

1 Coexistence of alleles: insights of Modern
2 Coexistence Theory into the maintenance of
3 genetic diversity

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1 Introduction

The question of how genetic variation is maintained, despite the effects of selection and drift, continues to be central to the study of evolutionary biology (Walsh & Lynch, 2018). Classical explanations include overdominance (heterozygote advantage) or frequency-dependent selection, but in the modern era of genomic data, all patterns of elevated variation than expected under neutrality tend to be categorized broadly as balancing selection, regardless of the evolutionary mechanism (Mitchell-Olds *et al.*, 2007). One of the evolutionary mechanisms coined under balancing selection is sexually antagonistic selection, which occurs when the direction of natural selection on traits or loci differs between the sexes (Connallon & Hall, 2018).

Sexually antagonistic selection has been identified as a powerful engine of speciation that generally prevents more than one allele to be fixed in a population (Gavrilets, 2014). The effect of sexually antagonistic selection, however, has been generally studied under strong simplifying assumptions such as constant population sizes and homogeneous environments (Kidwell *et al.*, 1977; Pamilo, 1979). Few studies have explored the effect of sexually antagonistic selection on the maintenance of polymorphism with more realistic assumptions, such as Connallon *et al.* (2018) that found that classical predictions break down when fluctuations in the environment combined with life-history traits allow local adaptations and promote the maintenance of genetic diversity. The effect of environmental fluctuations without local adaptation, however, has not been studied in the context of sexually antagonistic selection.

30 The contribution of environmental fluctuations to genetic variability remains a de-
31 bated issue. Classic theoretical models predict that temporal fluctuations in environmen-
32 tal conditions are unlikely to maintain a genetic polymorphism (Hedrick, 1974; 1986).
33 However, other studies have found that fluctuating selection can maintain genetic vari-
34 ance on sex-linked traits (Reinhold, 2000), or in populations where generations overlap
35 (Ellner & Hairston Jr, 1994; Ellner & Sasaki, 1996). Similarly, temporal changes in popu-
36 lation sizes have been shown to mitigate the effect of genetic drift in small populations
37 (Pemberton *et al.*, 1996), or populations with a seed bank (Nunney, 2002). Thus, both fluc-
38 tuations in selection and population sizes could dramatically change the effect of sexually
39 antagonistic selection in the maintenance of genetic diversity.

40 Importantly, progress requires more than just identifying if fluctuations increase or de-
41 crease genetic diversity, but to quantify how exactly they contribute to its' maintenance
42 (Ellner *et al.*, 2016). Modern coexistence theory (MCT) provides a powerful conceptual
43 framework to do so (Chesson, 2000b; 1994; Barabás *et al.*, 2018). Although its core ideas
44 were formalized in an ecological context (Chesson, 1994; 2000a), this framework provides
45 the necessary tools to examine the relative contributions of fluctuations to diversity main-
46 tenance, which can also be applied to evolutionary contexts (Ellner & Sasaki, 1996; Rein-
47 hold, 2000). From an ecological perspective, polymorphism is equivalent to the coexis-
48 tence of species, and the fixation of either one of the alleles is equivalent to competitive
49 exclusion. The coexistence of alleles, thus, can be examined through the same lens as the
50 coexistence of competing species.

51 Here, we seek to explicitly apply recent theoretical and analytical advances in MCT to

the question of how genetic variation is maintained under sexually antagonistic selection. Specifically, we aim to quantify the relative importance of different types of fluctuations to overall stable coexistence, or to exclusion of sexually antagonistic alleles. We extended a conceptualization of MCT (Ellner *et al.*, 2016; 2019) to examine how fluctuations in selection values, fluctuations in population sizes, and their interactions can stabilize or hinder the coexistence of alleles. In particular, we examined i) Can fluctuations in population sizes and selection values allow sexually antagonistic alleles to coexist when differences in their fitness would typically not allow them to? and ii) What is the relative contribution of different types of fluctuations that allow two sexually antagonistic alleles to be maintained in a population? Our study provides the tools to analyze evolutionary dynamics from an ecological perspective and contributes to answering long-lasting questions regarding the effect of non-constant environments on genetic diversity.

2 Methods

We first present the evolutionary consequences of sexually antagonistic selection in constant environments. We then present a model that describes the evolutionary dynamics of sexually antagonistic alleles, and show how changes in allele's frequencies can be expressed in terms of growth rates, a necessary condition for analyses done using MCT. We continue by simulating different scenarios of alleles invading a population, where we allowed population sizes, selection values, both, or neither to vary. Finally, we examine the results of our simulations through a MCT lense by calculating the contribution of each of these fluctuations in the coexistence of alleles across the parameter space of sexually

73 antagonist selection.

74 Sexually antagonistic selection

75 Most population genetic models of sex-dependent selection consider evolution at single,
76 biallelic loci with frequency and density independent effects on the relative fitness of
77 females and males (Wright, 1942; Kidwell *et al.*, 1977; Immler *et al.*, 2012). Consider a locus
78 with two alleles, j and k , that affect fitness in the haploid state. Assume allele j always has
79 a high fitness in females ($w_{jf} = 1$), but has variable fitness in males ($w_{jm} < 1$); and allele k
80 always has a high fitness in males ($w_{km} = 1$), but has variable fitness in females ($w_{kf} < 1$).
81 The selection against allele j in males is therefore $S_m = 1 - w_{jm}$, and the selection against
82 allele k in females is $S_f = 1 - w_{kf}$. Selection maintains both alleles in the population
83 under the condition that:

$$\frac{S_m}{1 + S_m} < S_f < \frac{S_m}{1 - S_m} \quad (1)$$

84 (Kidwell *et al.*, 1977; Pamilo, 1979; Connallon *et al.*, 2018). These inequalities can be used to
85 calculate the proportion of the selection parameter space (within the range $0 < S_m, S_f <$
86 1) that leads to polymorphism of sexually antagonistic alleles: in ≈ 0.31 of the parame-
87 ter space allele j will be fixed, in another ≈ 0.31 of the parameter space allele k will be
88 fixed, and in ≈ 0.38 of the parameter space polymorphism or coexistence of alleles can be
89 maintained.

90 Most of the models used to explore the evolutionary dynamics of sexual antagonism
91 assume constant population sizes and homogeneous environments (Kidwell *et al.*, 1977;

Pamilo, 1979; Immler *et al.*, 2012). In constant environments, the maintenance of polymorphism of sexually antagonistic alleles is solely determined by the values of S_m and S_f . If fluctuations in population sizes or selection values have an effect on the coexistence of sexually antagonistic alleles, it would be reflected in increases or decreases of the proportion of the parameter space of selection where polymorphism is maintained. Furthermore

Population dynamics of sexually antagonistic alleles

As a baseline, we used a model that captures the effects of sexually antagonistic selection. Our model consisted of a population that has discrete generations, and that is subject to the previously described sexual antagonism between allele j and k . The frequency each allele in each sex at the beginning of a life-cycle at time t given by:

$$p_{jm,t} = \frac{n_{jm,t}}{N_{m,t}} \quad (2)$$

$$p_{jf,t} = \frac{n_{jf,t}}{N_{f,t}} \quad (3)$$

$$p_{km,t} = \frac{N_{m,t} - n_{jm,t}}{N_{m,t}} \quad (4)$$

$$p_{kf,t} = \frac{N_{f,t} - n_{jf,t}}{N_{f,t}} \quad (5)$$

where $N_{m,t}$ and $N_{f,t}$ are the numbers of males and females in a population at time t , $n_{jf,t}$ is the number of females f with allele j , and $n_{jm,t}$ is the number of males m with allele j at time t , respectively.

109 The individuals in the population mate at random before selection occurs, and there-
 110 fore the frequency of offspring with allele j after mating, $p'_{j,t}$ can be expressed as:

$$p'_j = \frac{n_{jf,t}}{N_{f,t}} \frac{n_{jm,t}}{N_{m,t}} + \frac{1}{2} \frac{n_{jf,t}}{N_{f,t}} \frac{(N_{m,t} - n_{jm,t})}{N_{m,t}} + \frac{1}{2} \frac{(N_{f,t} - n_{jf,t})}{N_{f,t}} \frac{n_{jm,t}}{N_{m,t}}, \quad (6)$$

111 which upon rearranging and simplifying can be written as:

$$p'_{j,t} = \frac{(N_{m,t}n_{jf,t} + N_{f,t}n_{jm,t})}{2N_fN_m}. \quad (7)$$

112 Selection acts upon these offspring in order to determine the allelic frequencies in
 113 females and males in the next generation, $t + 1$. As an example the frequency of females
 114 with allele j after selection is given by:

$$p'_{jf,t+1} = \frac{n_{jf,t+1}}{N'_{f,t+1}} = \frac{p'_j w_{jf}}{p'_j w_{jf} + (1 - p'_j) w_{kf}} \quad (8)$$

115 The logarithmic growth rate of j in females, is therefore given by the number of fe-
 116 males with allele j after selection, divided by the original number of females carrying
 117 allele j :

$$r_{jf,t} = \ln \left(\frac{n'_{jf,t+1}}{n_{jf,t}} \right) \quad (9)$$

118 An equivalent expression for the per capita growth rate of allele j in males m can be
 119 obtained by exchanging f for m across the various subscripts in this expression.

120 Allelic coexistence in a sexual population, however, is ultimately influenced by growth

and establishment of an allele across both sexes. Therefore, the full growth rate of allele j across the entire population of females *and* males is given by

$$r_j = \ln \left(\frac{n'_{jf,t+1} + n'_{jm,t+1}}{n_{jf,t} + n_{jm,t}} \right). \quad (10)$$

Equivalently, there exists an expression for r_k . If the values of selection are within the bounds of Eqn.1, both alleles will have positive growth rates, and therefore be able to coexist. If one allele has a positive growth rate, while the other does not, then only one allele will be fixated into the population. We used this model as a baseline to perform simulations that allowed us to examine how different types of fluctuation change the expected effect of sexually antagonistic selection.

Simulations

Although the evolutionary dynamics of sexually antagonistic selection is often explored through changes in alleles' frequencies, MCT requires population dynamics to be expressed as growth rates of the competing alleles, as we show in Eqn.10. This is because MCT provides a framework to quantify what gives an allele a population growth rate advantage over the other allele when it becomes rare (i.e., when it is an invader) (Chesson, 1982; 2003; Barabás *et al.*, 2018). Our simulations, thus, consisted of performing invasion simulations of both alleles invading separately, allowing population sizes and fitness values to fluctuate, across the selection parameter space of sexually antagonistic selection. For simplicity, we first present our approach focusing on a fixed point in the selection parameter space.

140 Timeseries

141 We first incorporated the effects of fluctuations into our populatin dynamics model. To do
 142 so, we generated independent timeseries of fluctuations in fitness values and population
 143 sizes. In the case of fluctuations in selection values, for a given value of w_{jm} and w_{kf} (i.e.,
 144 a fixed point in the selection parameter space), we generated a timeseries of 500 timesteps
 145 made up of correlated fluctuations of w_{jm} and w_{kf} . Following the approach of Shoemaker
 146 *et al.* (2020) we controlled the effect size of fluctuations in fitness values (σ_w) and its '
 147 correlation (ρ_w) by using the Cholesky factorisation of the variance-covariance matrix:

$$C_w = \begin{bmatrix} \sigma_w^2 & \rho_w \sigma_w^2 \\ \rho_w \sigma_w^2 & \sigma_w^2 \end{bmatrix} \quad (11)$$

148 We multiplied Eqn. 11 by a (2×500) matrix of random numbers from a normal dis-
 149 tribution with mean 0 and unit variance, which yielded γ_j and γ_k . Then, we calculated
 150 the value of w_{jm} at time $t + 1$ as $w_{jm,t+1} = w_{jm}^{\gamma_{j,t}}$. We calculated the value of $w_{kf,t+1}$ analo-
 151 gously.

152 Similarly, we generated a timeseries of 500 timesteps made up of correlated fluctua-
 153 tions in population sizes. We chose values of N_m and N_f of 200 individuals each as the
 154 initial value of population sizes throughtout our simulations. We performed a Cholesky
 155 factorisation of the variance-covariance matrix, controlling the effect size of fluctuations
 156 in population sizes with σ_g and their correlation with ρ_g . We multiplied this factorisation
 157 by a random matrix of uncorrelated random variables, which yielded γ_m and γ_f . Finally,
 158 we calculated the number of males in the population at time $t + 1$ as $N_{m,t+1} = N_{m,t} + \gamma_{m,t}$.

We calculated the value of $N_{f,t+1}$ analogously.

Finally, we performed simulations that allowed our population dynamics model (Eqns. 2 to 10) to iterate for 500 timesteps. We started each simulation with the initial values of N_m and N_f described before and equal frequencies of allele j and allele k in each sex. For each timestep t in our simulations, the values of w_{jm} , w_{kf} , N_m and N_f used to calculate allele's frequencies in the next generation corresponded to the values calculated as described previously. This approach yielded a final timeseries that captured the dynamics of sexually antagonistic alleles, with flucting values of selection and population sizes.

Invasion simulations

We used the timeseries described previously to perform invasion simulations of both alleles. Each allele could invade via two different pathways: males and females. We explored all of the combinations of each allele invading through a different pathway (e.g., allele j invading through males, and allele k invading through females, and so on). Therefore, for every point in the parameter space of sexually antagonistic selection, we explored four different types of invasion.

For each timestep in the timeseries, we performed simulations of the two alleles invading separately via their respective pathway. To simulate invasion, we set the initial values of the invading allele to one individual, while the resident allele was set to the corresponding value of the timeseries, and we projected forward one generation. For example, if allele j was invading via males, then we would set $n_{jm} = 1$ and $n_{jf} = 0$, while the allele k would be the resident. The abundance of the resident was determined by the timestep

180 t of the timeseries. After one generation, we calculated the logarithmic growth rate of j
 181 allele invading as:

$$r_j = \ln \left(\frac{n_{jm,t+1} + n_{jf,t+1}}{1} \right) \quad (12)$$

182 Correspondingly, the logarithmic growth rate of the k allele as a resident would be
 183 given by:

$$r_k = \ln \left(\frac{n_{km,t+1} + n_{kf,t+1}}{n_{km,t} + n_{kf,t}} \right) \quad (13)$$

184 We treated each timestep of the timeseries independently, so we performed 500 inva-
 185 sion simulations, one for each timestep. Then, we calculated the mean invasion growth
 186 rate as the average of the 500 invasion growth rates, and the mean reasident growth rate
 187 as the average of the 500 resident growth rates. We determined alleles to be coexisting if
 188 both of them, invading via their respective pathway, had positive mean invasion growth
 189 rates, which is also called the mutual invasibility criterion.

190 **Functional decomposition**

191 To understand the relative contribution of fluctuations in population sizes and fitness
 192 values, we applied the functional decomposition framework we previously described. To
 193 do so, we performed another set of invasion simulations of each allele invading via its cor-
 194 responding pathway, but setting all of the fluctuating variables to their means. Then, we
 195 calculated invader and resident mean growth rates as previously described (e.g., Eqns.12
 196 and 13). When every variable was set to its mean, the average invasion and resident
 197 growth rate was equal to \mathcal{E}^0 .

Building upon this baseline, we performed another set of invasion simulations, but this time allowing variables to fluctuate one by one, to capture their main effects, and jointly, to capture their interactions. Then, we calculated the corresponding values of each \mathcal{E} term, as shown in Table 1. For simplicity, we only show the functional decomposition of j as an invader in Table 1, however, the functional decomposition of k as an invader is identical. This approach allowed us to capture the contribution of fluctuations to invader and resident growth rates, which we did for each allele invading a different pathway.

Having done the decomposition of invader and resident growth rates, we continued to do the invader-resident comparisons to calculate Δ values (e.g., ??). For each allele invading via a different pathway, we calculated 16 Δ values, one for each one of the \mathcal{E} terms. However, since the magnitude of each one of these values could vary considerably, to make them comparable, we normalized each Δ value by dividing it by the length of the Δ vector. For example, the normalized value of Eqn. ?? would be given by:

$$\Delta_j^{Nm*} = \frac{\Delta_j^{Nm}}{\sqrt{\sum_{i=1}^{16} (\Delta_i)^2}} \quad (14)$$

This normalization bounded Δ values from -1 to 1 .

The parameter space of sexually antagonist selection

To evaluate if fluctuations in fitness values and population sizes allow sexually antagonistic alleles to coexist when their fitness values would typically not allow them to, we applied the approach presented so far to the whole parameter space of selection

216 ($0 < S_m, S_f < 1$). To do so, we partitioned the parameter space in 2500 parts, each one
217 a combination of different w_{jm} and w_{kf} values. For each parameter combination, we se-
218 parately calculated each allele's mean invasion growth rate when invading through males
219 and females, as well as its functional decomposition. Then, we determined coexistence
220 outcomes using the mutual invasibility criterion. Finally, we calculated the proportion of
221 the parameter space that allowed alleles to coexist, for each allele invading via a different
222 sex.

223 We explored all of the combinations of low ($\sigma_w = 0.1$ and $\sigma_g = 1$), intermediate ($(\sigma_w =$
224 0.3 and $\sigma_g = 10)$) and high fluctuations ($\sigma_w = 0.7$ and $\sigma_g = 30$) in fitness values and
225 population sizes, with different extents of correlations between fluctuations (Table 2). As
226 a control simulation, we set $\sigma_w = 0.001$ and $\sigma_g = 0.001$, with no correlation between
227 fluctuations. For each one of the factorial combinations of σ_g , σ_w , ρ_g and ρ_w (Table 2),
228 we performed invasion simulations across the parameter space of selection. We did three
229 replicates per parameter combination, which resulted in 432 simulations.

Figures and tables

Table 1: Functional decomposition of the growth rate of allele j . Need to get rid of the sums and m because we are only presenting j . As well to add an overbar over r_j .

Term	Formula	Meaning
\mathcal{E}_j^0	$\bar{r}_j(\bar{N}_m, \bar{N}_f, \bar{w}_{jm}, \bar{w}_{kf})$	Growth rate at mean population size and fitness values.
$\bar{\mathcal{E}}_j^{N_m}$	$\bar{r}_j(N_m, \bar{N}_f, \bar{w}_{jm}, \bar{w}_{kf}) - \mathcal{E}_j^0$	Main effect of fluctuations in N_m
$\bar{\mathcal{E}}_j^{N_f}$	$\bar{r}_j(\bar{N}_m, N_f, \bar{w}_{jm}, \bar{w}_{kf}) - \mathcal{E}_j^0$	Main effect of fluctuations in N_f
$\bar{\mathcal{E}}_j^{w_{jm}}$	$\bar{r}_j(\bar{N}_m, \bar{N}_f, w_{jm}, \bar{w}_{kf}) - \mathcal{E}_j^0$	Main effect of fluctuations in w_{jm}
$\bar{\mathcal{E}}_j^{w_{kf}}$	$\bar{r}_j(\bar{N}_m, \bar{N}_f, \bar{w}_{jm}, w_{kf}) - \mathcal{E}_j^0$	Main effect of fluctuations in w_{kf}
$\bar{\mathcal{E}}_j^{N_m, N_f}$	$\bar{r}_j(N_m, N_f, \bar{w}_{jm}, \bar{w}_{kf}) - [\mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{N_m} + \bar{\mathcal{E}}_j^{N_f}]$	Interaction of fluctuations in N_m and N_f
$\bar{\mathcal{E}}_j^{w_{jm}, w_{kf}}$	$\bar{r}_j(\bar{N}_m, \bar{N}_f, w_{jm}, w_{kf}) - [\mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{w_{jm}} + \bar{\mathcal{E}}_j^{w_{kf}}]$	Interaction of fluctuations in w_{jm} and w_{kf}
$\bar{\mathcal{E}}_j^{N_m, w_{jm}}$	$\bar{r}_j(N_m, \bar{N}_f, w_{jm}, \bar{w}_{kf}) - [\mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{N_m} + \bar{\mathcal{E}}_j^{w_{jm}}]$	Interaction of fluctuations in N_m and w_{jm}
$\bar{\mathcal{E}}_j^{N_m, w_{kf}}$	$\bar{r}_j(N_m, \bar{N}_f, \bar{w}_{jm}, w_{kf}) - [\mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{N_m} + \bar{\mathcal{E}}_j^{w_{kf}}]$	Interaction of fluctuations in N_m and w_{kf}
$\bar{\mathcal{E}}_j^{N_f, w_{jm}}$	$\bar{r}_j(\bar{N}_m, N_f, w_{jm}, \bar{w}_{kf}) - [\mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{N_f} + \bar{\mathcal{E}}_j^{w_{jm}}]$	Interaction of variation in N_f and w_{jm}
$\bar{\mathcal{E}}_j^{N_f, w_{kf}}$	$\bar{r}_j(\bar{N}_m, N_f, \bar{w}_{jm}, w_{kf}) - [\mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{N_f} + \bar{\mathcal{E}}_j^{w_{kf}}]$	Interaction of fluctuations N_f and w_{kf}
$\bar{\mathcal{E}}_j^{N_m, w_{jm}, w_{kf}}$	$\bar{r}_j(N_m, \bar{N}_f, w_{jm}, w_{kf}) - [\mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{N_m} + \bar{\mathcal{E}}_j^{w_{jm}} + \bar{\mathcal{E}}_j^{w_{kf}}]$	Interaction of fluctuations in N_m , w_{jm} , and w_{kf}
$\bar{\mathcal{E}}_j^{N_f, w_{jm}, w_{kf}}$	$\bar{r}_j(\bar{N}_m, N_f, w_{jm}, w_{kf}) - [\mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{N_f} + \bar{\mathcal{E}}_j^{w_{jm}} + \bar{\mathcal{E}}_j^{w_{kf}}]$	Interaction of fluctuations in N_f , w_{jm} , and w_{kf}
$\bar{\mathcal{E}}_j^{N_m, N_f, w_{jm}}$	$\bar{r}_j(N_m, N_f, w_{jm}, \bar{w}_{kf}) - [\mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{N_m} + \bar{\mathcal{E}}_j^{N_f} + \bar{\mathcal{E}}_j^{w_{jm}}]$	Interaction of variation in N_m , N_f , and w_{jm}
$\bar{\mathcal{E}}_j^{N_m, N_f, w_{kf}}$	$\bar{r}_j(N_m, N_f, \bar{w}_{jm}, w_{kf}) - [\mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{N_m} + \bar{\mathcal{E}}_j^{N_f} + \bar{\mathcal{E}}_j^{w_{kf}}]$	Interaction of fluctuations in N_m , N_f , and w_{kf}
$\bar{\mathcal{E}}_j^{N_m, N_f, w_{jm}, w_{kf}}$	$\bar{r}_j(N_m, N_f, w_{jm}, w_{kf}) - [\mathcal{E}_j^0 + \bar{\mathcal{E}}_j^{N_m} + \bar{\mathcal{E}}_j^{N_f} + \bar{\mathcal{E}}_j^{w_{jm}} + \bar{\mathcal{E}}_j^{w_{kf}}]$	Interaction of variation in N_f , N_m , w_{jm} , and w_{kf}

Table 2: This is a caption

Parameter	Values	Description
σ_w	0.001, 0.1, 0.3, 0.5, 0.7, 0.9	Effect size of fluctuations in fitness values
σ_g	0.001, 1, 10, 20, 30, 50	Effect size of fluctuations in population sizes
ρ_w	-0.75, 0, 0.75	Correlation between fluctuations in fitness values
ρ_g	-0.75, 0, 0.75	Correlation between fluctuation in population sizes

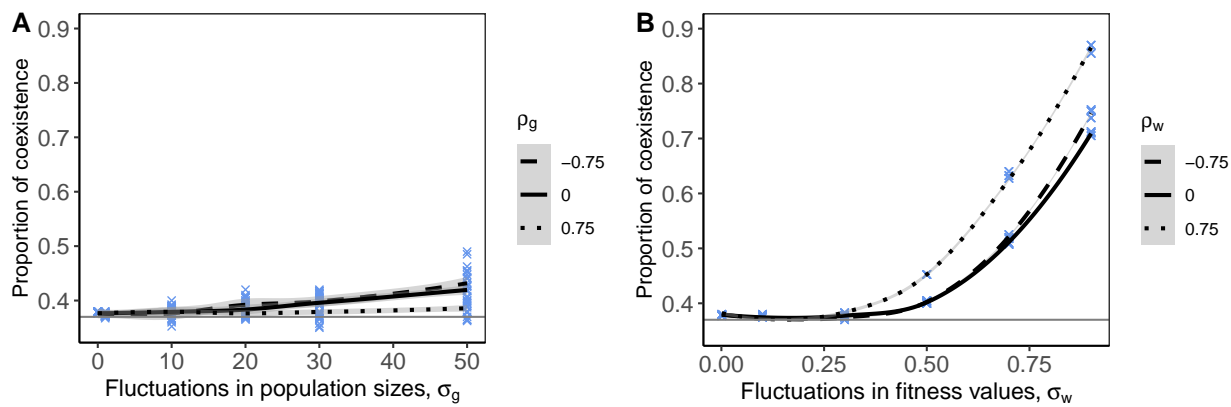


Figure 1

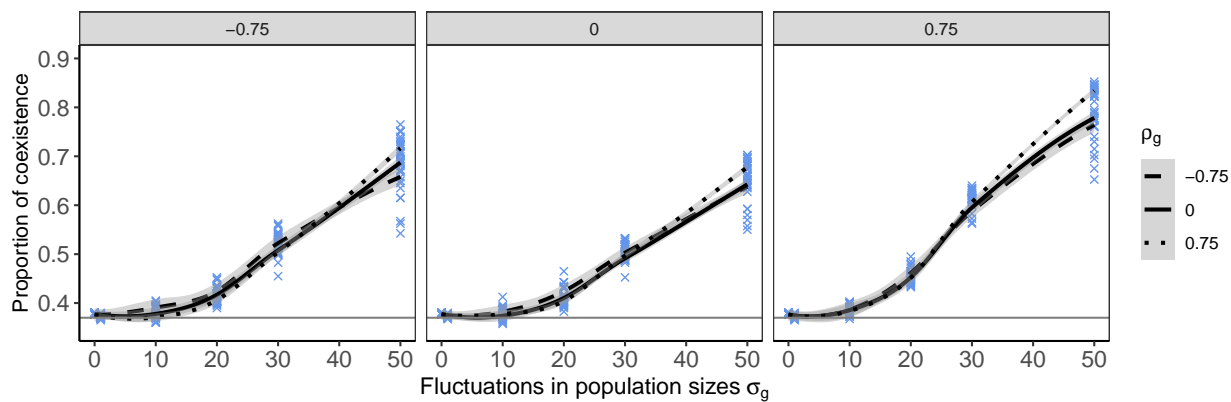


Figure 2

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