Effects of Evolution of Species Discrimination on Population Viability

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1 Introduction

Heterospecifc mating interactions can occur between closely related species that diverged

from a common ancestor and come under secondary contact

Heterospecific matings and courtship are costly, especially for females, as they often result

in inviable offspring. This phenomenon is known as reproductive interference. Males can

also incur costs if they spend sperm or time courting and mating with heterospecifics,

thus, reducing their reproductive potential

Previous studies have shown that reproductive interference can influence the co-existence

of species. Asymmetric reproductive interference reduces the fitness of the population

most affected, leading to more inviable offspring. This may lead to competitive exclusion.

Heterospecific matings negatively impact males' reproductive potential, creating selection

pressure for them to evolve discrimination. However, this discrimination reduces their

ability to lower the fitness of heterospecifics, weakening the species' overall competitive

ability.

Our aim is to demonstrate this phenomenon using a theoretical model where two species

initially symmetrically interfere with each other's reproduction. However, the males of

the two species differ in their ability to evolve discrimination. We do this by assuming

the male trait for discrimination has different additive genetic variance in each species;

thus the species with higher genetic variance shows a quicker evolutionary response to the same selection pressure

We show that the species evolving discrimination faster will be competitively excluded, illustrating a scenario of maladaptive evolution.

Objectives:

1. Demonstrating a scenario of maladaptive evolution, using reproductive interference as an example

2. Integrate concepts of reproductive interference (coexistence literature) and evolution of species discrimination under mate choice (RCD literature)

3. Add this dimension of eco-evolutionary feedback to this problem of reproductive interference - species discrimination

Methods

0.1   Model Assumptions

We model a scenario where recently diverged species come into secondary contact. The two species are present in sympatry, and there is ecological competition between them. (Interspecific competition > intraspecifc competition hence, unstable ecological equilibrium)

Tom: the model concerns a secondary contact zone, where members of the two species (or should we call these populations...) frequently interact...

Initially, males of both species are completely indiscriminate - i.e. they court conspecific and heterospecific males with equal probability.

The Model

Species and Mating Consider species 1 and 2. There are F_1 and F_2 females and M_1 and M_2 males. Females mate just once but they might reject some males that approach them before mating.

Female Acceptance A female of species i accepts an approaching heterospecific male $1 - y_i$

Male Discrimination Consider a male that discriminates with strength z_i. This impacts both the rate at which he approaches heterospecific females (the more he discriminates, the less he approaches them), but it might also impact the rate at which he approaches conspecific ones. This is the idea behind many Servedio papers: if you reject wrong type of mates, you might have more of a 'budget' to approach conspecifics.

Approach Rates For this reason, we could model his rate of approaching conspecifics as $1 + \alpha z_i$, while his rate of approaching heterospecifics is $1 - z_i$. The relevant range for both $1 - s$ and z is from 0 to 1.

Female Perspective From the perspective of a focal female of species 1, matings with conspecifics occur at a rate $M_1(1 + \alpha z_1)$ while matings with heterospecifics occur at a rate $M_2(1 - y_1)(1 - z_2)$. She is assumed to mate just once, thus this one mating is with a conspecific with a probability

$$\frac{M_1(1 + \alpha z_1)}{M_1(1 + \alpha z_1) + M_2(1 - y_1)(1 - z_2)} \tag{1}$$

The complementary probability is 1 minus that, and is (in the simplest case) assumed to lead to no offspring.

60 The other species' female perspective is derived similarly.

0.2 Male Fitness

62 Now, for males. What is male fitness? Heterospecific matings do not lead to anything (in

63 the simplest case), conspecific matings do.

64   The number of offspring in a breeding season, considering conspecific matings, can be

65 represented by the equation:

$$N_{t+1} = \frac{F_1 M_1 (1 + \alpha \bar{z_1})}{M_1 (1 + \alpha \bar{z_1}) + M_2 (1 - y_1)(1 - \bar{z_2})} \tag{2}$$

66   Number of offspring produced per unit male rating rate is:

$$\frac{N_{t+1}}{(1 + \alpha \bar{z_1})} = \frac{F_1 M_1}{M_1 (1 + \alpha \bar{z_1}) + M_2 (1 - y_1)(1 - \bar{z_2})} \tag{3}$$

67   Thus, the focal male is responsible for a portion of the total number of offsprings

68 produced, proportional to its own mating rate

$$N_{focal_{(t+1)}} = \frac{F_1 (1 + \alpha z_1)}{M_1 (1 + \alpha \bar{z_1}) + M_2 (1 - y_1)(1 - \bar{z_2})} \tag{4}$$

69   The average male fitness is $\frac{N_{t+1}}{M_1}$:

$$\bar{W} = \frac{F_1 (1 + \alpha z_1)}{M_1 (1 + \alpha z_1) + M_2 (1 - y_1)(1 - z_2)} \tag{5}$$

0.2.1 Breeder's Equation

71 We make use of the breeder's equation $\Delta \bar{z} = h^2 S$ to model the evolution of a trait (z),

72 in response to selection within a single generation. h^2 is the narrow-sense heritability of

73 the trait, or the proportion of phenotypic variance (V_P) in the trait made up by additive

74 genetic variance (V_A) across the population.

0.2.2 Evaluating Selection Differential for Male Discrimination from Fitness function

$$z_{\overline{t+1}} - \bar{z}_t = S_{diff}$$

77 Where $\bar{z}_{t+1}$, the mean value of the phenotypic trait in the next generation is

$$\bar{z}_{t+1} = \left(\frac{1}{\bar{W}_m} \int W_m(z) z p(z)\, dz\right)$$

78 For derivation of the above equation see 1.6

79 W_{z_1} (fitness) of the male with trait z_1 is

$$\frac{F_1(1 + \alpha_1 z_1)}{M_1(1 + \alpha_1 \bar{z}_1) + M_2(1 - s_1)(1 - \bar{z}_2)} \tag{6}$$

$$\frac{W_{z_1}}{\bar{W}_z} = \frac{(1 + \alpha_1 z_1)}{(1 + \alpha_1 \bar{z}_1)} \tag{7}$$

80 Assume that the traits follow a Gaussian distribution centered on $\bar{z}_1$ with variance σ_p^2

81 (phenotypic variance). (Note: Strictly, this is not true - (the traits should be between 0

82 and 1). But it can be an approximation if we assume that the variance is low)

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$$p(z_1) = \frac{1}{\sqrt{2\pi\sigma_p^2}} \exp\left(-\frac{(z_1 - \bar{z}_1)^2}{2\sigma_p^2}\right)$$

$$\int_{-\infty}^{\infty} \frac{W_{z_1}}{\bar{W}_z} p(z_1) dz_1 = \frac{(z_1 + \alpha_1 z_1{}^2)}{(1 + \alpha_1 \bar{z}_1)} p(z_1) dz_1 \tag{8}$$

$$\int_{-\infty}^{\infty} \frac{W_{z_i}}{W_z} p(z_1) dz_1 - \bar{z}_1 = \frac{\alpha_1 \sigma_p^2}{1 + \alpha_1 \bar{z}_1}. \tag{9}$$

The above selection differential is multiplied with h which is $\frac{\sigma_a^2}{\sigma_p^2}$ to obtrain $\Delta \bar{z}$

Thus,

$$\Delta \bar{z} = \frac{\alpha \sigma_a^2}{(1 + \alpha \bar{z})} \tag{10}$$

0.3 Evolution of Female permissivness to heterospecific courtship

Assumptions: There is no linkage between y_i of females and z_i of males. Both of these traits are autosomal and there is no sex-linkage

The female permissiveness $1 - y_i$ can be an evolving trait.

Previously, we described that from the female perspective, the number of offspring produced is equivalent to the probability of mating with a conspecifc Under the assumption that females can mate only once. We computed the conspecifc mating probabilty as follows: :

$$P_{conspecific} = \frac{M_1(1 + \alpha z_1)}{M_1(1 + \alpha z_1) + M_2(1 - y_1)(1 - z_2)}$$

This is equivalent to the expected number of offspring produced by a female with resistance trait value $1 - y_i$

$$W_f(y_i) = P_{conspecific} = \frac{M_1(1 + \alpha z_1)}{M_1(1 + \alpha z_1) + M_2(1 - y_i)(1 - z_2)}$$

0.3.1 Average Female Fitness

To compute the average fitness of females in the population, $\bar{W}_f$, we take the average over the distribution of y in the population. Since there is variation in y, the average fitness

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across all females can be written as:

$$\bar{W}_f = \frac{M_1(1 + \alpha\bar{z_1})}{M_1(1 + \alpha z_1) + M_2(1 - \bar{y})(1 - \bar{z_2})}$$

where $\bar{y}$ is the average value of y_i across all females in the population.

0.3.2 Calculating Trait Change using Selection Differential

Let's now derive the selection differential equation for females, using a similar approach as we did for males but with the trait y instead of z. We'll calculate the expected change in the female trait y over one generation due to selection.

The selection differential equation, but now applied to the female trait y is as follows:

$$\bar{y}_{t+1} - \bar{y}_t = S_{diff}$$

Where $\bar{y}_{t+1}$ is the mean value of the female phenotypic trait y in the next generation, and $\bar{y}_t$ is the current generation's average. The selection differential S_{diff} is the difference between the trait mean in the next generation and the current one.

In analogy to the male case, the mean trait in the next generation is given by:

$$\bar{y}_{t+1} = \frac{1}{\bar{W}_f} \int W_f(y) y p(y) \, dy$$

Where: - $\bar{W}_f$ is the average female fitness in the population. - $W_f(y)$ is the fitness of a female with trait y. - $p(y)$ is the probability distribution of the female trait y.

As derived earlier, $\bar{W}_f$ and $W_f(y)$ is:

$$W_f(y_i) = \frac{M_1(1 + \alpha z_1)}{M_1(1 + \alpha z_1) + M_2(1 - y_i)(1 - z_2)}$$

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113   And for the average trait value $\bar{y}$:

$$\bar{W}_f = \frac{M_1(1 + \alpha z_1)}{M_1(1 + \alpha z_1) + M_2(1 - \bar{y})(1 - z_2)}$$

114   The ratio of the individual fitness $W_f(y_i)$ to the average fitness $\bar{W}_f$ (selection gradient)

115   is:

$$\frac{W_f(y_i)}{\bar{W}_f} = \frac{M_1(1 + \alpha z_1)}{M_1(1 + \alpha z_1) + M_2(1 - y_i)(1 - z_2)} \cdot \frac{M_1(1 + \alpha z_1) + M_2(1 - \bar{y})(1 - z_2)}{M_1(1 + \alpha z_1)}$$

116   Simplifying this:

$$\frac{W_f(y_i)}{\bar{W}_f} = \frac{M_1(1 + \alpha z_1) + M_2(1 - \bar{y})(1 - z_2)}{M_1(1 + \alpha z_1) + M_2(1 - y_i)(1 - z_2)}$$

117   For small variations in y_i, i.e. (variance of y is small or $y_i - \bar{y} << 1$) this ratio can be

118   approximated by a linear expansion around $\bar{y}$: (For explanation see 1.6.2

$$\frac{W_f(y_i)}{\bar{W}_f} \approx 1 + \frac{M_2(1 - z_2)(y_i - \bar{y})}{M_1(1 + \alpha z_1) + M_2(1 - \bar{y})(1 - z_2)}$$

119   **Probability distribution assumption for Female Heterospecific Mating Resis-**

120   **tance Trait**   Assume that the trait y_i follows a Gaussian distribution centered on $\bar{y}$ with

121   variance σ_p^2 (the phenotypic variance):

122   (Assumption $\sigma_p^2 <<< 1$)

$$p(y_i) = \frac{1}{\sqrt{2\pi\sigma_p^2}} \exp\left(-\frac{(y_i - \bar{y})^2}{2\sigma_p^2}\right)$$

123   **Evaluating the Selection Differential**   Now we need to compute the integral for the

124   next generation's mean trait $\bar{y}_{t+1}$:

$$\bar{y}_{t+1} = \frac{1}{\bar{W}_f} \int_{-\infty}^{\infty} W_f(y_i) y_i p(y_i) \, dy_i$$

125   Using the approximation for $W_f(y_i)$, we get:

$$\bar{y}_{t+1} \approx \frac{1}{\bar{W}_f} \int_{-\infty}^{\infty} \left(1 + \frac{M_2(1-z_2)(y_i-\bar{y})}{M_1(1+\alpha z_1) + M_2(1-\bar{y})(1-z_2)} \right) y_i p(y_i) \, dy_i$$

126   This splits into two integrals:

$$\bar{y}_{t+1} \approx \frac{1}{\bar{W}_f} \left(\int_{-\infty}^{\infty} y_i p(y_i) \, dy_i + \frac{M_2(1-z_2)}{M_1(1+\alpha z_1) + M_2(1-\bar{y})(1-z_2)} \int_{-\infty}^{\infty} (y_i - \bar{y}) y_i p(y_i) \, dy_i \right)$$

127   Solving the Integrals

128   The first integral is just the mean $\bar{y}$, as $p(y_i)$ is centered at $\bar{y}$:

$$\int_{-\infty}^{\infty} y_i p(y_i) \, dy_i = \bar{y}$$

129   The second integral, involving $(y_i - \bar{y}) y_i$, is related to the variance σ_p^2:

$$\int_{-\infty}^{\infty} (y_i - \bar{y}) y_i p(y_i) \, dy_i = \sigma_p^2$$

130   **Final Expression for the Selection Differential**   Substituting these results into the

131   expression for $\bar{y}_{t+1}$, we obtain:

$$\bar{y}_{t+1} \approx \bar{y} + \frac{M_2(1-z_2)\sigma_p^2}{M_1(1+\alpha z_1) + M_2(1-\bar{y})(1-z_2)}$$

132   Thus, the selection differential is:

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$$S_{diff} = \bar{y}_{t+1} - \bar{y} = \frac{M_2(1 - z_2)\sigma_p^2}{M_1(1 + \alpha z_1) + M_2(1 - \bar{y})(1 - z_2)}$$

133   The above selection differential is multiplied with h which is $\frac{\sigma_a^2}{\sigma_p^2}$ to obtrain $\Delta\bar{z}$

134   Thus,

$$\Delta\bar{\bar{y}} = \frac{M_2(1 - z_2)\sigma_a^2}{M_1(1 + \alpha z_1) + M_2(1 - \bar{y})(1 - z_2)} \tag{11}$$

135   Thus, resistance y_i increases with each generation. The selection differential S_{diff}

136   is proportional to the phenotypic variance σ_p^2. There is stronger selection when the

137   heterospecifics are less discriminatory, and the heterospecfic : conspecific number is higher

Ecological Model

139   Previously, we derived the number of offsprings in the next generation in this model. This

140   turned out to be

$$N_{off_{(t+1)}} = \frac{F_1 M_1(1 + \alpha \bar{z}_1)}{M_1(1 + \alpha \bar{z}_1) + M_2(1 - y_1)(1 - \bar{z}_2)} \tag{12}$$

141   Assume both species have 1:1 sex ratio at all generations. Thus, $F = M$

$$N_{off_{(t+1)}} = \frac{\left(\frac{N_1}{2}\right)\left(\frac{N_1}{2}\right)(1 + \alpha \bar{z}_1)}{\left(\frac{N_1}{2}\right)(1 + \alpha \bar{z}_1) + \left(\frac{N_2}{2}\right)(1 - y_1)(1 - \bar{z}_2)} \tag{13}$$

142   This simplifies to...

$$N_{off_{(t+1)}} = \frac{\left(\frac{N_1}{2}\right)(N_1)(1 + \alpha \bar{z}_1)}{(N_1)(1 + \alpha \bar{z}_1) + (N_2)(1 - y_1)(1 - \bar{z}_2)} \tag{14}$$

143   **Offspring Competition**   Note that the above equation gives the production of offspring

144   from a single mating season; one also needs to include the intraspecific and interspecfic

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competition which will regulate the population.

For this purpose, one can use the Leslie-Grover Discrete competition equation

To sum it up, $N(t+1)$ depends on To sum it up, $N(t+1)$ depends on a) Resource Competition b)Mating Rates when there is incomplete species discrimination (Reproductive Interference)

$$N_1(t+1) = \left(\frac{b_1'}{1 + \alpha_{11}N_1(t) + \alpha_{12}N_2(t)} \right) \cdot \frac{\left(\frac{N_1}{2} \right) (N_1)(1 + \alpha\bar{z_1})}{(N_1)(1 + \alpha\bar{z_1}) + (N_2)(1 - y_1)(1 - \bar{z_2})} \quad (15)$$

Let $\frac{b_1'}{2}$ be b_1, then:

$$N_1(t+1) = \left(\frac{b_1 N_1(t)}{1 + \alpha_{11}N_1(t) + \alpha_{12}N_2(t)} \right) \cdot \left(\frac{N_1(1 + \alpha_1\bar{z_1})}{N_1(1 + \alpha_1\bar{z_1}) + N_2(1 - y_1)(1 - \bar{z_2})} \right) \quad (16)$$

Likewise, for species 2 the equation will become :

$$N_2(t+1) = \left(\frac{b_2 N_2(t)}{1 + \alpha_{22}N_2(t) + \alpha_{21}N_1(t)} \right) \cdot \left(\frac{N_2(1 + \alpha_2\bar{z_2})}{N_2(1 + \alpha_2\bar{z_2}) + N_1(1 - y_2)(1 - \bar{z_1})} \right) \quad (17)$$

1   Results and Analysis

1.1   Evolution of Male Discrimination Alone

The evolution of male discrimination results in an evolutionary suicide effect - where the species with greater evolvability goes extinct.
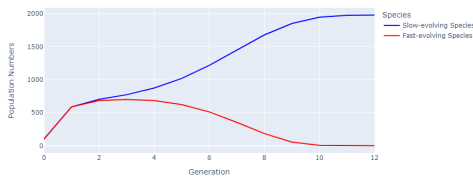

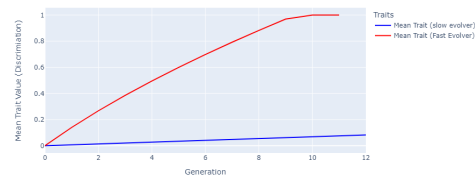Figure 1: Population Number Change of Both Species

Figure 2:Mean Male Discrimination Trait Change of Both Species

We aim to evaluate the conditions that promote or inhibit this evolutionary suicide effect. This analysis will provide insights into whether the effect is broadly applicable or if it occurs only under specific conditions, along with identifying other factors that may contribute to its likelihood.

1.2   Conditions

1. Evolvability effect v / s Female resistance

If the two species had females that were highly resistant to heterospecifc courtship, would it change outcomes of the fast evolver winning?

2. Evolvability Effect v/s Amount of genetic variation

Would the absolute amount of genetic variance influence the nature of this effect? i.e what would you predict about the competetive outcome of species can have a greater amount of trait change with unit generation in comparison to the ones with lower.

3. Evolvability effect v/s Conspecifc Mating Gain Factor

172   [Add conditions that promote/inhibit evolbability effect]

173   Furthermore, previous research indicates that the outcome of co-existence in cases of

174   reproductive interference is influenced by several factors. Our model is used to test various

175   alternative hypotheses, specifically assessing the relative significance of slow evolvability

176   effects compared to other dynamics that may operate between populations experiencing

177   mutual reproductive interference.

1.2.1   How Significant is the Evolvability Effect Compared to Other Factors Affecting Competitive Outcomes?

180   We characterise the significance of the evolvability effect under two scenarios a) When the

181   two species are in unstable ecological equilibrium and b) Stable ecological equilibrium

Unstable Ecological Equilibrium

183   1. **Relative Initial population size v/s relative evolvability of the two species**

184   Reproductive interference is characterized by positive frequency dependence, where

185   a population with a slightly higher initial size exerts more interference on the other

186   population. This results in reduced fecundity for the population with the smaller

187   size, creating a positive feedback loop that can drive the smaller population to

188   extinction.

189   Here, we evaluate the significance of evolutionary suicide effect caused by differing

190   evolvability between the two species and compare it to the effect of positive frequency

191   dependence driven by differences in initial population size, in determining the

192   outcome of co-existence

193   We adjusted the initial population size ratio between the fast and slow species from

194   10^{-3} to 10^3. For each population size ratio thus obtain the evolvability ratio of the

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195   two species were modified i.e the evolvability of sp. 1 was fixed at 0.01 while the

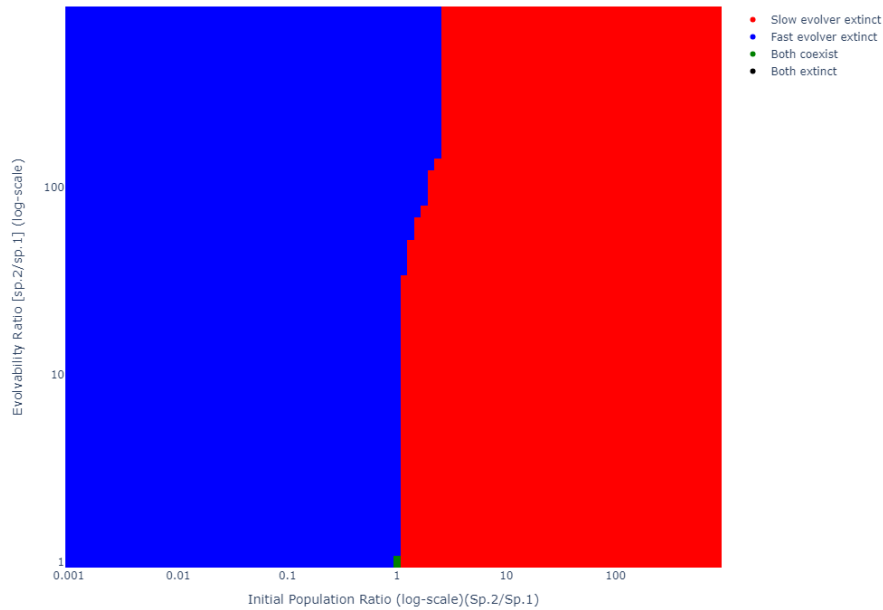196   evolvability of sp.2, 1 to 10^3 times that of sp.1

Figure 3: Initial population size v/s Evolvability Heatmap

197   Thus, based on the results of the simulation; it appears that the initial population

198   size largely determines the competitive outcome. A 6% increase in population size

199   of the fast evolving species makes it win rather than die by evolutionary suicide

200   The intuition behind this is that the positive frequency dependance effect acts only

201   on

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203   2. **Initial discrimination difference v/s Relative evolvability**, Asymmetric

204   reproductive interference, where one species disproportionately impacts another,

205   can lead to competitive exclusion.

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We investigate whether the relatively slow evolution of a species that initially discrim- inates more strongly can prevent its exclusion from the competitive environment.

The initial discrimination trait of the slower-evolving species varies between 0 (completely indiscriminate) and 1 (entirely discriminative). Meanwhile, the faster-evolving species is consistently regarded as indiscriminate, and the simulation is executed across various evolvability ratios.
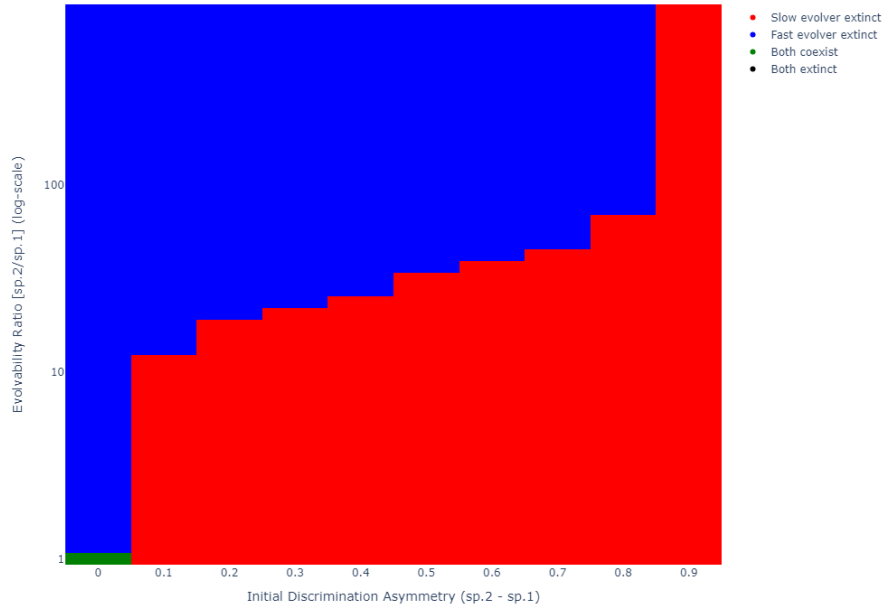

Figure 4: Initial Discrimination vs Evolvability Heatmap

[Insight from result]

3. **Relative interspecific competitive ability and Evolvability Ratios**

We explore the potential for evolutionary suicide of the faster-evolving species to reverse outcomes in scenarios where asymmetrical ecological interactions would typically lead to competitive exclusion.
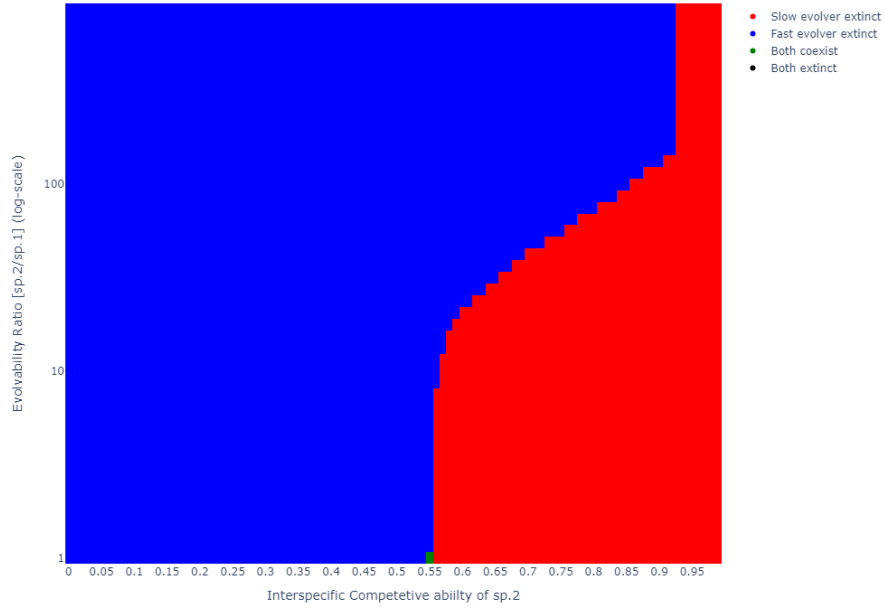
15

Figure 5: Interspecific Competitive Ability vs Evolvability

Across varying evolvability ratios, we rerun simulations while altering the competitive
ability of the high-evolvability species from 0.45 to 1. The interspecific competitive
ability of the slower-evolving species is held constant at 0.55, while the intraspecific
competition for both species remains fixed at 0.5.

[Insight from result]

Stable Ecological Equilibrium

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1.3 Evolution of Female Resistance

1.4 Evolution of Both Male Discrimination and Female Resistance

Discussion

Our study demonstrates that the evolution of male species discrimination can lead to competitive exclusion, although this outcome is restricted to certain parameter ranges, suggesting that other dynamics may be more significant. By developing a unified framework that integrates reproductive interference and species discrimination, we capture a nuanced eco-evolutionary feedback and reveal scenarios where rapidly evolving species may face disadvantages.

This finding underscores the complex and context-dependent nature of evolutionary outcomes, highlighting that rapid evolution does not always confer a competitive advantage. It is crucial to consider the role of evolution in various contexts and recognize that faster evolution is not always advantageous. In addition, accounting for all the different factors that contribute to the dynamics of a system is essential, as they influence the overall outcomes.

Our results highlight the intricate feedback between individual-level sexual selection and population dynamics. Specifically, selection pressures on males that improve their ability to discriminate between species can have adverse consequences at the population level, potentially leading to competitive exclusion.

Therefore, population-level selection can act against males evolving enhanced discrimination traits, creating a counterbalance to the benefits of individual sexual selection.

Thus, it is important to consider the evolution of discrimination when predicting the outcome of species that experience mutual reproductive interference. Faster evolution or

improved individual traits do not always translate into better population-level outcomes and can lead to counterintuitive results. Future empirical studies should focus on measuring the heritability of traits responsible for species discrimination to further understand their impact on coexistence and population dynamics.

1.5   Future Plans

1. Incorporate female permissivity evolutution of both species. Also think if the discrimination is sex linked or not. Evolution sex linked G matrix trait also sex linked

2. Understand emperical patterns of trait evolution. Try to test population level elimination hypothesis against evolution of male discriminatoion

Appendix

Appendix 1

1.6   Derivation of Selection Differential

Selection differential 'S' S is the selection differential, the difference in trait value between parents contributing offspring to the next generation and the population mean

The relationship is obtained by showing that the expression in brackets above is equal to s, the vector of selection differentials. To do this, we rewrite the expression in brackets as

$$\frac{1}{\overline{W}} \int W(z) z p(z)\, dz - \bar{z} \tag{S1}$$

$$= \int \frac{W(z) p(z)}{\overline{W}} z\, dz - \bar{z}$$

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But, by definition of a mean,

$$\bar{W} = \int p(z)W(z)\,dz,$$

so equation (9) can be rewritten as

$$\frac{1}{\bar{W}} \int W(z)zp(z)\,dz - \bar{z} = \frac{\int W(z)p(z)}{\int p(z)W(z)\,dz}z\,dz - \bar{z}.$$

Moreover, we can multiply the numerator and denominator of a ratio by N, the number of individuals in the population before selection, without changing that ratio:

$$\frac{1}{\bar{W}} \int W(z)zp(z)\,dz - \bar{z} = \frac{\int W(z)p(z)N}{\int p(z)W(z)N\,dz}z\,dz - \bar{z}.$$

But the ratio associated with the left-hand integral,

$$\frac{W(z)p(z)N}{\int p(z)W(z)N\,dz},$$

is just the number of individuals of phenotype z surviving selective mortality divided by the total number of surviving individuals in the population. In other words, it is the frequency of phenotype z among the selected individuals, which we will designate by $p'(z)$. Consequently, equation (10) is

$$\frac{1}{\bar{W}} \int W(z)zp(z)\,dz - \bar{z} = \int p'(z)z\,dz - \bar{z}.$$

But the expression involving the right-hand integral is just the mean phenotype among the selected individuals; therefore, the entire right-hand side of the equation is just the difference between the mean phenotype vector of the population before and after selection, which is the selection differential.

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279 **1.6.1 Gaussian Integral**

280 Given the expression to prove:

$$\int_{-\infty}^{\infty} \frac{z_1 + \alpha_1 z_1^2}{1 + \alpha_1 \bar{z}_1} p(z_1) dz_1 - \bar{z}_1 = \frac{\alpha_1 \sigma_p^2}{1 + \alpha_1 \bar{z}_1}$$

281 Assume $p(z_1)$ is a Gaussian distribution centered at $\bar{z}_1$ with variance σ_p^2:

$$p(z_1) = \frac{1}{\sqrt{2\pi\sigma_p^2}} \exp\left(-\frac{(z_1 - \bar{z}_1)^2}{2\sigma_p^2}\right)$$

282 We want to evaluate:

$$\int_{-\infty}^{\infty} \left(\frac{z_1}{1 + \alpha_1 \bar{z}_1} + \frac{\alpha_1 z_1^2}{1 + \alpha_1 \bar{z}_1}\right) p(z_1) dz_1$$

283 This can be split into two integrals:

$$\frac{1}{1 + \alpha_1 \bar{z}_1} \left[\int_{-\infty}^{\infty} z_1 p(z_1) dz_1 + \alpha_1 \int_{-\infty}^{\infty} z_1^2 p(z_1) dz_1\right]$$

284 Evaluate Each Integral

285 1. First Integral:

$$\int_{-\infty}^{\infty} z_1 p(z_1) dz_1 = \bar{z}_1$$

286 2. Second Integral:

$$\int_{-\infty}^{\infty} z_1^2 p(z_1) dz_1 = \sigma_p^2 + \bar{z}_1^2$$

287 Substitute these results back into the equation:

$$\frac{1}{1 + \alpha_1 \bar{z}_1} \left(\bar{z}_1 + \alpha_1(\sigma_p^2 + \bar{z}_1^2)\right)$$

288   Simplifying this expression leads to:

$$\frac{\alpha_1 \sigma_p^2}{1 + \alpha_1 \bar{z}_1} + \bar{z}_1$$

289   Hence, proved that

$$\int_{-\infty}^{\infty} \frac{z_1 + \alpha_1 z_1^2}{1 + \alpha_1 \bar{z}_1} p(z_1) dz_1 - \bar{z}_1 = \frac{\alpha_1 \sigma_p^2}{1 + \alpha_1 \bar{z}_1}$$

290   1.6.2   Approximation Female Fitness Ratio

291 To simplify this ratio, we use a Taylor series expansion around the mean value $\bar{y}$. This

292 involves expanding $W_f(y_i)$ in terms of $y_i - \bar{y}$, assuming the variations in y_i are small.

293   The ratio of fitness $\frac{W_f(y_i)}{\bar{W}_f}$ is:

$$\frac{W_f(y_i)}{\bar{W}_f} = \frac{\frac{M_1(1+\alpha z_1)}{M_1(1+\alpha z_1)+M_2(1-y_i)(1-z_2)}}{\frac{M_1(1+\alpha z_1)}{M_1(1+\alpha z_1)+M_2(1-\bar{y})(1-z_2)}}$$

294   Simplify this:

$$\frac{W_f(y_i)}{\bar{W}_f} = \frac{M_1(1 + \alpha z_1) + M_2(1 - \bar{y})(1 - z_2)}{M_1(1 + \alpha z_1) + M_2(1 - y_i)(1 - z_2)}$$

295   To approximate this ratio, expand it around $y_i = \bar{y}$ using a Taylor series. First, let's

296 write the denominator in a way that emphasizes how deviations from the mean $\bar{y}$ affect it:

$$Denominator = M_1(1 + \alpha z_1) + M_2(1 - y_i)(1 - z_2)$$

297   Expand the denominator around $y_i = \bar{y}$:

$$Denominator \approx M_1(1 + \alpha z_1) + M_2(1 - \bar{y})(1 - z_2) - M_2(1 - z_2)(y_i - \bar{y})$$

298   The linear expansion in y_i around $\bar{y}$ thus yields:

$$\frac{W_f(y_i)}{\bar{W}_f} \approx \frac{M_1(1+\alpha z_1) + M_2(1-\bar{y})(1-z_2)}{M_1(1+\alpha z_1) + M_2(1-\bar{y})(1-z_2) - M_2(1-z_2)(y_i-\bar{y})}$$

299   Simplify this expression by dividing the numerator and denominator by $M_1(1+\alpha z_1) +$

300    $M_2(1-\bar{y})(1-z_2)$:

$$\frac{W_f(y_i)}{\bar{W}_f} \approx \frac{1}{1 - \frac{M_2(1-z_2)}{M_1(1+\alpha z_1)+M_2(1-\bar{y})(1-z_2)}(y_i-\bar{y})}$$

301   For small deviations, this can be approximated linearly as:

$$\frac{W_f(y_i)}{\bar{W}_f} \approx 1 + \frac{M_2(1-z_2)}{M_1(1+\alpha z_1)+M_2(1-\bar{y})(1-z_2)}(y_i-\bar{y})$$

302   This linear approximation helps simplify the ratio for calculations and allows us to

303   use the variance to estimate the impact of trait variation on fitness.