EVOLUTION OF HELPING AND HARMING IN HETEROGENEOUS POPULATIONS

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There has been much interest in understanding how demographic factors can mediate social evolution in viscous populations. Here, we examine the impact of heterogeneity in patch quality—that is, the availability of reproductive resources for each breeder—upon the evolution of helping and harming behaviors. We find that, owing to a cancellation of relatedness and kin competition effects, the evolution of obligate and facultative helping and harming is not influenced by the degree of viscosity in populations characterized by either spatial or temporal heterogeneity in patch quality. However, facultative helping and harming may be favored when there is both spatial and temporal heterogeneity in patch quality, with helping and harming being favored in both high-quality and low-quality patches. We highlight the prospect for using kin selection theory to explain within-population variation in social behavior, and point to the need for further theoretical and empirical investigation of this topic.

KEY WORDS: dispersal, facultative behavior, kin selection, obligate behavior, reproductive value, scale of competition.

One of the major challenges for evolutionary biology is to explain the evolution of cooperative behavior (Maynard Smith and Szathmáry 1995; Hamilton 1996; West et al. 2007a). Natural selection favors those individuals who achieve greater personal reproductive success, relative to the other individuals in their population (Darwin 1859; Fisher 1930; Price 1970). All else being equal, a cooperative behavior that improves the reproductive success of another individual will reduce the actor's relative fitness, and hence it will be disfavored by natural selection. However, all else need not be equal. First, the actor may also derive a direct-fitness benefit, owing to mechanisms such as reciprocity (Trivers 1971) or by-product mutualism (West-Eberhard 1975). Such cooperation is termed "mutually beneficial" (West et al. 2007b). Second, the actor may derive an indirect-fitness benefit, as a consequence of being genetically related to the recipients of the cooperative behavior (Hamilton 1964). Such cooperation is termed "altruistic" (Hamilton 1964; West et al. 2007b).

One way in which relatedness may arise between social partners is if dispersal rates are low, such that individuals will tend to be genealogically close to their neighbors ("viscous" populations; Hamilton 1964, 1971). As this mechanism does not require discrimination of one's genetic relatives, it appears to provide a very general solution to the problem of altruistic cooperation. However, a problem with this idea is that limited dispersal may also exacerbate competition among social partners (Hamilton 1971; Queller 1992; West et al. 2002; Griffin et al. 2004). In the simplest scenario of an inelastic (i.e., saturated), viscous population, the relatedness and competition effects of limited dispersal exactly cancel, so that there is no net impact of the rate of dispersal upon the evolution of indiscriminate helping (Taylor 1992a, b; Kümmerli et al. 2009).

This has stimulated the development of a large body of theoretical—and, increasingly, empirical—research, examining factors that may decouple the relatedness and competition effects of dispersal. For example: population elasticity (Taylor 1992b; Alizon and Taylor 2008), overlapping generations (Taylor and Irwin 2000; Irwin and Taylor 2001), budding dispersal (Gardner and West 2006; Lehmann et al. 2006; Kümmerli et al. 2009), life-cycle and timing of the social behavior (Taylor 1992a; Lehmann and Rousset 2010), behaviors mediating patch extinction

probabilities (Lehmann et al. 2006), variable group size (Grafen 2007), trans-generational altruism (Lehmann 2007, 2010), dispersal-dependent social behavior (El Mouden and Gardner 2008), and sex-biased dispersal (Johnstone and Cant 2008; Gardner 2010).

All this work has concerned populations in which resources are evenly distributed among patches—that is, patches do not vary in their intrinsic quality. However, all natural populations are characterized by some degree of resource heterogeneity, and the impact of this variation has been of great interest to ecologists and evolutionary biologists (Levins 1968; Begon et al. 2006). The potential for resource heterogeneity to mediate the evolution of helping behaviors has been considered by Frank (1996, 2003, 2010), suggesting that individuals with greater resources will be favored to make greater investments into helping. However, Frank's models do not place the evolution of social behavior within an explicit viscous population setting, and so cannot address the issue of whether population viscosity drives the evolution of social behavior.

Here, we investigate the impact of heterogeneity in resource availability on the evolution of indiscriminate helping in viscous populations. We consider scenarios in which different patches have different resource availability at any given time and/or the same patch has different resource availabilities at different times, (i.e., spatial and/or temporal heterogeneity; cf Cohen and Levin 1991), and we describe the genetic structuring of the population that results from this variation, and its impact upon local competition for resources. In particular, we examine how relatedness and resource competition arise as a consequence of these demographic factors, how they become intertwined or decoupled within patches and across whole populations, and how they interact in mediating the evolution of helping and harming behaviors that are either obligate or facultatively adjusted to the availability of resources.

Model and Analysis
MODEL

We assume an infinite island model (Wright 1931), with social interactions among patchmates (Taylor 1992a). Each patch contains n haploid, asexual individuals. We consider two types of patches: high-quality patches that have high resource availability, and low-quality patches that have low resource availability. Individuals in high-quality patches each produce a large number $F_H = f(x, y)$ of offspring, and individuals in low-quality patches each produce a large number $F_L = s f(x, y)$ of offspring, where x is the individual's investment in the social behavior, y is the average investment among that individual's social partners, and $0 \leq s \leq 1$. Following reproduction, all adults die, and each surviving offspring disperses with probability m to a random patch

Table 1. A summary of model notation.

Symbol	Meaning
H	High-quality patch
L	Low-quality patch
O	Obligate social behavior
T	Corresponding to Taylor's (1992) analysis
P	Primary recipient
S	Secondary recipient
A_X	Potential for helping in condition X
α	Probability that a high-quality patch remains a high-quality patch
β	Probability that a low-quality patch remains a low-quality patch
c_X	Class-reproductive value in condition X
F_X	Fecundity of a breeding female in condition X
$\tilde{h}$	Probability that an individual chosen at random is native to the patch
h_X	Probability of philopatry in condition X
m	Migration rate
n	Patch size
π_X	History of resource quality in condition X
p	Frequency of high-quality patches in the population
r_X	"Others-only" relatedness of an individual in condition X
R_X	"Whole-group" relatedness of an individual in condition X
s	Quality ratio
τ	Temporal coefficient of correlation
v_X	Individual reproductive value of an individual in condition X
x	Level of helping of a focal actor
y	Average level of the neighbor's social behavior
z^*	Candidate evolutionary stable strategy for the social behavior

in the population, or else stays in the native patch with probability $1 - m$. Subsequent to dispersal, n offspring are chosen at random to become reproductively mature in each patch, with the remainder dying. Finally, patches may undergo changes in their resource availability: high-quality patches remain high quality with probability α or else become low quality with probability $1 - \alpha$; low-quality patches remain low quality with probability β, or else become high quality with probability $1 - \beta$. Model notation is summarized in Table 1.

HELPING AND HARMING

We classify social behaviors according to their impact upon fecundity. Specifically, the fecundity cost of the behavior is given by $-C \equiv \partial f / \partial x$ and the fecundity benefit of the behavior is given by $B \equiv \partial f / \partial y$, and we define helping behaviors as those

involving $B > 0$ and harming behaviors as those involving $B < 0$. We employ the Taylor–Frank neighbor-modulated fitness approach to kin selection analysis (Taylor and Frank 1996; Frank 1997, 1998; Rousset 2004; Taylor et al. 2007) to determine the direction of selection acting upon the social trait, assuming that the population is at ecological equilibrium (see Appendices A–E for details). The condition for the evolution of obligate helping and harming is given by

$$c_H(-C + r_{P|H}B - (B - C)r_{S|H}v_{S|H}) \\ + c_L(-C + r_{P|L}B - (B - C)r_{S|L}v_{S|L}) > 0, \tag{1}$$

where c_H and c_L denote the class-reproductive values for individuals in high-quality and low-quality patches, respectively (Fisher 1930; Taylor 1990, 1996; Grafen 2006); $r_{P|H}$ and $r_{P|L}$ denote the relatedness of the actor to her patchmates (the "primary" recipients of West and Gardner 2010), for actors in high-quality and low-quality patches, respectively; $r_{S|H}$ and $r_{S|L}$ denote the relatedness of the actor to those individuals who will compete for resources with the extra offspring produced in the actor's patch (the "secondary" recipients of West and Gardner 2010), for actors in high-quality and low-quality patches, respectively; and $v_{S|H}$ and $v_{S|L}$ denote the individual reproductive values of the secondary recipients, expressed relative to that of the actor and her patchmates, for actors in high-quality and low-quality patches, respectively (see Appendices C and E for details).

The conditions for the evolution of facultative helping and harming are given by

$$-C + r_{P|H}B - (B - C)r_{S|H}v_{S|H} > 0, \tag{2}$$

and

$$-C + r_{P|L}B - (B - C)r_{S|L}v_{S|L} > 0, \tag{3}$$

for individuals in high-quality patches and individuals in low-quality patches, respectively (see Appendix D for details).

Thus, an increase in investment into the social behavior impacts upon the actor's inclusive fitness in three ways. First, she suffers a personal cost C. Second, her primary recipients receive a benefit B, and this is weighted by the genetic relatedness r_P of the actor to these individuals. Third, the net increase $B - C$ in fecundity leads to a decrease of $B - C$ in the survival of the secondary recipients, and this is weighted by the genetic relatedness r_S of the actor to these individuals, and their relative reproductive value v_S. Note that this third term in inequality (2) and (3) can be rearranged in the form $\tilde{h}(B - C)\,\tilde{h}v\,R_S$, where $\tilde{h}$ is the probability that an offspring chosen at random after dispersal is native to the patch, this can be interpreted as follows: of the $(B - C)$ additional offspring created due to the social behavior, a fraction $\tilde{h}$ stays in the local patch and wins a breeding site, dis-

placing other native offspring which have on average a relatedness R and an expected relative reproductive value v_S to the actor. The product of relatedness and relative reproductive value is sometimes termed "life-for-life" relatedness (Hamilton 1972), and this describes how well the recipient transmits copies of the actor's genes to future generations, relative to the actor's ability to do this herself (cf. Williams 1996, p. 181).

Setting the LHS of each of these inequalities (1)–(3) equal to zero, we obtain the conditions for the actor to "break even," neither increasing nor decreasing her inclusive fitness. Rearranging these conditions into the form $C/B = A$, the quantity A represents the potential for helping (Gardner 2010) and its additive inverse $-A$ represents the potential for harming. If $A > 0$ there is potential for helping to be favored, and if $A < 0$ there is potential for harming to be favored, provided the cost is sufficiently small. From inequality (1), the potential for obligate helping is

$$A_0 = \frac{c_H(r_{P|H} - r_{S|H}v_{S|H}) + c_L(r_{P|L} - r_{S|L}v_{S|L})}{c_H(1 - r_{S|H}v_{S|H}) + c_L(1 - r_{S|L}v_{S|L})}. \tag{4}$$

From inequalities (2) and (3), the potentials for facultative helping are given by

$$A_H = \frac{r_{P|H} - r_{S|H}v_{S|H}}{1 - r_{S|H}v_{S|H}} \tag{5}$$

and

$$A_L = \frac{r_{P|L} - r_{S|L}v_{S|L}}{1 - r_{S|L}v_{S|L}}, \tag{6}$$

for actors in high-quality and low-quality patches, respectively.

Results and Discussion
SPATIAL HETEROGENEITY
We first consider populations in which resource availability varies across patches within generations but not across generations within patches (i.e., spatial heterogeneity only). We derive the following results:

Result 1
Spatial heterogeneity has no impact on the potential for obligate helping and harming, which is zero ($A_O = 0$) over the whole range of parameter values (see Appendix E for details). This extends Taylor's (1992a) cancellation result for homogeneous populations to obligate social behaviors in spatially heterogeneous populations.

Result 2
Spatial heterogeneity has no impact on the potential for facultative helping and harming, which is zero ($A_H = A_L = 0$) over the whole range of parameter values (see Appendix E for details). This extends Result 1 to facultative social behaviors.

Why does Taylor's (1992a) result for homogenous populations and obligate helping and harming extend to spatially heterogeneous populations with potentially facultative helping and harming? To understand this, we first consider the potential for facultative helping in high-quality patches, which is given by equation (5), that is, $A_H = (r_{P|H} - r_{S|H}v_{S|H})/(1 - r_{S|H}v_{S|H})$. Note that the relatedness of the actor to her primary recipients $r_{P|H}$ is equal to the product of philopatry $h_H = (1 - m)^2/(1 - m + m(p + (1 - p)s))^2$ for a high-quality patch—where p is the frequency of high-quality patches at equilibrium (see Appendix E for details)—and whole-group relatedness (Pepper 2000) R_H for a high-quality patch, because in the absence of temporal heterogeneity the actor's patch was of high quality in the previous generation. Also, the relatedness of the actor to her secondary recipients $r_{S|H}$ is equal to the product of philopatry h_H for a high-quality patch and whole-group relatedness R_H for a high-quality patch, because in the absence of temporal heterogeneity, the actor's patch remains high quality in the next generation. Moreover, the reproductive value of a secondary recipient—that is, an adult in the actor's patch in the next generation—is equal to the reproductive value of the actor, that is, $v_{S|H} = 1$. This is because both individuals are inhabitants of high-quality patches.

Hence, as in Taylor (1992a), the actor places equal value upon her primary and secondary recipients: $r_{P|H} = r_{S|H}v_{S|H}$ (Fig. 1), and consequently the potential for facultative helping is zero, $A_H = 0$ (see Appendix E for details). The same is true for facultative helping in low-quality patches: $h_L = ((1 - m)s)^2/((1 - m)s + m(p + (1 - p)s))^2$ and $v_{S|L} = 1$, hence $r_{P|L} = r_{S|L}v_{S|L}$, and $A_L = 0$ (Fig. 1; see Appendix E for details). As a consequence of this cancellation effect in both high-quality and low-quality patches, the potential for obligate helping is also zero, $A_O = 0$ (see Appendix for details). Since the potential for harming is given by the additive inverse of the potential for helping—that is, $-A$—the above cancellation also applies to the evolution of obligate and facultative harming behaviors.

TEMPORAL HETEROGENEITY
We next consider populations in which resource availability varies across generations within patches but not across patches within generations (i.e., temporal heterogeneity only). We assume that all patches become high quality with probability p, or become low quality with probability $1 - p$. We derive the following results:

Result 3
Temporal heterogeneity has no impact on the potential for obligate helping and harming, which is zero ($A_O = 0$) over the whole range of parameter values (see Appendix H for details). This extends Taylor's (1992a) cancellation result for homogeneous populations to obligate social behaviors in temporally heterogeneous populations.

Result 4
Temporal heterogeneity has no impact on the potential for facultative helping and harming, which is zero ($A_H = A_L = 0$) over the whole range of parameter values (see Appendix H for details). This extends Result 3 to facultative social behaviors.

Owing to the absence of spatial heterogeneity, the probability of philopatry is $h_H = h_L = h = (1 - m)^2$ for both high-quality and low-quality patches, whole-group relatedness is $R_H = R_L = R = 1/(n - (n - 1)(1 - m)^2)$ for both high-quality and low-quality patches, and the relative reproductive value of secondary recipients is $v_{S|H} = v_{S|L} = v_S = 1$ for actors in both high-quality and low-quality patches, that is, the same as in Taylor's (1992) model. Hence, the actor places equal value upon her primary and secondary recipients: $r_{P|H} = r_{S|H}v_{S|H} = r_{P|L} = r_{S|L}v_{S|L}$ (Fig. 2), and consequently the potential for helping is zero, $A_H = A_L = A_O = 0$ (see Appendix H for details). Again, a parallel argument can be made for the potential for harming, $-A$.

SPATIAL AND TEMPORAL HETEROGENEITY
We next consider populations in which resource availability varies both across patches within generations and across generations within patches (i.e., both spatial and temporal heterogeneity). We derive the following results:

Result 5
Spatial and temporal heterogeneity has no impact on the potential for obligate helping and harming, which is zero ($A_O = 0$) over the whole range of parameter values (see Appendix G for details). This extends Taylor's (1992a) cancellation result to obligate social behaviors in spatially and temporally heterogeneous populations.

Result 6
Spatial and temporal heterogeneity has an impact on the potential for facultative helping and harming, which may be nonzero ($A_H \neq 0$ and $A_L \neq 0$) depending upon parameter values (see Appendices C and E for details). Thus, selection may favor helping and harming that is facultatively adjusted according to the quality of the actor's patch, in spatially and temporally heterogeneous populations.

Why does Taylor's (1992a) result for homogenous populations and obligate helping and harming collapse when we consider populations that are both spatially and temporally heterogeneous with facultative helping and harming? Focusing our attention upon facultative helping in high-quality patches, we find that the potential for this behavior to be favored by natural selection is given by equation (5), that is, $A_H = (r_{P|H} - r_{S|H}v_{S|H})/(1 - r_{S|H}v_{S|H})$. If resource availability is heterogeneous through space and time, then the actor's high-quality patch may have been either high or low quality in the previous generation, and so her
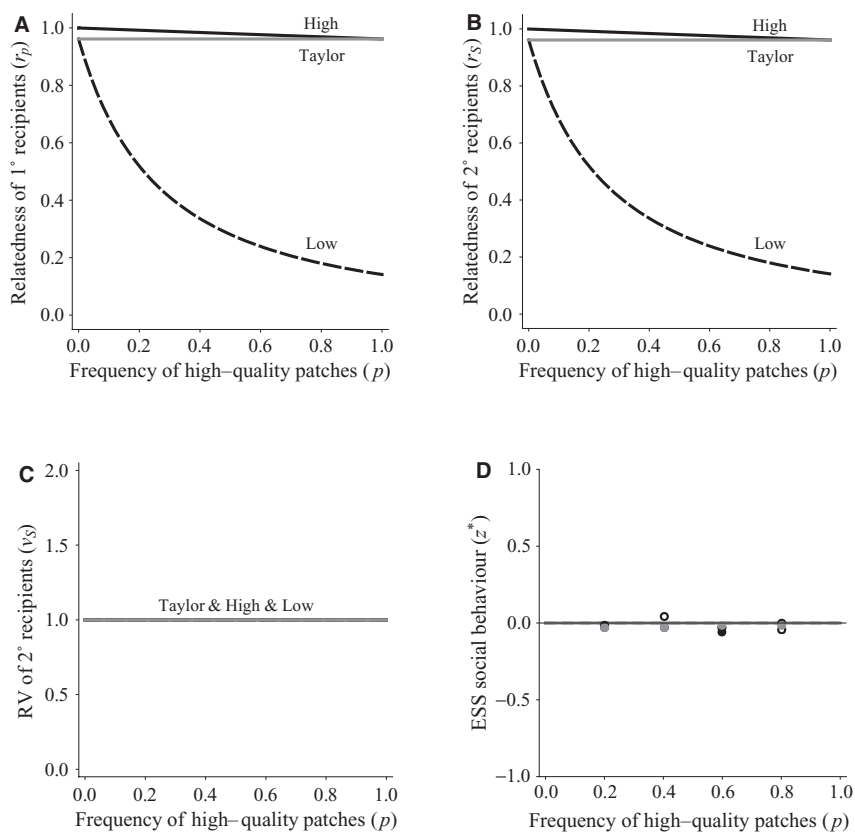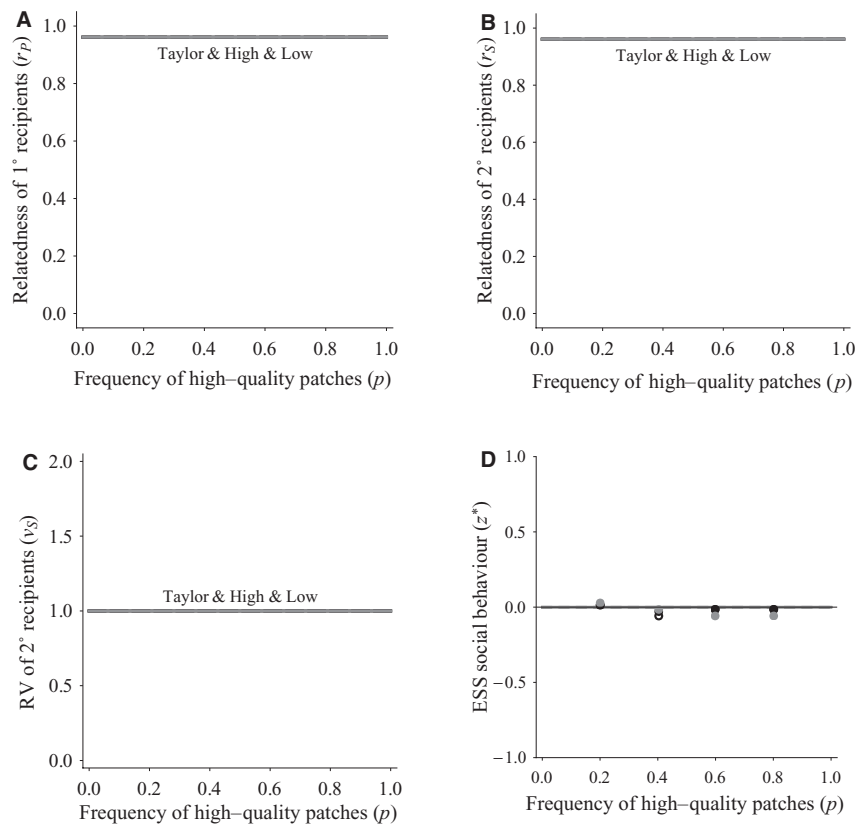
Figure 1. Impact of spatial heterogeneity upon relatedness, reproductive value, and the evolution of helping and harming. **(A)** The relatedness of primary recipients (r_P) as a function of the frequency of high-quality patches (p) is shown for high-quality patches ($r_{P|H}$; solid line), low-quality patches ($r_{P|L}$; dashed line), and Taylor's (1992) reference model ($r_{P|T}$; gray line). Relatedness of primary recipients is higher in high-quality patches owing to higher philopatry, and lower in low-quality patches owing to lower philopatry, relative to the reference model ($r_{P|L} < r_{P|T} < r_{P|H}$). **(B)** The relatedness of secondary recipients (r_S) as a function of the frequency of high-quality patches (p). Relatedness of secondary recipients is higher in high-quality patches owing to higher philopatry, and lower in low-quality patches owing to lower philopatry, relative to the reference model ($r_{S|L} < r_{S|T} < r_{S|H}$). Importantly, primary and secondary recipients are equally related ($r_{P|H} = r_{S|H}$, $r_{P|L} = r_{S|L}$). **(C)** The relative reproductive value of secondary recipients (v_S) is constant with respect to the frequency of high-quality patches (p), and is equal to that of the reference model ($v_{S|H} = v_{S|L} = v_{S|T} = 1$). **(D)** An illustration of how the equilibrium level of helping or harming depends upon the frequency of high-quality patches (p; see Appendix F for details). Analytical results (lines) and illustrative simulation data (circles) are shown for obligate behavior (gray line, solid gray circles), facultative behavior in low-quality patches (dashed line, open circles), and facultative behavior in high-quality patches (black line, solid black circles). In all panels, we assume $n = 2$, $s = 0.01$, $m = 0.01$, and $\tau = 1.00$.

relatedness to the primary recipients $r_{P|H}$ is a weighted average of the product of philopatry $h_H = (1 - m)^2/(1 - m + m(p + (1 - p)s))^2$ and whole-group relatedness R_H for high-quality patches and the product of philopatry $h_L = ((1 - m)s)^2/((1 - m)s + m(p + (1 - p)s))^2$ and whole-group relatedness R_L for low-quality patches (see Appendix E for details). In contrast, her relatedness $r_{S|H}$ to the secondary recipients is the product of the probability of philopatry h_H and whole-group relatedness R_H for her high-quality patch. Because we have $h_H \geq h_L$ we have that $r_{P|H} \leq r_{S|H}$ (see Appendix E for details). Moreover, the reproductive value of her secondary recipients—that is, adults in her

patch in the next generation—is not equal to her own reproductive value. Although she has the reproductive value of an individual in a high-quality patch, theirs is a weighted average of the reproductive value of an individual in a high-quality patch and that of an individual in a low-quality patch. Hence, $v_{S|H} \leq 1$ (see Appendix C for details).

Consequently, the actor may place different values upon her primary and secondary recipients: $r_{P|H} \neq r_{S|H}v_{S|H}$ (Fig. 3; see Appendix for details). Hence, the potential for facultative helping in high-quality patches may be nonzero, $A_H \neq 0$. The same is true for facultative helping in low-quality patches: $r_{P|L} \geq r_{S|L}$
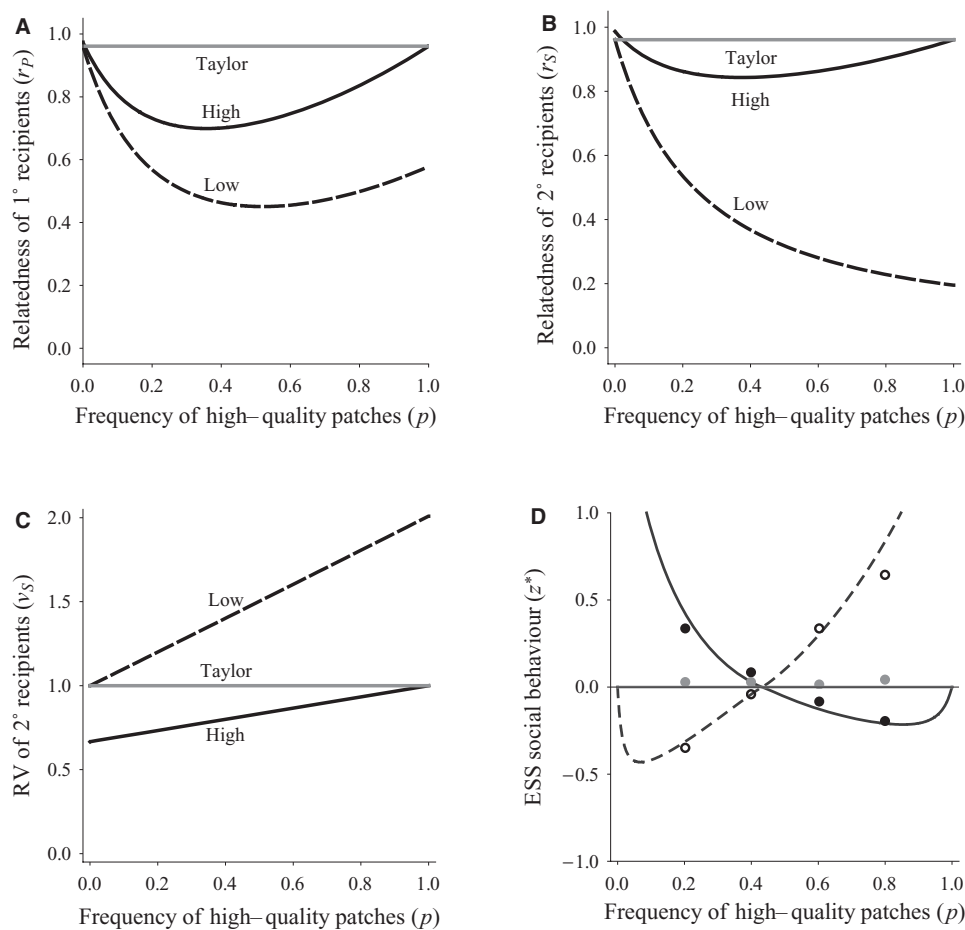
Figure 2. Impact of temporal heterogeneity upon relatedness, reproductive value, and the evolution of helping and harming. (A) The relatedness of primary recipients (r_P) as a function of the frequency of high-quality patches (p) is shown for high-quality patches ($r_{P|H}$; solid line), low-quality patches ($r_{P|L}$; dashed line), and Taylor's (1992) reference model ($r_{P|T}$; gray line). Relatedness of primary recipients in high-quality and low-quality patches is equal to that for the reference model ($r_{P|H} = r_{P|L} = r_{P|T}$). (B) The relatedness of secondary recipients (r_S) as a function of the frequency of high-quality patches (p). Relatedness of secondary recipients in high-quality and low-quality patches is equal to that for the reference model ($r_{S|H} = r_{S|L} = r_{S|T}$). Importantly, primary and secondary recipients are equally related ($r_{P|H} = r_{S|H} = r_{P|L} = r_{S|L}$). (C) The relative reproductive value of secondary recipients (v_S) is constant with respect to the frequency of high-quality patches (p), and is equal to that of the reference model ($v_{S|H} = v_{S|L} = v_{S|T} = 1$). (D) An illustration of how the equilibrium level of helping or harming depends upon the frequency of high-quality patches (p; see Appendix F for details). Analytical results (lines) and illustrative simulation data (circles) are shown for obligate behavior (gray line, solid gray circles), facultative behavior in low-quality patches (dashed line, open circles), and facultative behavior in high-quality patches (black line, solid black circles). In all panels, we assume $n = 2$, $s = 0.01$, $m = 0.01$.

and $v_{S|L} \geq 1$, so $r_{P|L} \neq r_{S|L} v_{S|L}$ and $A_L \neq 0$ (Fig. 3; see Appendices C and E for details). We find that there is potential for helping in high-quality patches and potential for harming in low-quality patches ($A_H > 0$, $A_L < 0$) when high-quality patches are relatively rare (low p), and potential for harming in high-quality patches and potential for helping in low-quality patches ($A_H < 0$, $A_L > 0$) when high-quality patches are relatively common (high p; Fig. 4). For example, in high-quality patches, the asymmetry in relatedness ($r_{P|H} < r_{S|H}$) favors harming, as the actor values secondary recipients more than primary recipients. By contrast, the asymmetry in reproductive value ($v_{S|H} < 1$) favors helping, as the actor values primary recipients more than secondary recipients.

The asymmetry in relatedness is largest when the frequency of high-quality patches (p) is intermediate, whereas the asymmetry in reproductive value is largest when the frequency of high-quality patches (p) is low. Thus, helping is more likely to evolve when high-quality patches are relatively rare (Fig. 4).

In addition, as the environment becomes more staid (temporal correlation increases) the asymmetry in reproductive value becomes more important than the asymmetry in relatedness. As a result, staid environments are favorable to the evolution of facultative helping in high-quality patches and to the evolution of facultative harming in low-quality patches. By contrast, as the population becomes more mixed (i.e., migration
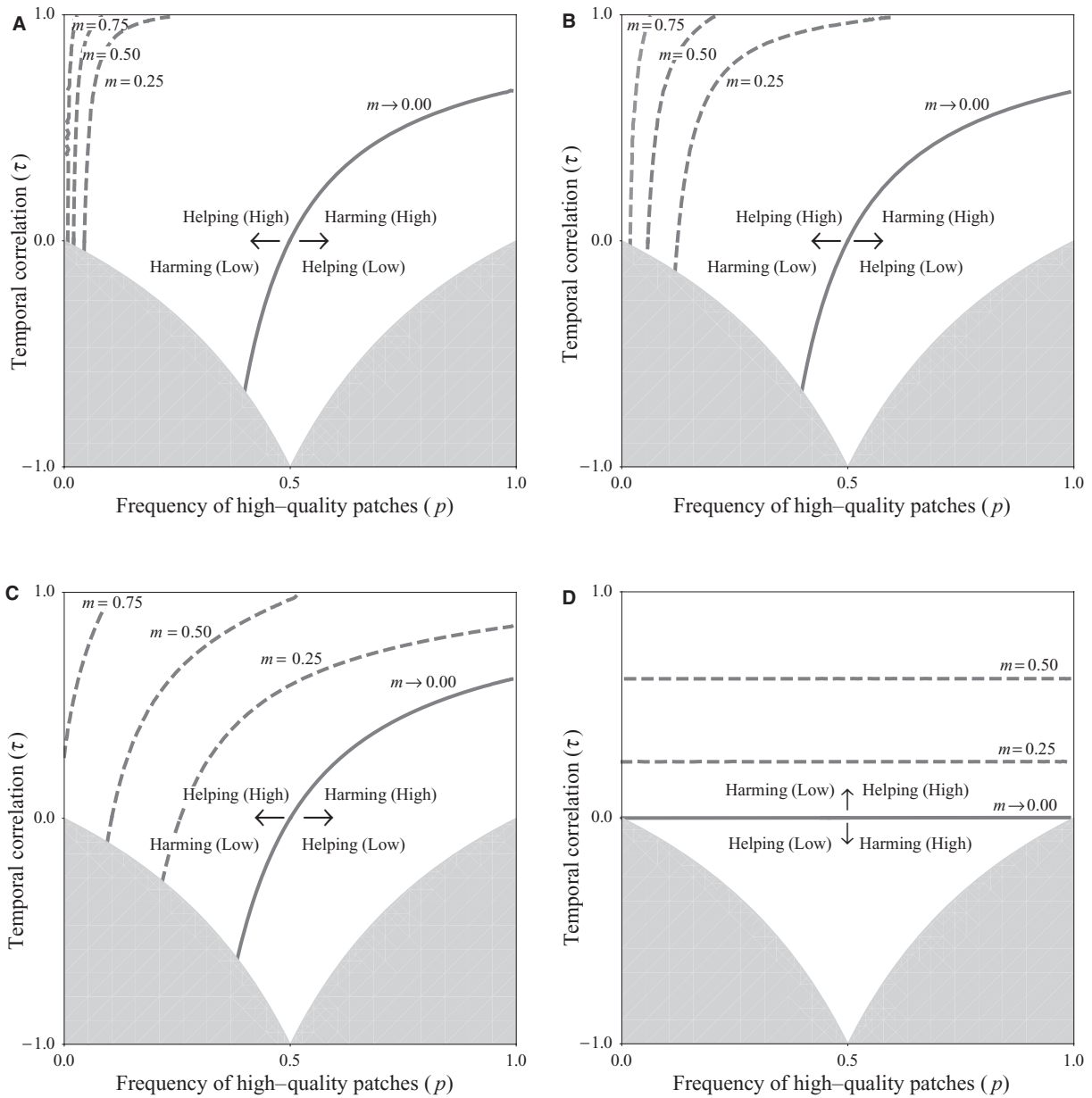
Figure 3. Impact of spatial and temporal heterogeneity upon relatedness, and reproductive value and the evolution of helping and harming. (A) The relatedness of primary recipients (r_P) as a function of the frequency of high-quality patches (p) is shown for high-quality patches ($r_{P|H}$; solid line), low-quality patches ($r_{P|L}$; dashed line), and Taylor's (1992) reference model ($r_{P|T}$; gray line). Relatedness of primary recipients may be higher or lower in high-quality patches, relative to the reference model, and is lower in low-quality patches, relative to the reference model ($r_{P|L} < r_{P|H}, r_{P|T}$). (B) The relatedness of secondary recipients (r_S) as a function of the frequency of high-quality patches (p). Relatedness of secondary recipients may be higher or lower in high-quality patches, relative to the reference model, and is lower in low-quality patches, relative to the reference model ($r_{S|L} < r_{S|H}, r_{S|T}$). Importantly, primary and secondary recipients may be unequally related ($r_{P|H} \neq r_{S|H}, r_{P|L} \neq r_{S|L}$). (C) The relative reproductive value of secondary recipients (v_S) as a function of patch frequency (p). In high-quality patches, the relative reproductive value of secondary recipients is less than or equal to that of the reference model; and in low-quality patches, the relative reproductive value is greater than or equal to that of the reference model ($v_{S|H} \leq v_{S|T} \leq v_{S|L}$). (D) An illustration of how the equilibrium level of helping or harming depends upon the frequency of high-quality patches (p; see Appendix F for details). Analytical results (lines) and illustrative simulation data (circles) are shown for obligate behavior (gray line, solid gray circles), facultative behavior in low-quality patches (dashed line, open circles), and facultative behavior in high-quality patches (black line, solid black circles). In all panels, numerical examples are given for $n = 2$, $s = 0.01$, $m = 0.01$, and $\tau = 0.10$.

rate increases), the asymmetry in relatedness becomes more important than the asymmetry in reproductive value. As a result, mixed populations are favorable to the evolution of facultative harming in high-quality patches and to the evolution of facultative helping in low-quality patches (Fig. 4).

However, although actors in high-quality patches place unequal value upon their primary and secondary recipients, and

actors in low-quality patches place unequal value upon their primary and secondary recipients, we find that actors place equal value upon their primary and secondary recipients when we take an average over actors in high-quality and low-quality patches. As the ecological dynamics is determined by a time-homogeneous Markov chain, the transition probabilities that mediate the value of primary recipients are identical to the transition probabilities

Figure 4. Impact of spatial and temporal heterogeneity upon the potential for facultative helping and harming. The continuous line represents a null potential for helping and harming ($A_H = A_L = 0$) for varying migration rates ($m \to 0.00$, $m = 0.25$, 0.50, and 0.75). (A, B, C) When high-quality patches are relatively rare (low p), there is potential for helping in high-quality patches ($A_H > 0$) and potential for harming in low-quality patches ($A_L < 0$). When high-quality patches are relatively common (high p), there is potential for harming in high-quality patches ($A_H < 0$) and potential for helping in low-quality patches ($A_L > 0$). (D) As the asymmetry in fecundity becomes negligible ($s \to 1$), the regions where helping or harming are favored become invariant in relation to the frequency of high-quality patches (p). Note that, in this case, selection is vanishing weak, and when $s = 1$ it vanishes altogether, recovering Taylor's (1992) result. The shaded region represents impossible parameter combinations (see Appendix A for details). Numerical examples are given for $n = 2$, (A) $s = 0.001$, (B) $s = 0.01$, (C) $s = 0.1$, and (D) $s \to 1$.

that mediate the value of secondary recipients (see Appendix G for details). Hence, although there is nonzero potential for facultative helping and harming in high-quality and low-quality patches ($A_H \neq 0, A_L \neq 0$), there is zero potential for obligate helping and harming ($A_O = 0$) in populations characterized by both spatial and temporal heterogeneity.

Conclusions

Population viscosity has been suggested to represent a very general mechanism by which kin selection can drive the evolution of cooperation at all levels of biological organization. However, the seminal result of Taylor (1992a) reveals that, in the simplest scenario of a homogeneous, inelastic island model of population structure, the cooperation-promoting effects of increased genetic relatedness exactly cancel with the cooperation-inhibiting effects of increased kin competition, so that population viscosity has no net effect on the evolution of cooperation. Here, we have shown that this result extends to heterogeneous populations, where certain patches have high resource availability and their residents enjoy high fecundity, and other patches have low resource availability and their residents suffer low fecundity. The potential for obligate helping—and harming—is zero irrespective of the degree of population viscosity, in populations characterized by spatial and/or temporal heterogeneity in resource availability. Only when social behavior is facultatively adjusted according to the actor's patch type and there is both spatial and temporal heterogeneity in resource availability does a nonzero potential for helping or harming arise.

Previous work on social evolution in unsaturated populations (e.g., Alizon and Taylor 2008; Wild et al. 2009; Lion and Gandon 2010) is superficially similar to the present saturated-population analysis, because empty breeding sites can be thought of as a type of resource that varies in its availability between patches. However, empty sites promote helping by easing competition for resources, owing to a feedback from the social behavior to the number of breeders per patch, and need not impact at all on the genetic relatedness of social partners (Wild et al. 2009; but see Alizon and Taylor 2008 and Lion and Gandon 2010). In contrast, the present model requires that each breeding spot is won at the expense of some other individual's chance of reproductive success, and helping behaviors may instead evolve owing to the way in which resource heterogeneity impacts upon the genetic structure of populations. Moreover, although the availability of empty sites in such models depends upon the social behavior exhibited by a patch's residents, the present model has assumed that resource availability is determined independently of the genetic strategies of the residents. The possibility of incorporating feedback, such that the probability of a patch transitioning from low to high qual-

ity depends upon the social behavior of its residents, represents an interesting avenue for future exploration.

Empirical data on the relationship between spatiotemporal heterogeneity in resource availability and social behavior are limited. Recent comparative studies have considered the relationship between temporal heterogeneity and cooperative breeding in birds, finding that greater seasonality is associated with a greater degree of sociality (Rubenstein and Lovette 2007; Cockburn and Russell 2011; Jetz and Rubenstein 2011). We suggest that future comparative studies should look for an interaction between spatial and temporal heterogeneity in resource availability. Moreover, there is ample scope for experimentally testing the predictions of our model using experimental evolution methods. The island model of population structure is very amenable to implementation in laboratory studies of microbial social behavior (Griffin et al. 2004; Kümmerli et al. 2009), and this experimental methodology could readily be extended to incorporate patch heterogeneity in space and time. More generally, we emphasize the potential for kin selection theory to explain variation within as well as between populations, and we suggest that future empirical studies consider the relationship between local environments and local sociality in addition to the relationship between global environments and whole-population measures of sociality.

Finally, we note some implications for the response of organisms' social behaviors to climate change and other relatively fast, anthropogenic impacts upon the natural environment. The main results of our analysis have concerned populations that are at ecological equilibrium, and adaptive evolutionary change may be relatively slow to track ecological upheavals. Hence, we predict that rapid degradation of the environment may be accompanied by maladaptive facultative changes in organisms' social behaviors. For example, over much of the range of parameter values, our model predicts that facultative harming behavior is favored in low-quality patches. Consequently, habitat deterioration might lead to an increase in mutually costly harming behaviors within ecologically threatened species, further contributing to their extinction risk. Such indirect consequences of habitat deterioration may pose an extra obstacle for conservation efforts.

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Appendix A
PATCH DYNAMICS

Given the assumptions described in the main text, transitions in patch quality can be represented as a matrix as follows:

$$P = \begin{pmatrix} \alpha & 1-\beta \\ 1-\alpha & \beta \end{pmatrix}. \tag{A1}$$

At equilibrium, the fraction of patches that are in the high-quality state is

$$p = \frac{1-\beta}{2-(\alpha+\beta)}, \tag{A2}$$

assuming $\alpha, \beta < 1$. Denoting patch quality at time t by T_t (equal to 1 for H and equal to 0 for L), the correlation coefficient describing the statistical association between a patch's quality at times t and $t+1$ is $\tau = \text{cov}(T_t, T_{t+1})/\sqrt{(\text{var}(T_t)\text{var}(T_{t+1}))}$, or

$$\tau = \alpha - (1-\beta), \tag{A3}$$

at ecological equilibrium. Note that when temporal correlation is negative ($\tau < 0$), it is no longer independent of the frequency of high-quality patches (p). For example, when $\tau = -1$, the frequency of high-quality patches must be equal to ½. Otherwise we would not have a stable distribution of high-quality patches over generations. Note also that this environmental change may be regarded as analogous to an extra phase of dispersal (cf Débarre and Gandon 2011), albeit a form of "budding" dispersal (Gardner and West 2006) where all patchmates "travel" together to the new environment.

Appendix B
REPRODUCTIVE SUCCESS

In a high-quality patch, each offspring of a focal breeding female stays in the native patch with probability $1-m$. The expected number of her non-dispersing offspring that successfully win a breeding site in the patch is given by $(1-m)\,E^\bullet_{H \to H}$, where

$$E^\bullet_{H \to H}$$
$$= \frac{f(x_H, y_H)}{(1-m)f(Y_H, Y_H) + m(pf(z_H, z_H) + (1-p)f(z_L, z_L)s)}, \tag{A4}$$

where Y_H is the average trait value in the focal patch, and z_H and z_L are the population average trait values in high- and low-quality patches, respectively. Each offspring of the same focal mother migrates to a high-quality patch with probability mp. The expected number of her offspring that disperse to a high-quality patch and successfully win a breeding site in the patch is given by

$m\,p\,E^\circ_{H \to H}$, where:

$$E^\circ_{H \to H}$$
$$= \frac{f(x_H, y_H)}{(1-m)f(z_H, z_H) + m(pf(z_H, z_H) + (1-p)f(z_L, z_L)s)}. \tag{A5}$$

Finally, each offspring of the same focal mother migrates to a low-quality patch with probability $m(1-p)$. The expected number of her offspring that disperse to a low-quality patch and successfully win a breeding site in the patch is given by $m\,(1-p)\,E^\circ_{H \to L}$, where:

$$E^\circ_{H \to L}$$
$$= \frac{f(x_H, y_H)}{(1-m)f(z_L, z_L)s + m(pf(z_H, z_H) + (1-p)f(z_L, z_L)s)}. \tag{A6}$$

We also derive corresponding expressions for a focal mother in a low-quality patch. These expressions define a matrix $\mathbf{E}$ which is given by

$$\mathbf{E} = \begin{pmatrix} E_{H \to H} & E_{L \to H} \\ E_{H \to L} & E_{L \to L} \end{pmatrix}$$
$$= \begin{pmatrix} (1-m)E^\bullet_{H \to H} + mpE^\circ_{H \to H} & mpE^\circ_{L \to H} \\ m(1-p)E^\circ_{H \to L} & (1-m)E^\bullet_{L \to L} + (1-p)E^\circ_{L \to L} \end{pmatrix}. \tag{A7}$$

Matrices $\mathbf{P}$ and $\mathbf{E}$ combine to define the reproductive success matrix, which is given by

$$\mathbf{w} = \begin{pmatrix} w_{H \to H} & w_{L \to H} \\ w_{H \to L} & w_{L \to L} \end{pmatrix} = \mathbf{PE}. \tag{A8}$$

In the context of class-structured populations, the reproductive success of an adult breeding female must take into account the relative contribution of individuals in different classes for gene frequency change (Fisher 1930; Price 1970; Taylor 1990; Grafen 2006). Thus, the reproductive success of a focal individual in a high-quality patch is given by

$$W_H = w_{H \to H} + \frac{v_L}{v_H}w_{H \to L}, \tag{A9}$$

where v_H and v_L are the reproductive value of individuals in high-quality and low-quality patches, respectively. Likewise, the reproductive success of a focal adult breeding female in a low-quality patch is

$$W_L = w_{L \to L} + \frac{v_H}{v_L}w_{L \to H}. \tag{A10}$$

The expected reproductive success of an individual is given by the class-specific reproductive success (W_H and W_L), weighted by the respective class-reproductive values

(c_H and c_L), which is given by

$$W = c_H W_H + c_L W_L. \quad (A11)$$

Class-reproductive value is defined as the product of the frequency of individuals in a given patch quality-type and those individuals' reproductive value ($c_H = p\upsilon_H$; $c_L = (1 - p)\upsilon_L$).

Appendix C
REPRODUCTIVE VALUE

Individuals reproductive values are given by the left-eigenvector of matrix **w** (defined in eq. A8) assuming a neutral population (Taylor 1990; Grafen 2006), and are normalized such that $c_H + c_L = 1$ (Taylor 1990; Taylor et al. 2007). Hence, a gene drawn at random from the population has an expected reproductive success W_H with probability c_H, and an expected reproductive success W_L with probability c_L. If there is no heterogeneity in the population (i.e., $s = 1$) then there are no differences in the reproductive values ($v_H = v_L$). However, as heterogeneity emerges in the population (i.e., $0 < s < 1$), it is easy to show that $v_H > v_L$, because individuals in high-quality patches have higher fecundity than individuals in low-quality patches. Reproductive values of secondary recipients are given by: $v_{S|H} = (\alpha v_H + (1 - \alpha)v_L)/v_H$ and $v_{S|L} = (\beta v_L + (1 - \beta)v_H)/v_L$. Note that, because $v_H \geq v_L$, we have $v_{S|H} \leq 1$ and $v_{S|L} \geq 1$.

Appendix D
HAMILTON'S RULE AND THE POTENTIAL FOR HELPING AND HARMING

To determine how selection acts on the trait of interest, we use the Taylor-Frank approach (Taylor and Frank 1996; Frank 1998; Taylor et al. 2007). We assume that the genetic variation is segregating at a locus responsible for the social behavior. We denote the genic value for a focal gene drawn from this locus by g (Price 1970; Falconer 1981). Assuming a vanishingly small genetic variation, the direction of natural selection acting on the social trait is given by

$$\frac{dW}{dg} = c_H \frac{dW_H}{dg} + c_L \frac{dW}{dg}. \quad (A12)$$

The derivative in the first term of the RHS of this equation can be expanded as follows:

$$\frac{dW_H}{dg} = \frac{\partial W_H}{\partial x_H}\frac{dx_H}{dg_H}\frac{dg_H}{dg} + \frac{\partial W_H}{\partial y_H}\frac{dy_H}{dg'_H}\frac{dg'_H}{dg} + \frac{\partial W_H}{\partial Y_H}\frac{dY_H}{dG_H}\frac{dG_H}{dg},$$
$$(A13)$$

where g'_H denotes social partners' average genetic value excluding self, and G_H denotes social partners' average genetic value includ-

ing self, genetic values being the average of an individual's genic values. All the derivatives and partial derivatives are evaluated at $x = y = Y = z$ (Taylor and Frank 1996; Frank 1997, 1998; Taylor et al. 2007). The partial derivatives give the marginal effects of the mutant phenotypes. The correlations between the phenotype and the genetic breeding values represent the genotype-to-phenotype mapping defined as $dx_H/dg_H = dy_H/d\ g'_H = dY_H/dG_H = \gamma_H$, and this is arbitrarily set to unity ($\gamma_H = 1$). The correlations between breeding values are coefficients of consanguinity. These correlations when normalized to the actor's coefficient of consanguinity give the kin selection coefficient of relatedness (Bulmer 1994). The same expansion can be made for the direction of selection acting on low-quality patches (dW_L/dg). Note that selection acting on the social trait not only depends upon the direction of selection (dW_X/dg), but also upon the class-reproductive values (c_X). As a consequence, we may have $dW_X/dg \neq 0$, but $c_X = 0$, in which case selection acting on the trait in the context X is null.

For obligate social behaviors, the condition for the evolution of higher breeding values is given by $dW/dg > 0$. For facultative social behavior, the condition for the evolution of higher breeding values in high-quality patches and low-quality patches is given by $dW_H/dg > 0$ and $dW_L/dg > 0$, respectively. This gives the inequalities (1)–(3) in the main text.

Appendix E
RELATEDNESS

Here, we derive the kin selection coefficients of relatedness for haploid populations. We assume vanishingly small genetic variation in the population. To determine the average relatedness structure in the population, we define a recursion equation (Wright 1969; Taylor 1992a; Rousset 2004). In a neutral and equilibrium population, the relatedness of a focal offspring to her sisters is 1 with probability $1/n$. The relatedness to her native patchmates is the relatedness among their mothers, which is given by r. These are native to the focal patch with probability h, which is the probability that we choose at random two offspring that have not dispersed. Therefore among offspring, relatedness is given by

$$Q = h\left(\frac{1}{n} + \left(1 - \frac{1}{n}\right)r\right). \quad (A14)$$

A patch in a high-quality state was a high-quality patch in the previous generation with probability π_H, and was a low-quality patch with probability $1 - \pi_H$. A low-quality patch was a low-quality patch in the previous generation with probability π_L, and a high-quality patch with probability $1 - \pi_L$. The recursion

equations are given by

$$\begin{cases} r'_{\mathrm{H}} = \pi_{\mathrm{H}} Q_{\mathrm{H}} + (1 - \pi_{\mathrm{H}}) Q_{\mathrm{L}} \\ r'_{\mathrm{H}} = (1 - \pi_{\mathrm{L}}) Q_{\mathrm{H}} + \pi_{\mathrm{L}} Q_{\mathrm{L}} \end{cases}, \qquad (A15)$$

Solving the system of equation (A15) for equilibrium, $r'_{\mathrm{H}} = r_{\mathrm{H}}$ and $r'_{\mathrm{L}} = r_{\mathrm{L}}$, we get the kin selection coefficients of relatedness, which are given by

$$r_{\mathrm{H}} =$$
$$\frac{\pi_{\mathrm{H}} h_{\mathrm{H}}(n - h_{\mathrm{L}}(n-1)) + (1 - \pi_{\mathrm{H}}) h_{\mathrm{L}} n + (1 - \pi_{\mathrm{L}})(n-1)}{(n - \pi_{\mathrm{H}} h_{\mathrm{H}}(n-1))(n - h_{\mathrm{L}}(n-1)) + (1 - \pi_{\mathrm{L}}) h_{\mathrm{L}}(n-1)(n - h_{\mathrm{H}}(n-1))},$$
$$(A16)$$

and

$$r_{\mathrm{L}} =$$
$$\frac{h_{\mathrm{L}}(n - \pi_{\mathrm{H}} h_{\mathrm{H}}(n-1)) + (1 - \pi_{\mathrm{L}})((h_{\mathrm{H}} + h_{\mathrm{L}})n - h_{\mathrm{H}} h_{\mathrm{L}}(n-1))}{(n - \pi_{\mathrm{H}} h_{\mathrm{H}}(n-1))(n - h_{\mathrm{L}}(n-1)) + (1 - \pi_{\mathrm{L}}) h_{\mathrm{L}}(n-1)(n - h_{\mathrm{H}}(n-1))}$$
$$(A17)$$

for high-quality patches and low-quality patches, respectively. "Whole-patch" relatedness coefficients are determined by substituting these values into the expression $R = 1/n + (1 - 1/n)r$, for the corresponding patch quality types. Relatedness of primary recipients is given by $r_{\mathrm{P|H}} = r_{\mathrm{H}}$ and $r_{\mathrm{P|L}} = r_{\mathrm{L}}$ for high-quality patches and low-quality patches, respectively. Relatedness of secondary recipients is given by $r_{\mathrm{S|H}} = h_{\mathrm{H}} R_{\mathrm{H}}$ and $r_{\mathrm{S|L}} = h_{\mathrm{L}} R_{\mathrm{L}}$ for high-quality patches and low-quality patches, respectively. Let us denote the denominator of (A16) and (A17) as D. After some algebra, it is easy to show that $r_{\mathrm{P|H}} - r_{\mathrm{S|H}} = -(h_{\mathrm{H}} - h_{\mathrm{L}})n(1 - \alpha)/D$ and that $r_{\mathrm{P|L}} - r_{\mathrm{S|L}} = (h_{\mathrm{H}} - h_{\mathrm{L}})n(1 - \alpha)/D$. Thus, because $h_{\mathrm{H}} \geq h_{\mathrm{L}}$, we have $r_{\mathrm{P|H}} \leq r_{\mathrm{S|H}}$ and $r_{\mathrm{P|L}} \geq r_{\mathrm{S|L}}$.

In spatially heterogeneous populations ($\tau = 1$), a high-quality patch was always a high-quality patch in the previous generation ($\pi_{\mathrm{H}} = 1$), and a low-quality patch was always a low-quality patch in the previous generation ($\pi_{\mathrm{L}} = 1$). Hence, the coefficients of relatedness of equations (A16) and (A17) reduce to $r_{\mathrm{H}} = h_{\mathrm{H}}/(n - (n-1)h_{\mathrm{H}})$ and $r_{\mathrm{L}} = h_{\mathrm{L}}/(n - (n-1)h_{\mathrm{L}})$. This gives the following identity between others-only and whole-group relatedness: $r_{\mathrm{H}} = h_{\mathrm{H}} R_{\mathrm{H}}$ and $r_{\mathrm{L}} = h_{\mathrm{H}} R_{\mathrm{L}}$. As a consequence in spatial heterogeneous populations, the relatedness of primary recipients is equal to the relatedness of secondary recipients (see main text). Note also that $r_{\mathrm{H}} - r_{\mathrm{L}} = (h_{\mathrm{H}} - h_{\mathrm{L}})n/((n - (n-1)h_{\mathrm{H}})(n - (n-1)h_{\mathrm{L}}))$. Since $h_{\mathrm{H}} \geq h_{\mathrm{L}}$, relatedness in high-quality patches is always larger or equal to relatedness in low-quality patches ($r_{\mathrm{H}} \geq r_{\mathrm{L}}$).

Appendix F
EVOLUTIONARILY STABLE STRATEGY AND SIMULATIONS

We wrote the code for the simulations in the language C++ (see Supporting Information). The protocol of the simulations closely follows the specifications of the model assumptions. However, instead of an infinite number of patches we now have a finite number of patches that we set to 5000. Each patch accommodates $n = 2$ breeding individuals. Thus, the total population size is 10,000. Each individual's genotype is represented as a real number on the interval $[-1,1]$, where positive values indicate level of investment into helping and negative values indicate level of investment into harming. At initialization, all genotypes are set to 0. In every subsequent generation, we choose 10 individuals at random for mutation: we add to their genotypic value a random Gaussian-distributed quantity with mean 0 and variance 0.015. To make quantitative predictions about the candidate evolutionarily stable strategy (ESS; Maynard Smith and Price 1973) for the social behavior (z^*), one needs to specify the marginal fecundity cost and the marginal fecundity benefits. The marginal fecundity cost is assumed to decrease monotonically with the investment in the social behavior, such that $-C = \partial f(x,y)/\partial x = -k$, where k is a scaling factor. The marginal fecundity benefits are assumed to have diminishing returns with the investment in the social behavior such that $B = \partial f(x,y)/\partial y = \mathrm{sign}(y)k\eta\mu|y|^{(\mu-1)}$, where η is a scaling factor, and μ controls the rate at which the benefits saturate with the investment in the social behavior. In the analytical model, a candidate ESS is found when the ratio between the marginal fecundity cost and the marginal fecundity benefits exactly matches the potential for helping ($C/B = A$). The candidate ESS is then given by $z^* = \mathrm{sign}(A)(\eta\mu|A|)^{1/(1-\mu)}$. In the simulation model, we let the population evolve up to 500,000 generations, and we compute the average genotypic value across all individuals in the final generation. In Figures 1–3, we provide illustrative numerical solutions for z^*, along with illustrative simulation data. Here, we assumed $\eta = 20$, $\mu = 0.1$, and $k = 0.015$.

Appendix G
CANCELLATION OF OBLIGATE SOCIAL BEHAVIOR

The life-for-life relatedness of primary recipients is $\rho_{\mathrm{P|H}} = r_{\mathrm{P|H}}$ and $\rho_{\mathrm{P|L}} = r_{\mathrm{P|L}}$ for high-quality and low-quality patches, respectively. The life-for-life relatedness of secondary recipients is $\rho_{\mathrm{S|H}} = r_{\mathrm{S|H}} v_{\mathrm{S|H}}$ and $\rho_{\mathrm{S|L}} = r_{\mathrm{S|L}} v_{\mathrm{S|L}}$. For obligate behaviors, the life-for-life coefficients of primary recipients is given by

$$\rho_{\mathrm{P}} = c_{\mathrm{H}} \rho_{\mathrm{P|H}} + c_{\mathrm{L}} \rho_{\mathrm{P|L}}, \qquad (A18)$$

and the life-for-life relatedness of a secondary recipient is given by

$$\rho_{\mathrm{S}} = c_{\mathrm{H}} \rho_{\mathrm{S|H}} + c_{\mathrm{L}} \rho_{\mathrm{S|L}}. \qquad (A19)$$

In Taylor's (1992a) model, these are $\rho_{\mathrm{P}} = r = hR$, and $\rho_{\mathrm{S}} = aR$, where a is the proportion of competition that occurs

locally (scale of competition; Frank 1998; Gardner and West 2006; Van Dyken 2010). As $h = a$, we have $\rho_P = \rho_S$, as actors value primary recipients as much as secondary recipients there is no selection for social behaviors. In our model, we find that same symmetry: $h_H = a_H$, and $h_L = a_L$. As the ecological dynamics is determined by a time-homogeneous Markov chain, we find additional symmetries. To see how these explain the cancellation result for obligate behavior, let us denote the different probabilities (P) in the life-for-life relatedness as follows: $P(X_{t-1} = H \mid X_t = H) = \pi_H$, $P(X_{t-1} = L \mid X_t = H) = 1 - \pi_H$, $P(X_{t-1} = L \mid X_t = L) = \pi_L$, $P(X_{t-1} = H \mid X_t = L) = 1 - \pi_L$, $P(X_{t+1} = H \mid X_t = H) = \alpha$, $P(X_{t+1} = L \mid X_t = H) = 1 - \alpha$, $P(X_{t+1} = L \mid X_t = L) = \beta$, $P(X_{t+1} = H \mid X_t = L) = 1 - \beta$, $P(X_t = H) = p$, and $P(X_t = H) = 1 - p$. Using this notation, the life-for-life coefficients of relatedness for obligate behavior can be written as follows:

$$
\begin{aligned}
\rho_P = {} & P(X_t = H)(P(X_{t-1} = H \mid X_t = H)h_H R_H v_H \\
& + P(X_{t-1} = L \mid X_t = H)h_L R_L v_H) \\
& + P(X_t = L)(P(X_{t-1} = H \mid X_t = L)h_H R_H v_L \\
& + P(X_{t-1} = L \mid X_t = L)h_L R_L v_L)
\end{aligned}
\tag{A20}
$$

and

$$
\begin{aligned}
\rho_S = {} & P(X_t = H)(P(X_{t+1} = H \mid X_t = H)h_H R_H v_H \\
& + P(X_{t+1} = L \mid X_t = H)h_H R_H v_L) \\
& + P(X_t = L)(P(X_{t+1} = H \mid X_t = L)h_L R_L v_H \\
& + P(X_{t+1} = L \mid X_t = L)h_L R_L v_L).
\end{aligned}
\tag{A21}
$$

We can show that life-for-life relatedness of primary recipients is equal to the life-for-life relatedness of secondary recipients. For example, first note that from Bayes' theorem, we have that $P(X_{t-1} = L \mid X_t = H) = P(X_t = H \mid X_{t-1} = L)P(X_{t-1} = L)/P(X_t = H)$; second as the ecological dynamics is described by a time-homogeneous Markov chain, we have $P(X_t = H \mid X_{t-1} = L) = P(X_{t+1} = H \mid X_t = L)$, as a result we have $P(X_t = H)P(X_{t-1} = L \mid X_t = H) = P(X_t = L)P(X_{t+1} = H \mid X_t = L)$. This can be shown to hold for all other terms in the life-for-life coefficients of relatedness. Thus, as in Taylor's (1992a) model of obligate social behavior in homogeneous populations, we find that the average life-for-life relatedness of primary recipients is equal to the average life-for-life relatedness of secondary recipients ($\rho_P = \rho_S$). This identity prevents the evolution of social behaviors.

Appendix H
TEMPORAL HETEROGENEITY

Here, we assume that within a generation, all patches have the same quality-state, that is, the population is in the high-quality state or the population is in the low-quality state. Independently of the current state, the population becomes high quality with probability p or becomes low quality with probability $1 - p$. The matrix $\mathbf{P}$ is now defined by setting $\alpha = p$ and $\beta = 1 - p$. As before, we solve the matrix for its right-eigenvector, and this gives $u_H = p$ and $u_L = 1 - p$. However, the interpretation is now different: u_H and u_L represent the expected fraction of generations that the population, on the long run, spends on the high-quality state and on the low-quality state, respectively. We also need to determine the contribution of high-quality individuals and low-quality individuals to the future genetic composition of the population, that is, the individual reproductive values. The reproductive value of a high-quality individual is determined as follows: the fecundity of focal high-quality individual is 1; with probability p her offspring reproduce as high-quality individuals, in which case they have reproductive value v_H; with probability $1 - p$ her offspring reproduce as low-quality individual, in which case they have reproductive value v_L; hence, at equilibrium, we get the following identity: $v_H = p v_H + (1 - p) v_L$. Therefore, reproductive values are identical and can be normalized such that $v_H = v_L = 1$. Class-reproductive values are given by: $c_H = u_H v_H = p$ and $c_L = u_L v_L = 1 - p$. Because within each generation there is no heterogeneity, and because reproductive values are identical, the class-specific fitness expressions are identical (W_H and W_L), and are given by

$$
W_X = \frac{(1 - m) f(x_X, y_X)}{(1 - m) f(Y_X, Y_X) + m f(z_X, z_X)} + \frac{m f(x_X, y_X)}{f(z_X, z_X)}.
\tag{A22}
$$

As before, we use the Taylor–Frank approach (Taylor and Frank 1996) to determine the direction of natural selection acting on the social traits. Relatedness coefficients are again given by equation (A15) with $\pi_H = 1 - \pi_L = p$, $\pi_L = 1 - \pi_H = 1 - p$, and $h_H = h_L = (1 - m)^2$. As a result, $r_H = r_L = r_{P|H} = r_{P|L} = h R_H = h R_L = h R = h/(n - (n - 1)h)$. Relatedness of secondary recipients is given by $r_{S|H} = r_{S|L} = h R_H = h R_L = h R$. Hence, $r_{P|H} = r_{S|H}$ and $r_{P|L} = r_{S|L}$. Specific patch dynamics are given for concreteness and clarity. However, the various measures of value—that is, relatedness and reproductive value—are independent of the particular dynamics and the correlation between population states over generations.

Supporting Information

The following supporting information is available for this article:

Supporting Text. Simulation code.

Supporting Information may be found in the online version of this article.

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```
//**********************************************************************//
//                                                                      //
//  Illustration of the algorithm used for the simulations in Rodrigues & Gardner "Evolution of  //
//  helping and harming in heterogeneous populations"                   //
//  The illustration is given for facultative behaviour in high-quality patches  //
//  and the temporal heterogeneity case.                                //
//                                                                      //
//  Generation of random numbers is required for three distribution types:  //
//   uniform, binomial and normal;                                      //
//  Code for these distributions can be easily found on-line.           //
//                                                                      //
//**********************************************************************//

//*** Header file ***//

#include <iostream>
#include <fstream>
#include <stdlib.h>
#include <sstream>
#include <math.h>
#include <time.h>
#include <vector>
#include <assert.h>
#include <stdio.h>
#include <ctime>
#include <cmath>
#include <cstdlib>
#include <string>

using namespace std;

#ifndef tempH_Header_h
#define tempH_Header_h

const int P = 5000; // Number of patches in the population
const int N = 2;    // Number of breeding adults per patch

// Declaration of functions

void initiate();    // Initiate individual's genotype
void reset();       // Vital rates
void onegen();      // Selection
void mutation();    // Mutation

// Definition of structures used in the main file

struct deme
{
    float genotype[N];       // Genotype of a focal individual
    float newGenotype[N];    // New genotype of a focal individual
    float fecundity[N];      // Fecundity of a focal individual
```

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```cpp
    float benefits[N];        // Fecundity benefits of a focal individual
    float quality;            // Patch quality
    int natives;              // Number natives that win a breeding site
    float stay;               // Competitiveness of natives
    float productivity;       // Patch productivity
};

struct rnd               // Random generators
{
    float uni();                          // Uniform distribution
    float norm(float mu, float var);      // Normal distribution
    int bino(int NT, float M);            // Binomial distribution
};

//*** Main file ***//

#include "Header.h"
#include <iostream>
#include <iostream>
#include <fstream>

using namespace std;

int G = 500000;                // Number of generations
float popProductivity = 0;     // Population productivity
float m = 0.01;                // Base-line migration rate
float s = 0.01;                // Quality asymmetry
float pH = 0.8;                // Probability of high-quality
float q = 1;                   // Patch quality
float k = 0.005;               // Constant affecting costs and benefits
float a = 20;                  // Constant affecting benefits
float b = 0.1;                 // Diminishing benefits parameter
int mutR = 10;                 // Mutation rate
float mutS = 0.015;            // Mutation size

deme patch[P];                 // Initialisation of deme structure

int main (int argc, const char * argv[])
{
    initiate();
    for(int gen=0;gen<G;gen++)
    {
        onegen();
    }
    return 0;
}

//*** Initial genotype ***//

void initiate()
{
```

```
        for (int i=0;i<P;i++)
        {
            for(int j=0;j<N;j++)
            {
                patch[i].genotype[j]=0.0;
            }
        }
        reset();
        return;
    }

//*** Patch quality and vital rates ***//

void reset()  // Sets the fecundity rates in the population
{
    popProductivity = 0;
    if(rnd.uni() < pH) // Definition of patch quality
    {
        q = 1;
    }
    else
    {
        q = s;
    }
    for(int i=0;i<P;i++)
    {
        patch[i].productivity = 0;
        patch[i].quality = q;
        for (int j=0;j<N;j++)
        {
            if(patch[i].quality == 1)  // Facultative helping in high-quality patches
            {
                patch[i].fecundity[j]=patch[i].quality*(1-k*abs(patch[i].genotype[j]));
                patch[i].benefits[j]=0;
                for(int l=0;l<N;l++)
                {
                    if(l!=j)
                    {
                        if(patch[i].genotype[l]!=0)
                        {

patch[i].benefits[j]+=patch[i].quality*k*a*(patch[i].genotype[l]/(abs(patch[i].genotype[l])))*pow
(abs(patch[i].genotype[l]),b)/float(N-1);
                        }
                    }
                }
                patch[i].fecundity[j]+=patch[i].benefits[j]; // Sets individuals' fecundity
            }
            else  // No selection in low-quality patches
            {
                patch[i].fecundity[j] = patch[i].quality;  // Sets individuals' fecundity
```

```
        }
        patch[i].productivity+=patch[i].fecundity[j];  // Sets patch productivity
      }
      popProductivity+=patch[i].productivity;          // Sets population productivity
    }
    return;
}

//*** Selection ***//

void onegen()  // Competition for breeding sites
{
    for(int i=0;i<P;i++)
    {
      float rProd = 0;
      float cProd = 0;
      int jb = 0;
      int ib = 0;
      patch[i].stay = ((1-m)*patch[i].productivity)/((1-
m)*patch[i].productivity+m*popProductivity/float(P));
      patch[i].natives = rnd.bino(N,patch[i].stay); // Sets number of natives that win a breeding
site
      for(int j=0;j<patch[i].natives;j++) // Competition among natives for breeding sites
      {
        cProd = 0;
        rProd = 0;
        jb = 0;
        rProd = patch[i].productivity*rnd.uni();
        if(rProd > 0)
        {
          while (cProd < rProd)
          {
            cProd+=patch[i].fecundity[jb];
            jb++;
          }
          jb--;
        }
        patch[i].newGenotype[j] = patch[i].genotype[jb];
      }
      for(int j=patch[i].natives;j<N;j++)  // Competition between patches for breeding sites
      {
        cProd = 0;
        ib = 0;
        rProd = 0;
        rProd = popProductivity*rnd.uni();
        if(rProd > 0)
        {
          while (cProd < rProd)
          {
            cProd+=patch[ib].productivity;
            ib++;
```

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```
            }
            ib--;
        }
        cProd = 0;
        jb = 0;
        rProd = patch[ib].productivity*rnd.uni(); // Competition between individuals for breeding
sites
        if(rProd > 0)
        {
            while (cProd < rProd)
            {
                cProd+=patch[ib].fecundity[jb];
                jb++;
            }
            jb--;
        }
        patch[i].newGenotype[j] = patch[ib].genotype[jb];
    }
}
for(int i=0;i<P;i++)  // Sets the genotypes for the new generation
{
    for(int j=0;j<N;j++)
    {
        patch[i].genotype[j]=patch[i].newGenotype[j];
    }
}
mutation();
reset();
return;
}

//*** Mutation ***//

void mutation()
{
    float mstep = 0;
    int ib, jb;
    for(int i=0;i<mutR;i++)
    {
        ib = rand()%P;
        jb = rand()%N;
        mstep = rnd.norm(0.0,mutS);
        patch[ib].genotype[jb]+=mstep;
        if(patch[ib].genotype[jb]>=1)patch[ib].genotype[jb]=1.0;
        if(patch[ib].genotype[jb]<=-1)patch[ib].genotype[jb]=-1.0;
    }
    return;
}
```