Three-phase transition to reproductive isolation

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Introduction

Inputs:

- Adaptive dynamics: selection for adaptive diversification!
- Dieckmann-Doebeli (1999) model (and others): selection for reproductive isolation!
- Analytically tractable model by Pennings et al. (2008): Reproductive isolation often remains intermediate, sexual selection may help, however.

Goal:
Re-investigate Dieckmann-Doebeli nearer to the quantitative genetics limit to understand the mechanism more clearly.
Three-phase transition to reproductive isolation

Intro

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Lotka-Volterra ecology

Continuous ecological trait: $x$

Population dynamics:

$$\frac{dn_i}{dt} = \left[r(x_i) - \sum_a a(x_i, x_j) n_j \right] n_i$$

$$r(x) = K_{\text{max}} e^{-\left[\frac{x^2}{2w^2}\right]^k}$$

Stabilizing selection; $k > 1$: platykurtic

$$a(x_i, x_j) = e^{-\frac{(x_i-x_j)^2}{2\sigma^2}}$$

weakening competition
with increasing trait difference
Evolutionary branching
Genetic assumptions

Modified from Dieckmann & Doebeli (1999):

Multilocus traits:

- Ecological trait: $2 \times 32$ loci
- Mating trait: $2 \times 16$ loci

Two alleles per locus (0, or 1), additive, random recombination.

Assortative mating according to the ecological trait:

- Hermaphrodite individuals choose a mate in their female role.
- The larger the mating trait of the mother, the smaller the trait difference she accept between herself and her mate.

Individual-based simulation in continuous time:

- Constant birth rate
- Death rate determined by Lotka-Volterra competition
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Reference simulation: Ecological trait

Three phases

- First: fast to the middle, widened trait distribution
- Second: slow, gradual transition to bimodality
- Third: fast completion of segregation
Three-phase transition to reproductive isolation

Reference simulation: Mating trait

**Three phases**

- First: fast increase of assortativity
- Second: minimal additional change
- Third: fast further increase of assortativity
Three-phase transition to reproductive isolation

Reference simulation

Reference simulation: Additive variance

Three phases
- First: no significant change of variance
- Second: accelerating loss of genetic variance
- Third: seems to be initiated by the loss of genetic variance
Offspring **phenotypic** deviation becomes small only when the parental **genetic** difference becomes so!!!!
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Reference simulation: Sources of selection

Ecological selection diminishes and sexual selection takes over for the third phase.
Dependence on population size, mutation rate and cost of assortativity

Three-phase transition to reproductive isolation

Parameter dependence
Three-phase transition to reproductive isolation

Parameter dependence

Dependence on competition width and kurtosis

\[ \sigma_A = 0.250 \]

\[ \sigma_c = 1.0 \]

\[ \sigma_c = 0.75 \]

\[ \sigma_c = 0.5 \]

\[ \sigma_c = 0.25 \]
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Parameter dependence

Same with smaller additive variance

\[
\sigma_A = 0.158
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Parameter dependence

The Gaussian case
Suggested interpretation

- Large segregation variance keep homogenizing the population even if assortativity is perfect.
- Stabilizing selection (ecological, or sexual) decreases additive/segregation variance, but this process is slow.
- Run-away sexual selection completes isolation, but it is initiated only when the genetic variance is sufficiently small.
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Theory background 1: Quantitative genetics (Bulmer) limit

The limit:
- Number of loci $\rightarrow \infty$
- Per locus gene effect $\rightarrow 0$
- Additive/segregation variance = const.

In this limit:
- Speed of directional evolution = const.
- Speed of change of allele frequencies $\rightarrow 0$
- Speed of change of variance $\rightarrow 0$ !!!!

Evolution of variance is slow in our case, because the number of loci are high!

Theory background 2: Instability of sexual continuum

With constant mating and segregation kernel (Noest, 1997)

Stabilizing mechanisms:

- Ecological stabilization: above the scale of competition width!
- Stabilization by difference between parent and offspring (by difference between parents + segregation + mutation): below the scale of this difference!

Destabilizing mechanism:

- Sexual destabilization: above the scale of mating width!

Run-away sexual selection is arrested until segregation variance becomes sufficiently low!
Three-phase transition to reproductive isolation

- Interpretation

- Conclusion

- Three phases:
  1. fast initial diversification,
  2. prolonged partial isolation,
  3. fast final segregation.

- Interpretation:
  1. Need for selective elimination of additive/segregation variance.
  2. Decrease of additive variance is slow for high number of loci.
  3. Run-away sexual selection concludes the process.

- Parameter dependence:
  Clear adaptive speciation is sufficiently generic!

- Partial segregation tends to be transitory, but it can be sustained for long time!
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Interpretation

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