Evolution of assortative mating

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Outline of the talk

- Species and speciation
  Assortment
- Modifiers of small effect
  Multilocus formalism
- A model of evolution of assortment
  Results
- Conclusions

Introduction

Species is the basic unit for taxonomy, ecology and conservation biology. Traditionally, we can distinguish two species as genetically distinct organisms, whose offspring would be inviable.

Speciation is the process by which a species splits into two.

In recent years there has been an increased interest in studies of speciation.

However, there is not a general framework under which we can identify the genetical mechanisms which leads towards reproductive isolation.

Most of the recent literature is based on simulations. Although a great deal of progress has been made, this kind of studies have not helped to a general understanding.

It seems clear that to understand speciation, we need to disentangle the *genetic* mechanisms leading to divergence between species.

For speciation to occur, the species must have already some degree of reduced gene flow, so that they can evolve different combinations of genes. Furthermore, some ecological or geographical isolation is required, such that these different combinations can coexist.

Allopatric speciation occurs when a population is separated by a geographical barrier into two subpopulations. Lack of gene flow due to geographic isolation together with different selective forces leads to two different species.

Sympatric speciation occurs within the range of dispersal of the species (ie, without geographic isolation). Disruptive selection leads to reduced gene flow by reproductive isolation.

Assortment

By assortment, we mean assortative mating generated by an ecological constraint, such as body size, host choice or flowering time in plants.

This mechanism generates frequency-dependent selection.

Specifically, we think of individuals mating according to their similarity in a trait z, such that the mating probability is proportional to $|z - z'|$

Modifiers of weak effect

A modifier is a locus which is not under direct selection. Its effect is to alter the associations or selection in the other loci in which we are interested.

The importance of a modifier of weak effect is that it will generate simple linear equations, and thus we can decompose and study separately the different effects that the modifier may have.

It has proved of extreme use in describing the evolution of recombination.

Multilocus formalism

Barton and Turelli (1991), and later on Kirkpatrick et al (2002), developed a framework which allows a complete study of multilocus systems.

It provides exact solutions for *all* the relevant variables via recursion equations, in a population described by multiple alleles and multiple loci.

Relevant variables: frequencies of each allele and associations between loci.

Following Kirkpatrick et al (2002), fitness can be defined as

$$\frac{w}{\bar{w}} = 1 + \sum_{U,V} a_{U,V}(\zeta_U \zeta_V^* - D_U D_V), \tag{1}$$

where $a_{U,V}$ is the selection coefficient acting on the set of loci U on females and the set of loci V on males.

The ζ's are such that $\zeta_j = X_j - \mathrm{p_j}$ is the deviation from a reference value $\mathrm{p_j}$, and $\zeta_U = \prod_{j \in U} \zeta_j$, and $\zeta^*_V = \prod_{j \in V} \zeta^*_j$.

D_U is the association between the set of loci U, defined as $D_U = \mathrm{E}\left[\zeta_U\right]$.
Note $D_\emptyset = 1$.

The natural reference value $\mathrm{p_j}$ is the frequency of the allele j in the population p_j, and that is the one we will use in this work.

Selection and recombination

The effect of selection on the association D_A is

$$D'_A = D_A + \sum_{U \subseteq W} a_U (D_{AU} - D_A D_U), \qquad (2)$$

and after transmission

$$D''_A = \sum_{S+T=A} \tilde{r}_{S,T} D'_{S,T}, \qquad (3)$$

where $\tilde{r}_{S,T}$ is the proportion of gametes produced with the set S from the mother and T from the father.

A model for evolution of assortment

Our interest lies on the effect that a small perturbation (modifier of weak effect) on the selection for assortment will have on the equilibrium of the population.

The accumulation of small effects may lead to speciation, which we will measure according to D.

A model for evolution of assortment

Assortment is “regulated” by a trait z which is characterised by two biallelic loci j and k. Both loci have the same contribution to the trait.

Individuals mate according to their similarity in z. For simplicity, we assume the loci j and k are in equilibrium, and at frequencies $p_j = p_k = \frac{1}{2}$, and j and k are symmetric.

In general, we would have to consider all the selection coefficients.

However, we start by the simpler case in which the following selection coefficients are not zero: $a_{j,j}$, $\tilde{a}_{j,k}$, $a_{k,k}$, $\tilde{a}_{jk,\emptyset}$, $a_{jk,jk}$.

If j and k are exchangeable, then $a_{j,j} = a_{k,k} = \tilde{a}_{j,k} = a_{1,1}$. Similarly, $a_{2,0} = \tilde{a}_{jk,\emptyset}$, and $a_{2,2} = a_{jk,jk}$.

On a's and D_{jk}

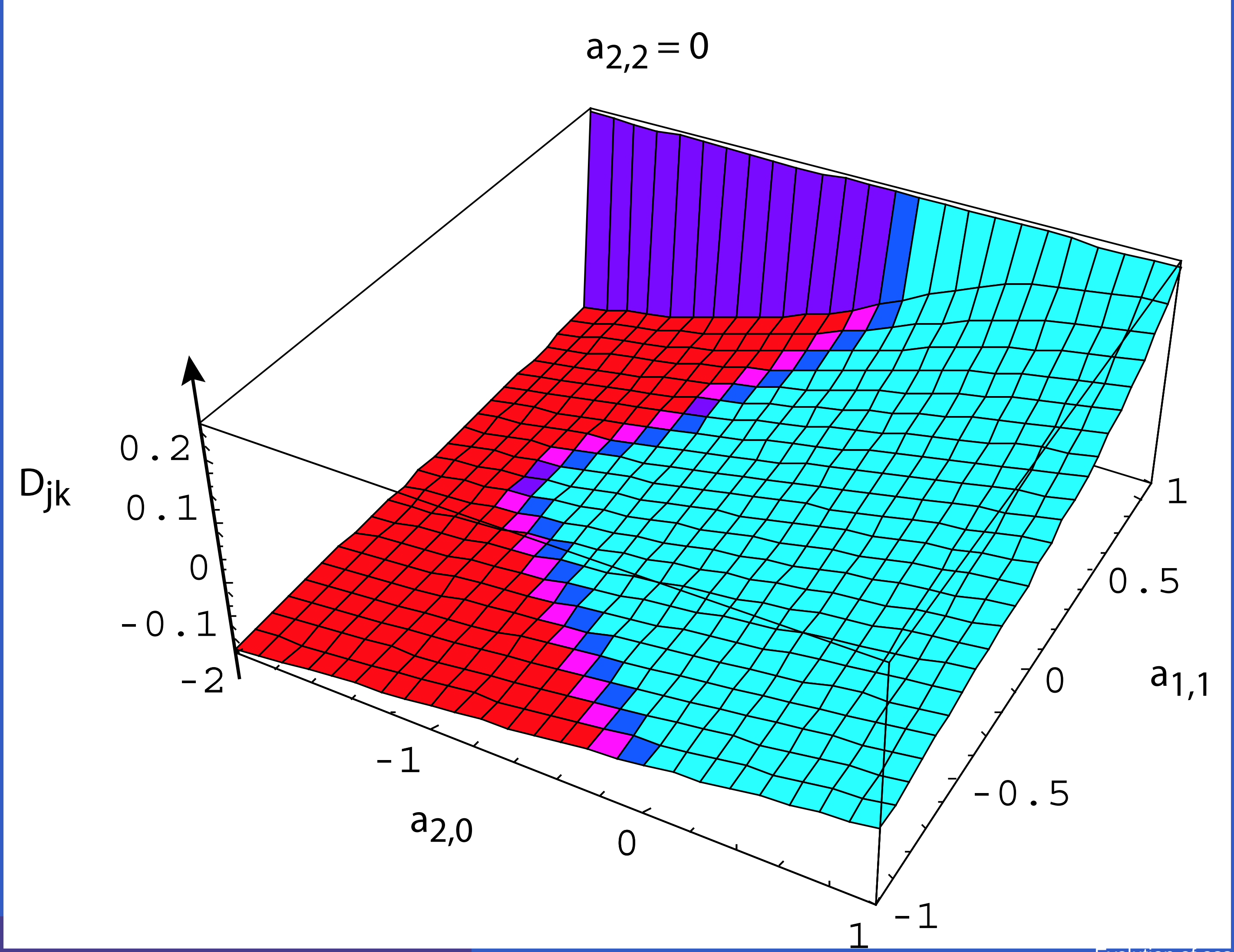
If the trait in consideration regulates body size:

- $a_{jk,\emptyset}$: viability selection.
  Selects for extreme/intermediate sizes
- $a_{j,j}$, $\tilde{a}_{j,k}$ and $a_{k,k}$: assortative mating.
  Preferential mating between similar sizes.
- $a_{jk,jk}$: selection due to assortative mating and epistatis

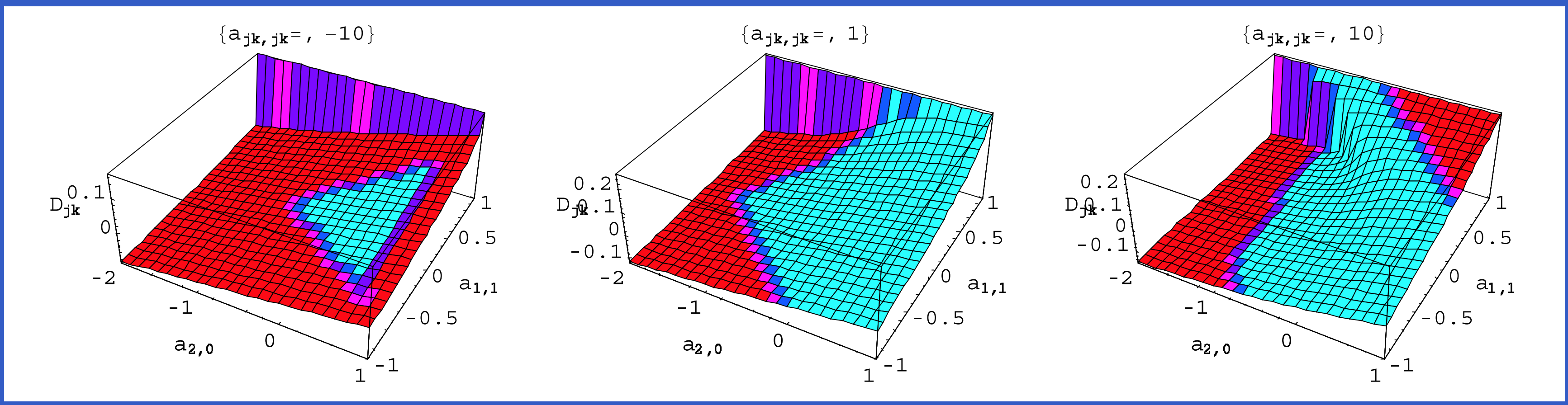
D_{jk} is our measure of reproductive isolation:

- panmictic population: $D_{jk} = 0$
- complete isolation(speciation): $D_{jk} = \frac{1}{4}$

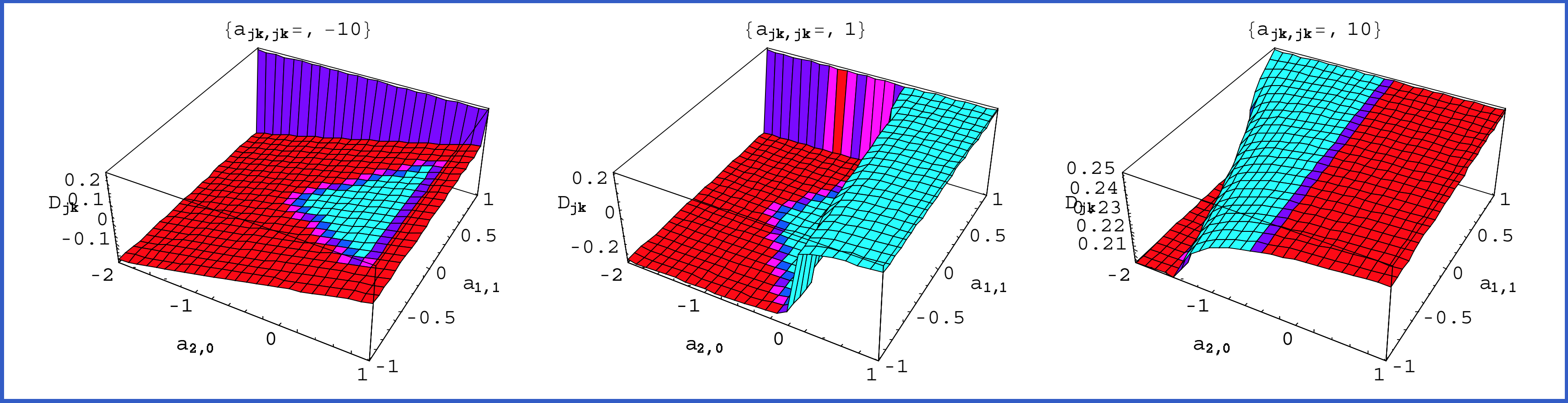
D_{jk}



D_{jk}


{a_{jk,jk}=, -10}
{a_{jk,jk}=, 1}
{a_{jk,jk}=, 10}
D_{jk}
a_{2,0}
a_{1,1}

$r = 0.5$


{a_{jk,jk}=, -10}
{a_{jk,jk}=, 1}
{a_{jk,jk}=, 10}
D_{jk}
a_{2,0}
a_{1,1}

$r = 0.03$

A modifier i

We then introduce a modifier locus i, which will affect the selection acting on j and k.

Thus, it will perturb the already existing selection by $\tilde{a}_{ij,j}$, $\tilde{a}_{ij,k}$, $\tilde{a}_{ik,j}$, $\tilde{a}_{ik,k}$, $\tilde{a}_{ijk,jk}$.

We assume the modifier to have a small effect, such that $a_{iU,V} \sim \epsilon$ and $D_{iU,V} \sim \epsilon$, and we keep leading orders in ϵ.

From here, we can study the change in frequency of the modifier Δp_i and its association with j and k, D_{ijk}.

This will allow us to know whether the modifier can invade or not, and whether it can go to fixation.

Ultimately, our interest is to know whether the modifier increases the association D_{jk}, since it is our measure of the degree of reproductive isolation between emerging species.

Change in frequency of the modifier

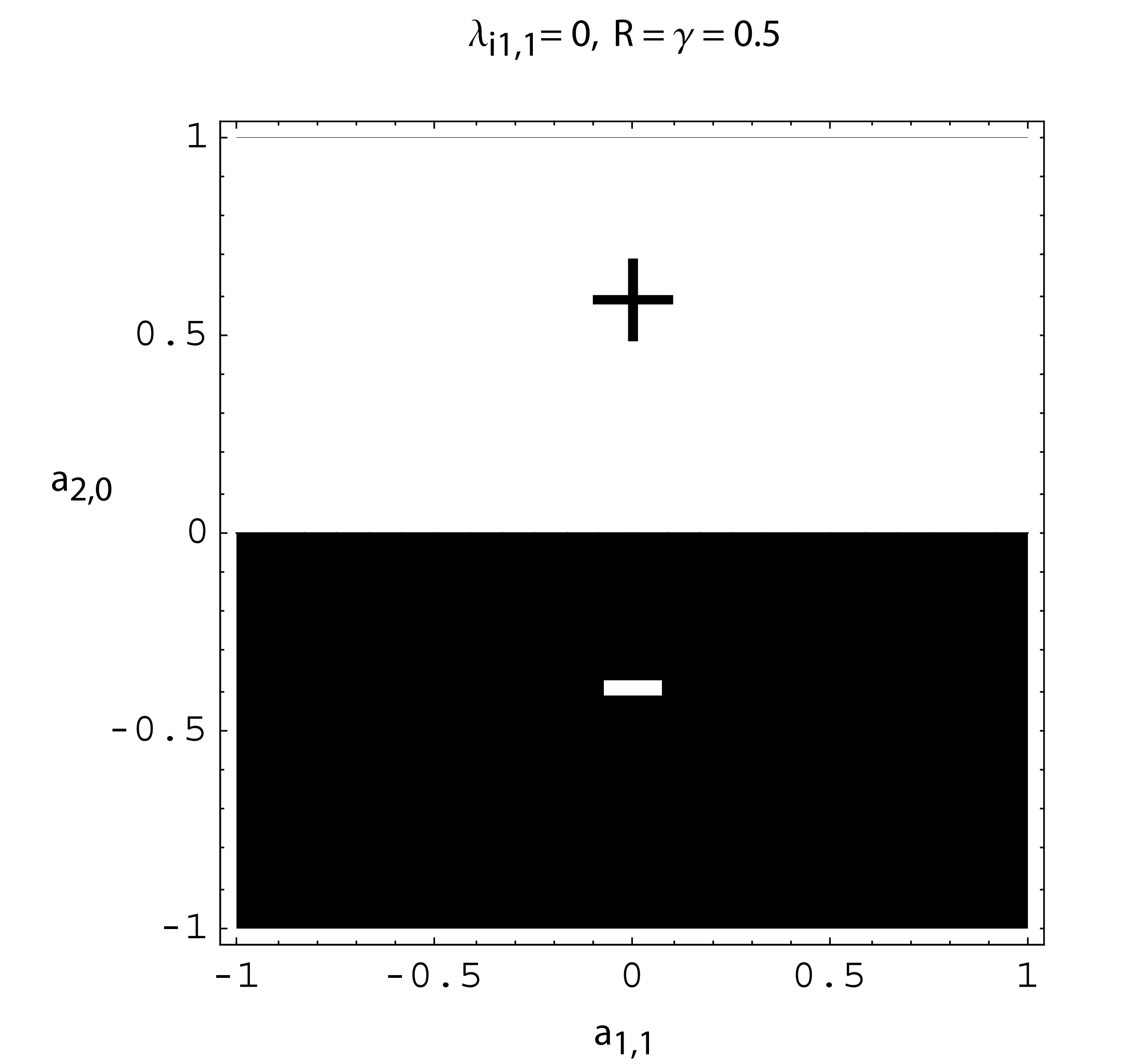
The change in frequency of the modifier can be written as

$$\frac{\Delta p_i}{pq_i} = \lambda_{i1,1} a_{i1,1} + \lambda_{i2,2} a_{i2,2}, \tag{4}$$

where the λ's are functions of the selection coefficients affecting j and k, and the different recombination rates.

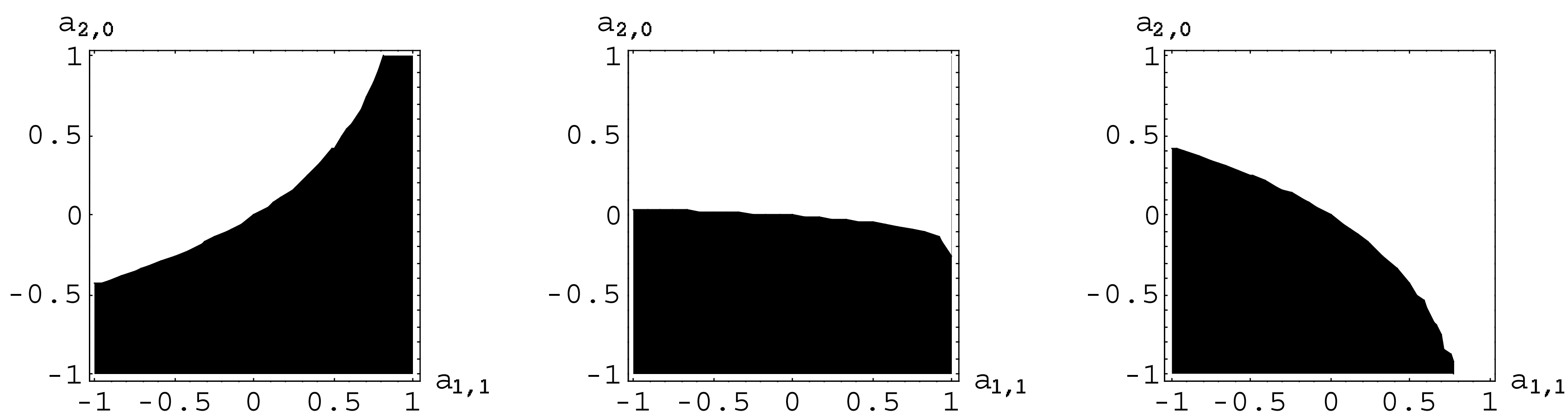
As the modifier is of weak effect, so long as its frequency increases, it will go to fixation.

Study of λ's



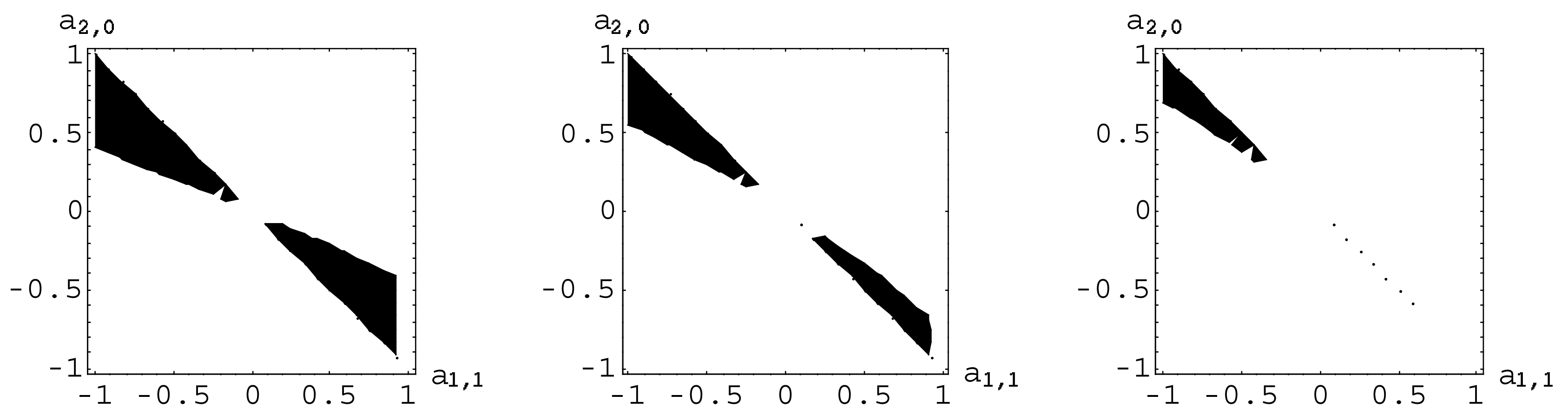
Invasion?

Contribution from $\lambda_{i1,1}$ for free recombination



$\lambda_{i1,1}$; R = γ = 0.5 and $a_{2,2}$ = −10, 1, 10 (from left to right)

Contribution from $\lambda_{i2,2}$ for free recombination



$\lambda_{i2,2}$; R = γ = 0.5 and $a_{2,2}$ = −10, 1, 10 (from left to right)

Note this is the smallest contribution.

Summary and conclusions

An accumulation of n modifiers of small effect may lead to complete reproductive isolation

- Multilocus formalism allows us to describe our system exactly
- Modifiers of weak effect lead to linear equations, which allow us to analyse separately the different contributions
- A modifier of assortment can lead to higher values of D_{jk}, to a greater reproductive isolation

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