Linked selection and the evolution of altruism in a family-structured population

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Abstract

Altruism is defined as when an individual increases the fitness of another at a cost to their own fitness. Much research on the evolution of altruism focuses on hypotheses based on the role of a single locus or multilocus quantitative trait in kin selection, group selection, and reciprocity. Very few studies of altruism have explored how linked selection, or selection at loci neighboring an altruism locus, impacts the evolution of altruism. While linked selection can decrease the efficacy of selection at neighboring loci, it is also possible it might have other effects including promoting selection for altruism by increasing relatedness in regions of low recombination. Here, we used population genetic simulations to study how negative selection at linked loci, or background selection, affects the evolution of altruism. When altruism occurs between full siblings, we found that background selection interfered with selection on the altruistic allele, increasing its fixation when the altruistic allele was disfavored and reducing its fixation when the allele was favored. Background selection has the same effect on other, nonsocial, genes, suggesting that altruistic genes may not be affected by linked selection differently from other types of genes in family-structured populations.

Keywords: social evolution, kin selection, altruism, linked selection

Introduction

Altruism is the phenomenon where an organism helps another's fitness at the expense of its own fitness (Hamilton 1964; Taylor 1992; Rousset 2004; Lehmann and Keller 2006). This type of behavior is found in many species from microbes like *Dictyostelium discoideum* (Strassmann *et al*. 2000; Noh *et al*. 2018) to aphids (Benton and Foster 1992; Uematsu *et al*. 2010), ants (Hamilton 1972; Bourke and Franks 1995), and primates including humans (Burkart *et al*. 2007; Warneken *et al*. 2007; Silk and Boyd 2010) . The existence of altruism despite its costs to survival or reproduction has spawned a tremendous amount of evolutionary theory. Multiple explanations have been proposed, such as kin selection and reciprocal altruism or reciprocity (Hamilton 1964; Trivers 1971; Maynard Smith 1974; Axelrod and Hamilton 1981). The foundational research on the evolution of altruism occurred squarely in the "pre-genomic" era — before the evolutionary consequences of selection at loci genetically linked to the locus of interest were seriously considered. Since then, the immense theoretical (e.g., Hamilton 1970; Queller 1985; Taylor and Frank 1996; Rousset and Billiard 2000; Lehmann and Keller 2006; Ohtsuki *et al*. 2006; Tarnita *et al*. 2009; Úbeda and Gardner 2010; Rankin 2011; Akçay and Van Cleve 2012; Van Cleve 2015, 2017, 2020; Allen *et al*. 2017; Akçay 2018; McAvoy *et al*. 2020) and empirical (Krakauer 2005; Boomsma 2009; Strassmann *et al*. 2011; Lukas and Clutton-Brock 2012; Bourke 2014; Nadell *et al*. 2016; Griesser *et al*. 2017; Ostrowski 2019) progress on the evolution of altruism has largely ignored the potential influence of selection on linked genes whose expression is not related to cooperation or social behavior.

In general, selection on non-neutral mutations generates a stochastic evolutionary force that decreases genetic diversity at linked sites (i.e., linked loci). This can be seen in background selection (Charlesworth *et al*. 1993; Hudson and Kaplan 1995), which is caused by linked genes with small deleterious effects, or in a selective sweep (Maynard Smith and Haigh 1974; Kaplan *et al*. 1989), which is caused by a linked gene with a strong beneficial effect. Linked selection is most influential in genomic regions with low recombination rates. Another factor affecting genetic diversity is spatial structure and limited migration between local populations or demes (Crow and Kimura 1970): when migration among demes is weak, individuals tend to reproduce in the same deme as their parents, and they are more likely to have identical alleles than individuals in different demes. This results in a decrease in local genetic diversity within demes and an increase in genetic relatedness as measured by the F_{ST} statistic (Wright 1931, 1951), which compares genetic identity within demes to genetic identity between demes. Linked selection can also occur in spatially structured populations. Both background selection (Hu and He 2005) and selective sweeps (Slatkin and Wiehe 1998; Bierne 2010) can increase genetic homogeneity among linked loci within demes as measured by an increased F_{ST}.

Genetic relatedness is also one of the key ingredients in the evolution of altruism. Hamilton (1964) showed that the total effect of natural selection on an altruistic allele (assuming additive genetic effects and weak selection; Rousset and Billiard 2000; Lehmann and Rousset 2014) is given by the

inclusive fitness effect: $-c + r\,b$ where c is the fitness cost to the helping individual, b is the fitness benefit to the individual helped, and r is the genetic relatedness between the two (Hamilton 1964), which can be measured by F_{ST} (Hamilton 1964, 1970; Rousset 2004). Hamilton's rule states that an altruistic allele is favored by selection when $c/b < r$ (i.e. the inclusive fitness effect is greater than zero). Because linked selection within a genomic region may increase genetic relatedness in that region, Hamilton's rule suggests that it might also increase the range of cost/benefit ratios where an altruistic allele in that genomic region may evolve by natural selection. In fact, both theoretical and empirical research in asexual microbial systems suggest that selective sweeps caused by linked beneficial mutations unrelated to the social interaction can promote the evolution of altruism (Hammarlund *et al*. 2016) and protect communities from invasion by "selfish" cheaters (Morgan *et al*. 2012).

We investigated how linked selection modulates selection on altruism in a family-structured population of sexual, recombining diploids, by tracking the fixation probability of a single altruistic allele. Family-structured populations are ones where fitness-relevant interactions occur among direct family members (full siblings in our simulations) and genetic relatedness is high between siblings within families (e.g., $r = 1/2$ for full siblings) and low between families ($r = 0$ for our simulations, which is typical for outbred populations). Since family-structured populations were the original context for Hamilton's theory of kin selection (Hamilton 1964), they provide a good base case for the effect of linked selection via background selection. We found that background selection did not increase the range of cost/benefit ratios (c/b) under which an altruistic allele is favored. Instead, background selection interfered only with the strength of natural selection; it increased fixation probabilities when the altruistic allele was disfavored under Hamilton's rule and decreased fixation probabilities when the altruistic allele was favored. Thus, in contrast to expectations from selective sweeps in asexual microbial systems, background selection effects social traits within families as it does all other traits – by increasing the power of drift and decreasing the efficacy of selection.

Methods

We wrote and executed all simulations in SLiM 3 (Haller and Messer 2019) using a non-Wright-Fisher model with a base carrying capacity of 1000 diploid individuals each with a 100kb-long genome. Since the simulation uses absolute fitness, the actual population size is not exactly 1000, but instead depends on both the load of deleterious nonsocial mutations and the percent of altruistic individuals. Recombination occurred along the genome at a rate of $\rho = 10^{-8}$ per base pair. To represent background selection, slightly detrimental mutations occur at a rate of $u = 5\times10^{-8}$ per base pair. Across simulations, we modulated the strength of background selection by varying the fitness effect of deleterious mutations (dominance coefficient $h = 0.5$) from –0.006 to –0.014 in 0.002 intervals, as well as two

controls models in which we prevent background selection by introducing only neutral or strongly deleterious mutations ($s = 0$ and $s = -1$, respectively, with $h = 0.5$, and $u = 5\times10^{-8}$/bp)

For time efficiency, ten seed populations were generated by running the simulation for 5000 generations without the altruistic allele, which was sufficient to reach mutation-selection balance for deleterious variants (Supplementary Figure S1). All simulations start by loading these seed populations. Then, one copy of the altruistic allele is inserted into a random chromosome at base-pair 1000. This occurs after offspring are created for the generation, but before individuals die, such that the population size is larger than the carrying capacity, including roughly 1000 parents and 2000 offspring. Accordingly, the initial frequency and the fixation probability of a neutral allele inserted by this method is 1/6000.

During the reproduction phase of each generation, every member of the population is paired with another, if possible, and they produce a litter of four full siblings. Within the litter, a single pair of siblings is examined for an altruistic interaction. The altruistic allele is completely dominant, so if one sibling has at least one copy of the altruistic allele, their fitness suffers a cost, c, while the fitness of the chosen sibling is increased by a benefit, b. Two altruistic siblings may help each other, incurring both cost and benefit. Unless otherwise noted, the cost of helping was kept at $c = 0.1$. The benefit b varied, leading to a range of cost/benefit ratios where altruism was favored and disfavored. One million replicates were run for each data point.

We compared simulation results to fixation probabilities from population genetic theory. For the two cases without background selection (neutral linked mutations with $s = 0$ and strong deleterious linked mutations with $s = -1$), the fixation probability of an allele with dominance coefficient h and selection coefficient $\mathscr{S}$ in a diploid population of effective size N_e is (Ewens 2004, eqn. 3.30)

$$p_{\text{fix}} = \frac{\int_0^{p_0} exp(-2N_e \mathcal{S} x(2h + x(1-2h)))dx}{\int_0^1 exp(-2N_e \mathcal{S} x(2h + x(1-2h)))dx} \tag{1}$$

where p_o is the initial frequency of the allele. Since the family-structured model in our SLiM simulations is not an exact Wright-Fisher model, we needed to calculate the appropriate effective population size N_e. In particular, the family structure and sampling created a different variance in reproductive success, σ^2, than is typical for a Wright-Fisher model. The effective size is $N_e \approx N/\sigma^2$ (Ewens 2004, eqn. 3.107), and we measured the reproductive variance $\sigma^2 \approx 0.75$ in our simulations, which yields $N_e \approx 1333$. The selection coefficient $\mathscr{S}$ for the altruistic allele can be derived from the expected change in allele frequency and is approximately the inclusive fitness effect $-c + r\,b$ (Rousset and Billiard 2000; Roze and Rousset 2004). In our simulations, since only one of the two pairs of siblings have the opportunity for altruism, our selection coefficient is one half the inclusive fitness

effect: $\mathscr{S} = (-c + r\,b)/2 = (-c + 0.5\,b)/2$. Using this expression for $\mathscr{S}$, $h = 1$, $p_0 = 1/6000$, and $N_e = 1333$, we integrated equation (1) in Mathematica (Wolfram Research, Inc. 2021) to generate the predicted fixation probabilities in Figure 1. The vertical black lines represent the 95% binomial confidence intervals around the predicted fixation probabilities.

For the cases with background selection (linked mutations with $-0.014 \leq s \leq -0.006$ in our simulation), we predicted the fixation probabilities of the altruistic allele assuming that the only effect of background selection is a change in the effective population size N_e in equation (1), which we call $N_{e,bg}$. The expression for $N_{e,bg}$ in this case is derived from equation (7)in Hudson and Kaplan (1995) by setting their $L_1 = 0$ and $L_2 = l$ (since the altruistic allele in the simulation is on one end of the chromosome) and obtaining

$$N_{e,bg} = N_e e^{-U/(2(|sh|+R))} \tag{2}$$

where U is the total diploid rate of deleterious mutation in the genomic region, R is the length of the genomic region in Morgans, and N_e is the effective size without background selection. In terms of the per base mutation rate u and recombination rate ρ, $U = 2\,u\,l$ and $R = \rho\,l$, where l is the length of the genomic region. We used values of $N_e = 1333$, $R = 10^{-8} \times 10^{5} = 10^{-3}$, $U = 2 \times 5 \times 10^{-8} \times 10^{5} = 10^{-2}$, $h = 0.5$, and varied the value of s (see Figure 1) in equation (2) to generate $N_{e,bg}$ values for fixation probabilities calculated using equation (1).

Results

Generally, we found that background selection did not increase the range of cost/benefit ratios under which altruism is favored relative to Hamilton's rule with $r = 1/2$. Rather, background selection increased the altruistic allele's fixation probability when the allele was disfavored under Hamilton's rule with $r = 1/2$ and decreased its fixation probability when the allele was favored (Figure 1). The effect was more extreme when there was stronger selection for or against the allele; for example, when the benefit of being helped was 0.19, fixation occurred rarely with background selection present and never without it (Figure 1). The allele was effectively neutral when the inclusive fitness effect ($-c + r\,b$) was zero, which occurred in two cases: when both the benefit and cost were 0 and when the benefit and cost canceled one another, which occurred when the benefit $b = 0.2$, cost $c = 0.1$, and relatedness $r = 0.5$. In both these cases, background selection doesn't seem to affect fixation probabilities (Figure 1). These effects are consistent with background selection only affecting the fixation probability of the altruistic allele through a change in the effective population size N_e. Further confirmation of this can be seen in Figure 1 where the predicted fixation probabilities assuming background selection only affects N_e are generally consistent with the simulation results.

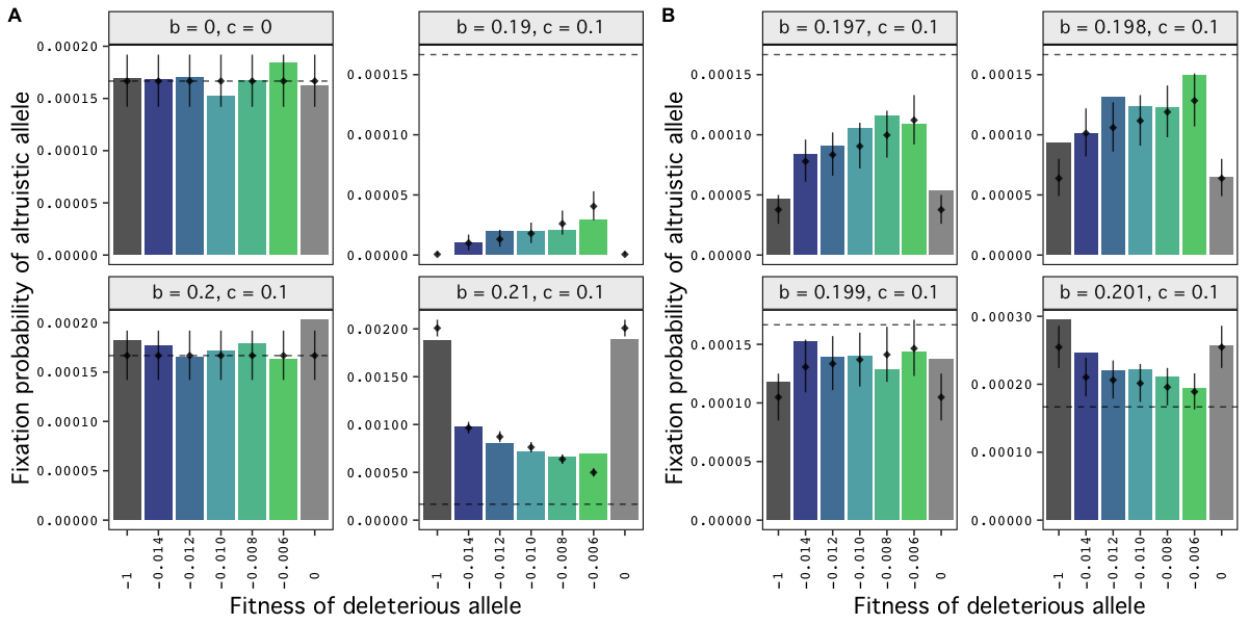

Figure 1. The effect of background selection on the fixation probability of the altruistic allele depends on whether the allele is selected for by Hamilton's rule. Simulations of altruism between full siblings ($r = 1/2$) are plotted by the cost (c) and benefit (b) to fitness of an altruistic interaction. Shown in A) are two scenarios when the altruistic allele is expected to be neutral by Hamilton's rule (leftmost column), a scenario when it is expected to be detrimental (upper right), and a scenario when it is expected to be beneficial (lower right). In B) benefit is varied by smaller increments around the expected neutral value of 0.2. The horizontal dashed line is the fixation probability of a neutral allele due to drift, 1/6000; vertical lines indicate the 95% binomial confidence interval for the predicted fixation probabilities (see Methods for details). In general, background selection does not affect fixation probability in the neutral cases, increases fixation probability when the altruistic allele is expected to be detrimental, and decreases fixation probability when the allele is expected to be beneficial.

Term	Estimate	Std. Error	z value	p-value
intercept	-58.84288	0.5694923	-103.32514	$<2\times10^{-16}$
benefit	250.44186	2.7503363	91.05863	$<2\times10^{-16}$
BGS	18.61980	0.6845086	27.20170	$<2\times10^{-16}$
benefit × BGS	-92.90784	3.3200609	-27.98377	$<2\times10^{-16}$

Table 1. A general linear model found that the benefit value, the presence of background selection (BGS), and their interaction were all significant predictors of the altruistic allele's fixation probability. The model used a logit link function. The response variable, fixation probability, was binomially distributed, while the benefit was numeric and the presence of background selection was categorical. All p-values were too small to be computationally represented and were instead given as 0 in R.

The effect of both the benefit value and the presence of background selection on the fixation probability of the altruistic allele were confirmed statistically by fitting the simulation data to a generalized linear mixed model using a logit link function and with a binomially distributed response variable, fixation probability. The two predictor variables were the benefit b, which was numeric, and a categorical variable BGS that indicated the presence or absence of background selection. BGS was false when fitness was -1 or 0, and true otherwise. As shown in Table 1, the benefit b, BGS, and the interaction between the benefit and BGS all significantly affected fixation probability.

To confirm that background selection did not affect the cost to benefit ratio under which altruism was favored and instead only affected the strength of selection for or against the allele, we ran simulations with both a higher and a lower recombination rate. As expected, varying recombination rate did not affect the cost/benefit ratios under which the altruistic allele was favored. Instead, the smaller recombination rate of 10^{-12} increased the effect of background selection and the larger recombination rate of 10^{-4} erased the effect of background selection (Supplementary Figure S2).

Discussion

Research into the evolution of genes that affect altruism has largely ignored the genomic context of those genes, such as the possibility that linked selection might affect their evolutionary fates. Since background selection can increase genetic relatedness in the genomic regions where it occurs, we examined the effect of background selection on a genomic region that contains an altruistic allele. We used simulations where altruism was determined by a single allele and altruistic individuals could help their full siblings. We found that whether the altruistic allele was positively or negatively

selected for was not affected by background selection, and could still be predicted by the classic condition for the evolution of altruism for family-structured populations, which is Hamilton's rule or $c/b < r$. Background selection was seen instead in its effect on the effective population size N_e: stronger background selection due to weaker recombination or weaker purifying selection in the genomic region (small s values) decreases N_e. Decreased N_e weakens the effect of selection at the altruistic allele relative to genetic drift and shifts the fixation probability closer to the neutral value. Fixation probabilities calculated assuming background selection only affects N_e reasonably fit the simulation data and confirm the limited role of background selection in this scenario. Background selection is well-known to increase the fixation probability of weakly deleterious alleles and decrease the fixation probability of weakly beneficial alleles (Birky and Walsh 1988; Charlesworth 1994).

The lack of an effect of background selection on whether the altruistic allele was under positive or negative selection can be explained by considering how background selection affects genetic relatedness in a family-structured population. Background selection can affect relatedness among individuals randomly sampled from the population but it should have no effect on the relatedness value of $r = 1/2$ between siblings within a family because selection on deleterious alleles acts only on adults and has no effect on the frequency of alleles within sibships. Altruism in this model occurs between siblings, and hence the sibling relatedness value is what matters in Hamilton's rule. Thus, background selection can only affect N_e. These results suggest that background selection may have a more powerful effect on when altruism evolves in demographic scenarios where helping occurs between individuals whose relatedness can be affected by linked selection. One such scenario may be in spatially-structured populations when individuals help others in their local deme and linked selection increases genetic relatedness above the level set by limited migration.

Support for the potential importance of this effect of linked selection comes from one of the few previous studies into how genomic context affects the evolution of social traits: Hammarlund et al. (2016) simulated mutations that confer a benefit in a new environment and are located on a non-recombining chromosome that also contains a social locus. Their results show that these beneficial mutations can favor the evolution of altruistic alleles in a spatially-structured population. While their scenario does involve linked selection, cooperation evolves in their scenario in a different way than the mechanism proposed here. Specifically, they assume that the size of each group in the population is positively related to the frequency of cooperation in that group, since more cooperative groups are likely to be more ecologically productive. Groups with more cooperators have more individuals, which increases the total chance that an adaptive mutation arises in a group with more cooperators relative to a group with fewer cooperators. Given complete linkage between the beneficial loci and social locus, cooperative alleles can hitchhike alongside the beneficial alleles and rise in frequency with the beneficial alleles in a process the authors call the "Hankshaw effect". However, this effect is temporary; eventually a non-cooperative mutation will occur at the social locus and it will fix given the cost of cooperation. Thus, cooperation is only maintained in the long term

with a constant source of beneficial mutations due to, for example, regular fluctuations in the environment. Moreover, their hitchhiking mechanism requires that the selection coefficient of a beneficial allele outweighs the cost of cooperation. In contrast, the hypothesis here is that linked selection more generally (due to either background selection or selective sweeps) might have an effect because it increases genetic relatedness in regions linked to a social locus. Nevertheless, their result is intriguing and does suggest that selection on linked, "nonsocial", mutations can impact the evolution of sociality.

Limited recombination is also crucial when social traits coevolve with other traits that affect cooperation or altruism (e.g., Lehmann *et al*. 2007; Rousset and Roze 2007; Hochberg *et al*. 2008; Parvinen 2013; Mullon *et al*. 2016, 2018). For example, punishment of non-cooperators stabilizes cooperation in the right scenarios (Boyd and Richerson 1992; Fehr and Gächter 2002; Boyd *et al*. 2003; Hauert *et al*. 2007). However, costly punishment itself cannot evolve unless some punishers are also cooperators (the type who benefit from not being punished), which requires genetic linkage between cooperation and punishment loci. Low recombination rates allow this linkage to build over time, which can aid a coevolutionary increase in the frequencies of both punishment and cooperation (Lehmann *et al*. 2007). Migration also has an important effect on the evolution of altruism, since it causes gene flow and shapes and other measures of genetic relatedness. Multiple models show that completely linked cooperation and dispersal loci can coevolve to a monomorphic equilibrium composed of individuals who cooperate and disperse at intermediate rates (Hochberg *et al*. 2008; Parvinen 2013; Mullon *et al*. 2016). Moreover, a few of these models show that evolutionary branching can occur under some parameters leading to a dimorphic population composed of weakly dispersing cooperators and strongly dispersing non-cooperators (Parvinen 2013; Mullon *et al*. 2016). Intriguingly, a recent simulation analysis showed (Mullon *et al*. 2018) that the stability of this social polymorphism depends on weak recombination between the cooperation and dispersal loci, and strong recombination leads to a return of stability of the monomorphic equilibrium.

Altruism is a complex behavior that can be subject to more evolutionary forces than non-social traits. However, our simulations show that altruism in a family-structured population is affected by background selection in the same way as simpler non-social traits are affected: background selection decreases the strength of selection for or against the linked trait. That said, altruism occurs in many more situations than portrayed by this single-population, sibling-helping-sibling model, and background selection may have a different effect in different scenarios. Further research into more complex population structures, different types of altruistic and cooperative interactions, and other kinds of linked selection may reveal more unique effects.

Data Availability Statement

All code for reproducing the SLiM simulations and Mathematica calculations are archived at https://github.com/vancleve/sib_altruism_background_selection.

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Supplementary Figures

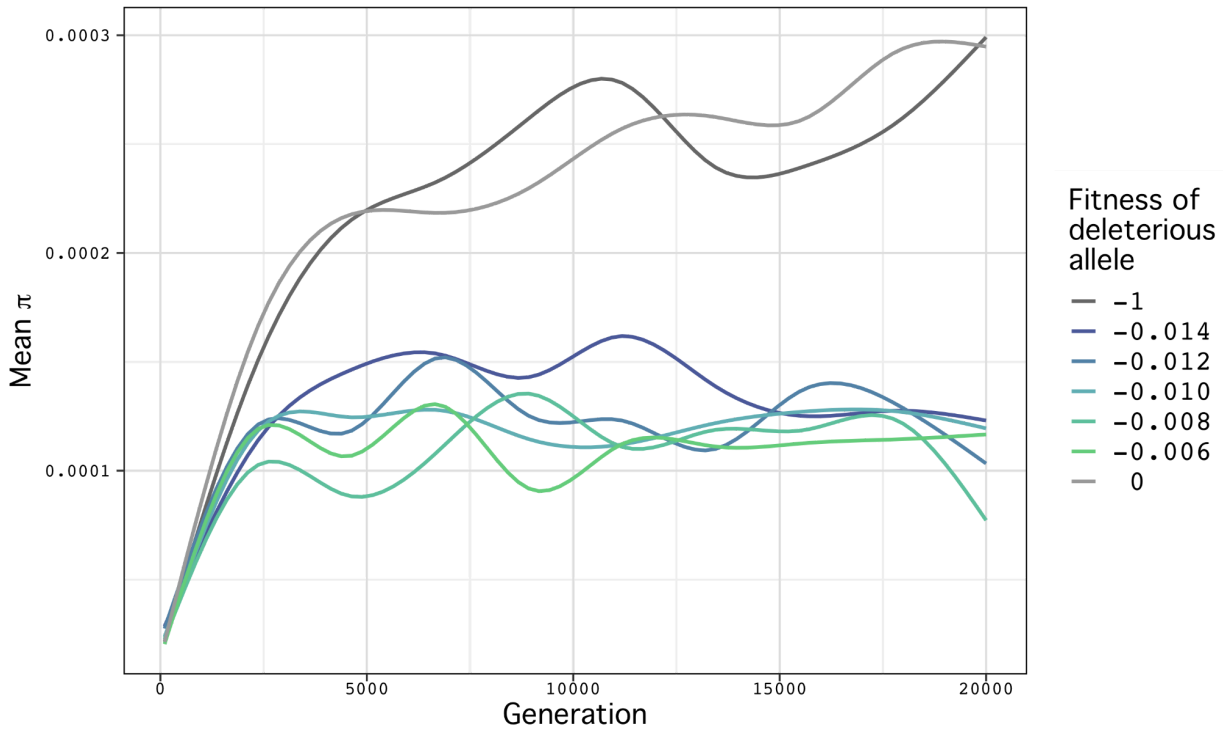

Figure S1. Genomic heterozygosity (π) over 20,000 generations in the presence and absence of background selection. 10 simulations were run for each fitness value for the detrimental mutations, and the mean π for each value is plotted. Background selection causes π to level off earlier and lower. For all fitness values, the greatest increase in π slows by generation 5000.

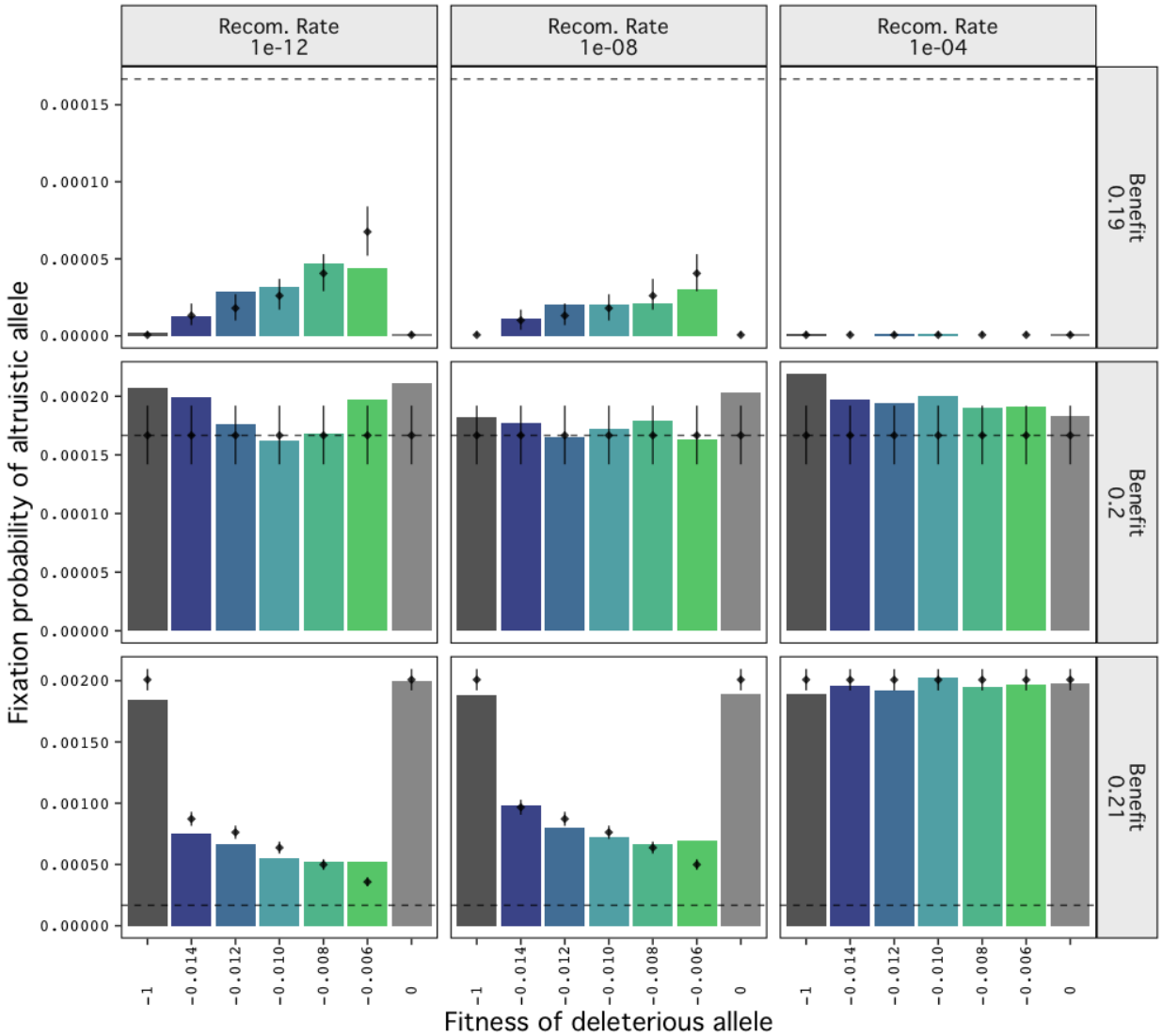

Figure S2. Varying recombination rate did not affect the cost/benefit ratios under which the altruistic allele is favored ($c/b < 0.5$ or $b > 0.2$ in the figure) and disfavored ($b < 0.2$ in the figure). Rather, the effect of background selection was stronger with a lower recombination rate of 10^{-12} while the higher recombination of 10^{-4} rate eliminated the effect of background selection. For the benefit $b = 0.2$, the allele was neutral at all recombination rates. The horizontal dashed line is the fixation probability of a neutral allele due to drift; vertical black lines indicate the 95% binomial confidence interval for the predicted fixation probabilities (see Methods for details).