_{i-1} |
| External birth in $i - 1$ patch (focal born) | $2\beta_i / i$ | 0 |
| External birth in $i - 1$ patch (nonfocal born) | $(i-2)\beta_i / i$ | G_{i-1} |
| Death in $i + 1$ patch ($i \leq n - 1$) | γ_i | G_{j+1} |
| Total | $\alpha_i + \beta_i + \gamma_i$ | |

This gives us the following recursive formula for G_i

$$G_i = \frac{1}{\alpha_i + \beta_i + \gamma_i} \left[\alpha_i \frac{2 + (i^2 - i - 2)G_{i-1}}{i(i-1)} + \beta_i \frac{(i-2)G_{i-1}}{i} + \gamma_i G_{i+1} \right] \quad (2 \leq i < n) \tag{A5}$$

$$G_n = \frac{1}{\alpha_n + \beta_n} \left[\alpha_n \frac{2 + (n^2 - n - 2)G_{n-1}}{n(n-1)} + \beta_n \frac{(n-2)G_{n-1}}{n} \right]$$

If we set all these to zero, for $2 \leq i \leq n$, we get a set of $n - 1$ equations in G_2, G_3, \dots, G_n , which can be solved to give the G_i .

Optimal dispersal rates. The previous calculations all involve the dispersal strategies (the m_i). As stated earlier, we assume that there is a constraint on the dispersal strategy such that we can replace all h_i by $1 - m_i$. To find the optimal value of m_i , we evaluate the consequences of a slight variation of m_i on the fitness of an individual in an i -type patch. If a focal increases its m_i by δm_i , there are three consequences on the fitness of the focal (see Table A2):

1. the focal gets more births in distant patches: $\delta m_i (\sum_{j=0}^{n-1} p_j (1 - x_j) v_{j+1})$
2. there are less local births, which affects the focal: $-\delta m_i (1 - x_i) (2v_{i+1} - v_i)$
3. and its patch mates: $-\delta m_i (i - 1) (1 - x_i) (v_{i+1} - v_i) G_i$

Thus, we can evaluate the value dm_i by which m_i should be modified to maximize the fitness of breeders in patches of type i :

$$dm_i = \delta m_i \left[\left(\sum_{j=0}^{n-1} p_j (1 - x_j) v_{j+1} \right) - (1 - x_i) (2v_{i+1} - v_i + (i - 1)(v_{i+1} - v_i)G_i) \right] \tag{A6}$$

If we choose initial values for the m_i and update them by dm_i , after several iterations the system converges toward a stable state (note that at each iteration we need to update the values of p_i, G_i , and v_i). We find that, with an even number of sites per patch, $m_i = 0$ if $i < n/2$ and $m_i = 1$ if $i \geq n/2$. With an odd number of sites per patch, $m_i = 0$ if $i < (n + 1)/2$ and $m_i = 1$ if $i \geq (n + 1)/2$. An easy way to check this result is to use these optimal values as initial values and check that the value of the dm_i is positive for patches where $m_i = 1$ and negative for patches where $m_i = 0$. Such a ‘bang-bang’ distribution is not surprising because the choice of where to send the offspring is made instantaneously on one offspring, which precludes any type of bet-hedging. Note that Cadet et al. (2003) find a similar pattern in their model in which full sites have a different dispersal rate from other sites.