Temporal Waves of Genetic Diversity in a Spatially Explicit Model of Evolution: Heaving Toward Speciation

Guy A. Hoelzer[1], Rich Drewes[2] and René Doursat[2,3]

[1]Department of Biology, [2]Brain Computation Laboratory,
[3]Department of Computer Science and Engineering
University of Nevada, Reno

Heaving Toward Speciation

1. Introduction
2. Model
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Heaving Toward Speciation

1. Introduction
   - Classical Framework: Biological Species Concept
   - Different Geographical Modes of Speciation
   - Common Themes in Textbook Speciation Models
   - Previous Ideas About Self-Organized Speciation
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1. Introduction

➢ Classical Framework: Biological Species Concept

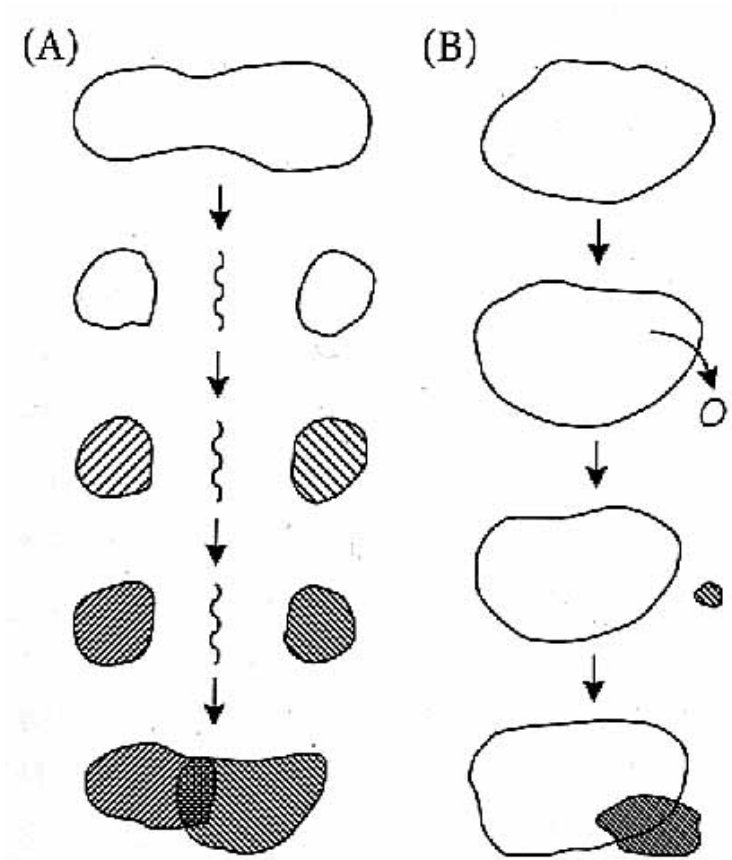
- ✓ "Species are groups of actually or potentially interbreeding populations, which are reproductively isolated from other such groups." —Ernst Mayr (1942)
- ✓ although limited to sexual species, Mayr's biological/isolation species concept is the most widely accepted definition of species among evolutionary biologists (replacing morphology)
  - conspecifics are able to interbreed and produce viable offspring, but members of different species are not
  - when subpopulations become so genetically different that they can no longer interbreed, *speciation* has occurred

→ *outbreeding depression: offspring viability decreases with genetic distance*

1. Introduction

➢ Different Geographical Modes of Speciation

- ✓ in space — *allopatric* speciation occurs when populations become geographically separated
- ✓ natural selection is a powerful evolutionary force in large populations (dichopatric or vicariant)
- ✓ genetic drift might be more powerful in small populations (peripatric or "founder effect")



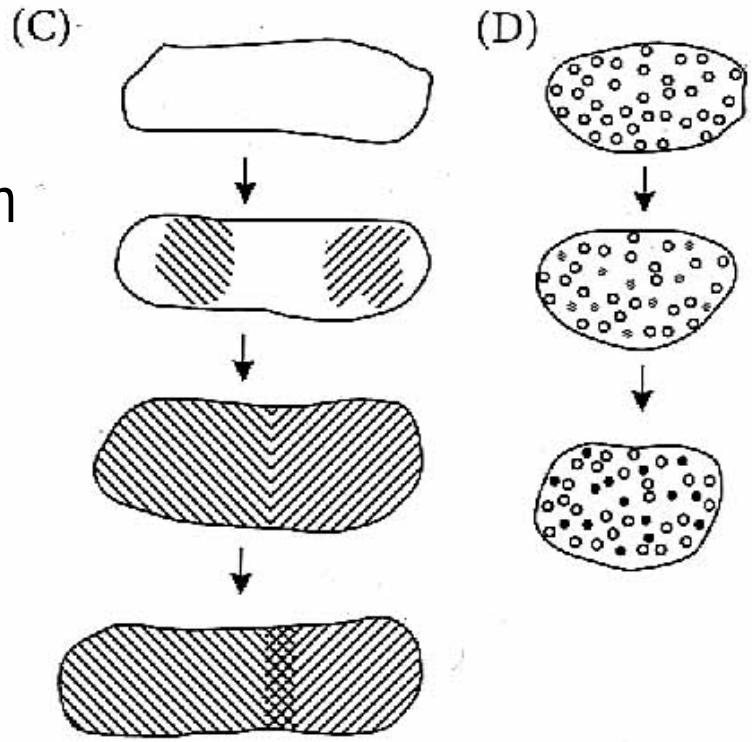
allopatric 1 (dichopatric)

allopatric 2 (peripatric)

1. Introduction

➢ Different Geographical Modes of Speciation (cont'd)

- ✓ cases where gene flow is not interrupted, but still reduced by habitat variation and divergent local adaptation
- ✓ in *parapatric* speciation, species occupy contiguous ranges (e.g., ring species: seagulls, etc.)
- ✓ *sympatric* species overlap, exploiting discretely different microhabitats



parapatric speciation

sympatric speciation

1. Introduction

➢ Common Themes in Textbook Speciation Models

- ✓ common theme among all these categories:
  - speciation is induced by divisive, external factors (physical barrier, habitat variation, assortative mating)
  - the inherent tendency of biological populations would be to remain unified in the absence of these factors

→ *the conventional wisdom is that it is the environment that tears species apart*

- ✓ the dogma of relaxation toward a well-mixed equilibrium is reminiscent of pre-oscillatory chemistry: disbelief in the possibility of spontaneous, *intrinsic* heterogenization

1. Introduction

➢ Previous Ideas About Self-Organized Speciation

- ✓ "species selection" focuses on the traits of species that can influence speciation/extinction rates (Stanley, Jablonski)
  - rate of colonizing new places
  - inherent tendency for isolation of subpopulations

→ *our model is based on the genetic dynamics within populations and does not rely on such species-level traits*

Heaving Toward Speciation

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2. Model
   - Representing Space and Spatial Constraints
   - Genomics and Sexual Reproduction
   - Offspring Viability Under Outbreeding Depression
   - Model Mechanics, Reproduction, Stabilization
3. Results
4. Conclusion

2. Model

➢ Overview

- ✓ we describe a model of a spatially extended biological population
- ✓ spatiality corresponds to the “isolation by distance” concept (Wright, 1943) — gene flow is short compared to system’s size

→ *our model suggests that biological populations inherently and regularly tend toward dividing themselves into daughter species* ***without*** *the influence of external factors*

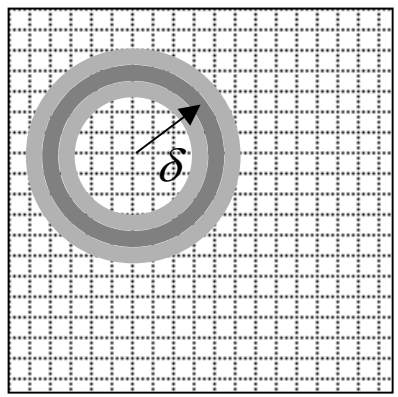
- ✓ these daughter species will be
  - parapatrically distributed
  - reproductively incompatible

2. Model

➢ Representing Space and Spatial Constraints

- ✓ $N \times N$ square grid with a homogeneous environment
  - the results presented here are based on the grid wrapped on a torus
- ✓ each grid cell can contain up to a predetermined number of individuals
  - cells are limited to 0 or 1 individual in the results here
- ✓ dispersal occurs <u>within</u> a distance d, drawn from a Gaussian distribution with mean and standard deviation δ

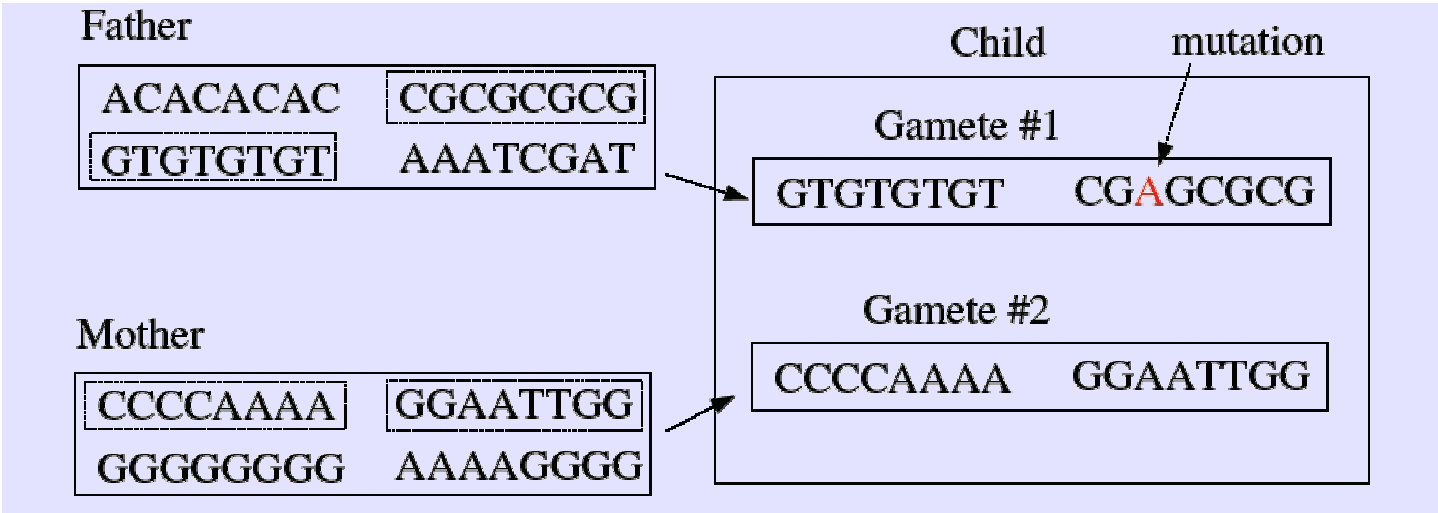
→ *we call it the δ-neighborhood, used for migration and to select potential mates*



2. Model

➢ Genomics and Sexual Reproduction

- ✓ diploid hermaphrodites, in which haploid genomes consist of 2 chromosomes of 200 nucleotide bases (G,A,T,C) each

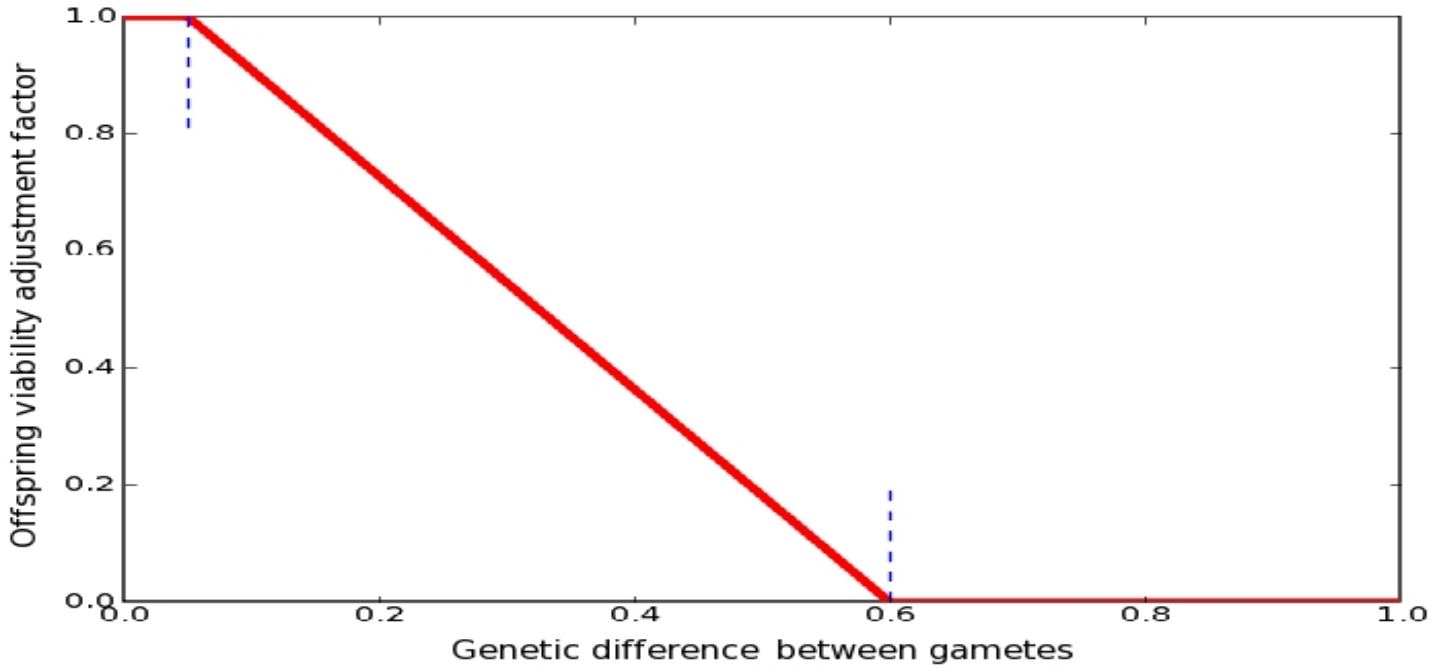


- ✓ each parent produces a haploid gamete by randomly selecting one of the chromosomes from each diploid pair
- ✓ when producing a gamete, some random point mutations are introduced according to a constant mutation probability

2. Model

➢ Offspring Viability Under Outbreeding Depression

- ✓ when outbreeding depression is invoked, offspring viabilities are not equal, but function of the genetic difference between gametes



→ *in this work we will compare the behavior of the model* ***with*** *and* ***without*** *invoking outbreeding depression*

2. Model

➢ Model Mechanics

- ✓ initial conditions
  - grid space is 80% filled — emptiness is not traditionally found in cellular automata models, yet is an important feature that will allow future species to separate
  - all individuals are genetically identical (exact same genome) — all the creation of diversity will be endogenous
- ✓ migration
  - individuals migrate to a cell chosen at random within the probabilistic δ-neighborhood, where δ typically equals 1.5

2. Model

➢ Reproduction

- ✓ each member of the population is selected once to be the "father" in a mating; for each father, the "mother" is chosen within its δ-neighborhood
- ✓ the number of potential offspring resulting from each mating is given by a Poisson distribution with mean 1
- ✓ generations do not overlap (all parents die after reproduction)
- ✓ each offspring is placed in a random grid cell within the δ-neighborhood of the mother
- ✓ if no grid cell within range has a vacancy, then the offspring of this mating are lost

2. Model

➢ Population Size is Stabilized

- ✓ the population size stays about the same from generation to generation because
  - each individual is the father in exactly one mating and the mother in an average of one mating
  - each mating has an average of one offspring
- ✓ to compensate for fluctuations (Poisson, viability, vacancy) and maintain the initial population size:
  - either supernumerary offspring are culled,
  - or parents are selected for additional mating at random

Heaving Toward Speciation

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   - Spatial Self-Organization: The Essence of Parapatric Speciation
   - Distribution of Empty Space
   - Mismatch Distribution Histograms
   - Isolation-by-Distance Scatter Plots
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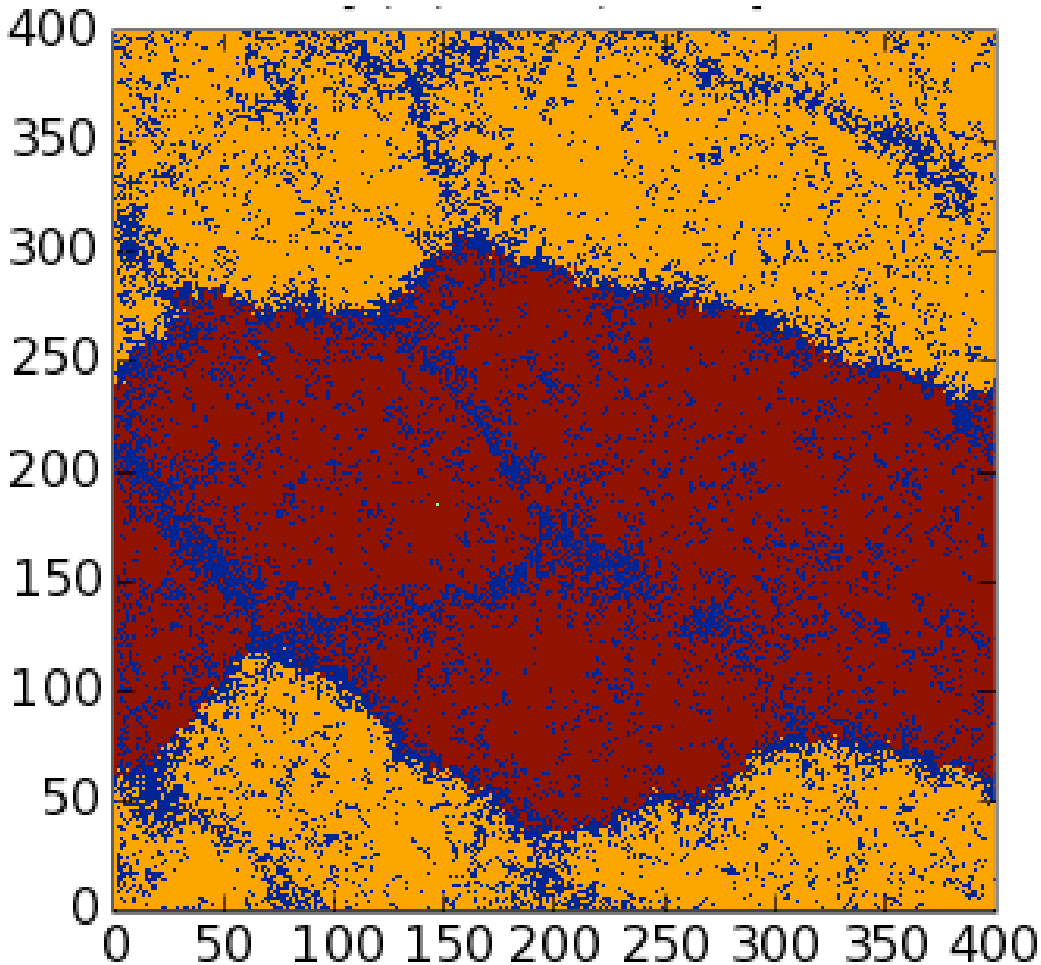
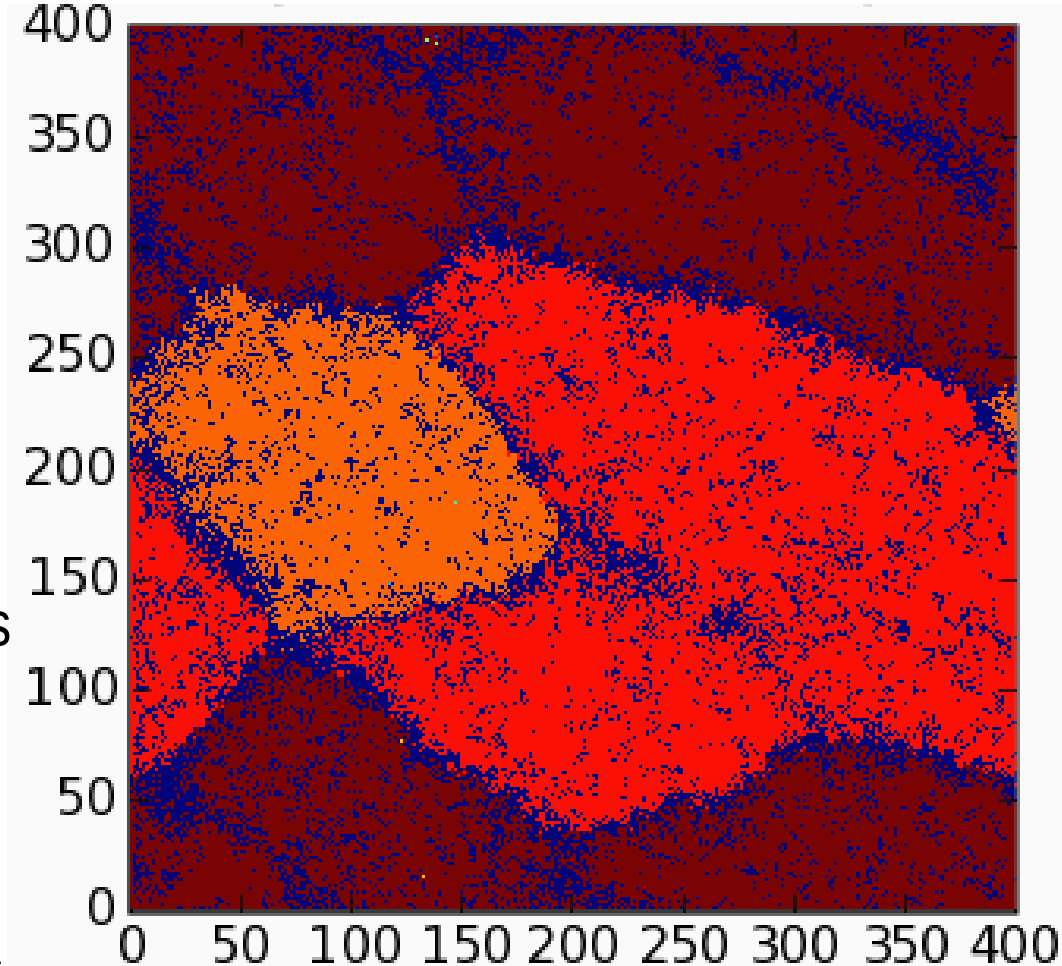
3. Results

- Spatial Self-Organization: The Essence of Parapatric Speciation
  - ✓ all haplotypes sharing a color are part of a graph where:
    - the nodes are individuals
    - graph edges are discovered pair differences smaller than .6 threshold = outbreeding thresh.



3. Results

- Spatial Self-Organization: The Essence of Parapatric Speciation (cont'd)
  - ✓ here, threshold .3 < outbreeding thresh.
  - ✓ different random seeds also show cluster consistency
  - ✓ outbreeding depression sharpens natural tendency toward spatial order
  - ≈ *inhibition at distance as in Turing patterns*

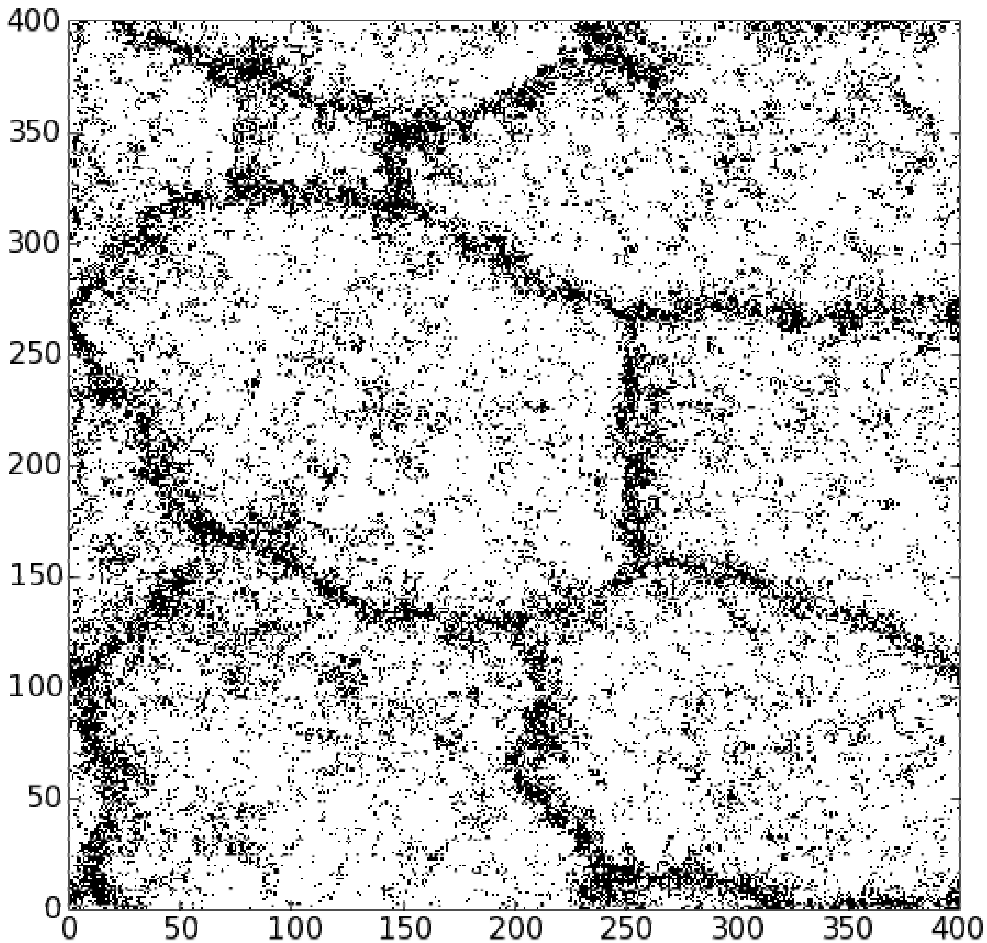


3. Results

➢ Distribution of Empty Space

- ✓ the interstitial areas in the color plots are actually empty space (not isolated individuals)

→ *subpopulations isolate themselves from each other to pursue different evolutionary paths*

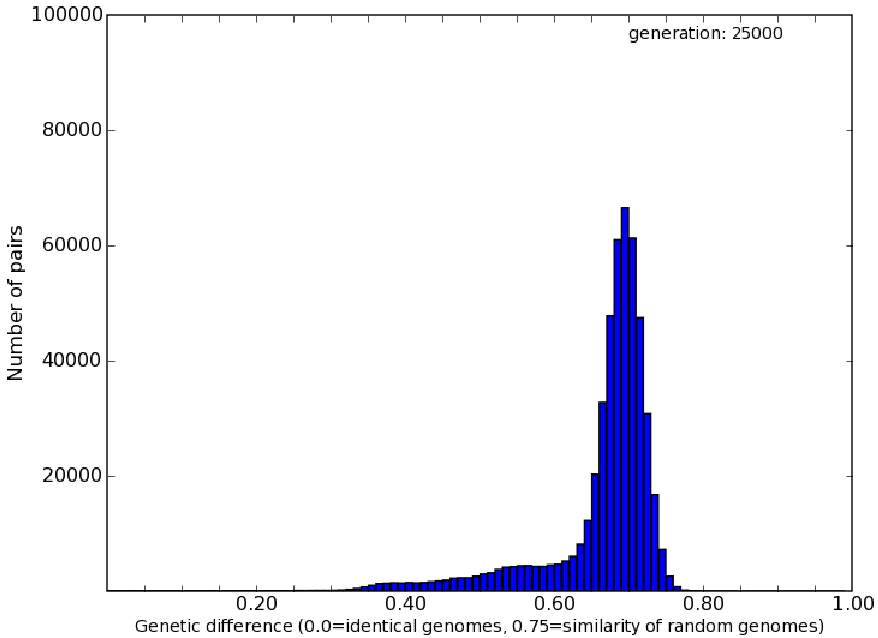


3. Results

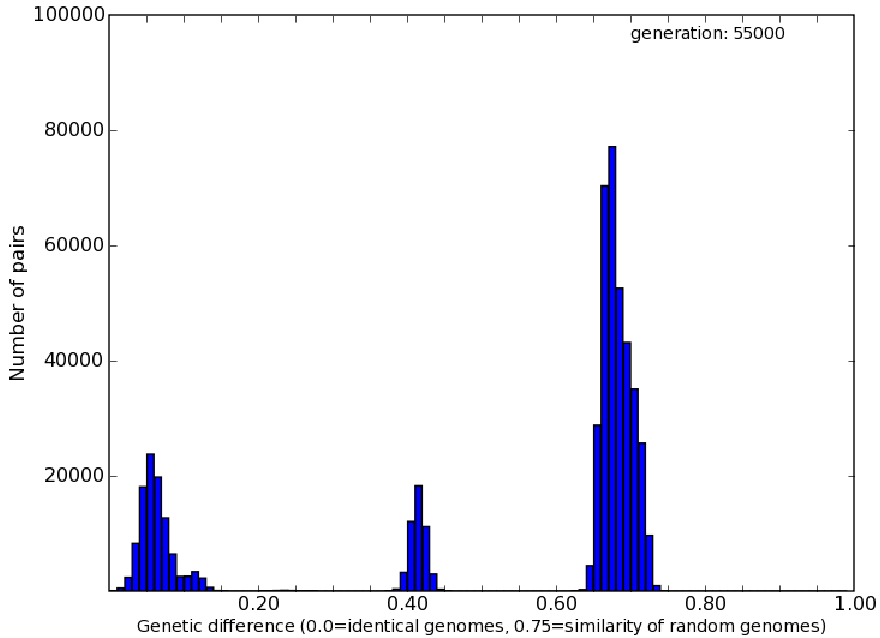
➢ Mismatch Distribution Histograms

✓ we sample gametes (haplotypes) uniformly at random on the grid and plot the frequency histogram of **pairwise** differences

→ *histogram bars start at* 0 *and move to the right*



without outbreeding depression:
global randomization march to .75

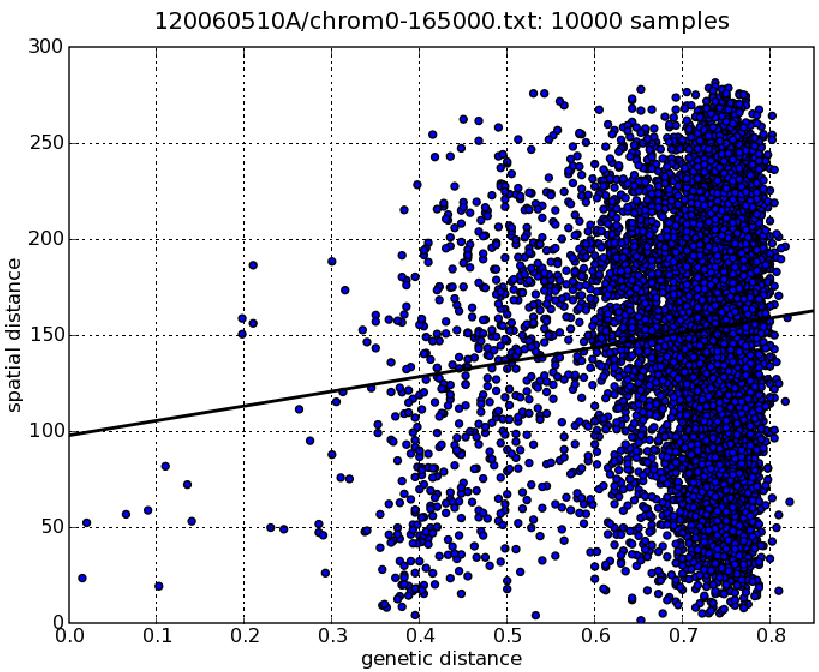


with outbreeding depression:
→ *emergence of multimodality = subpopulations*

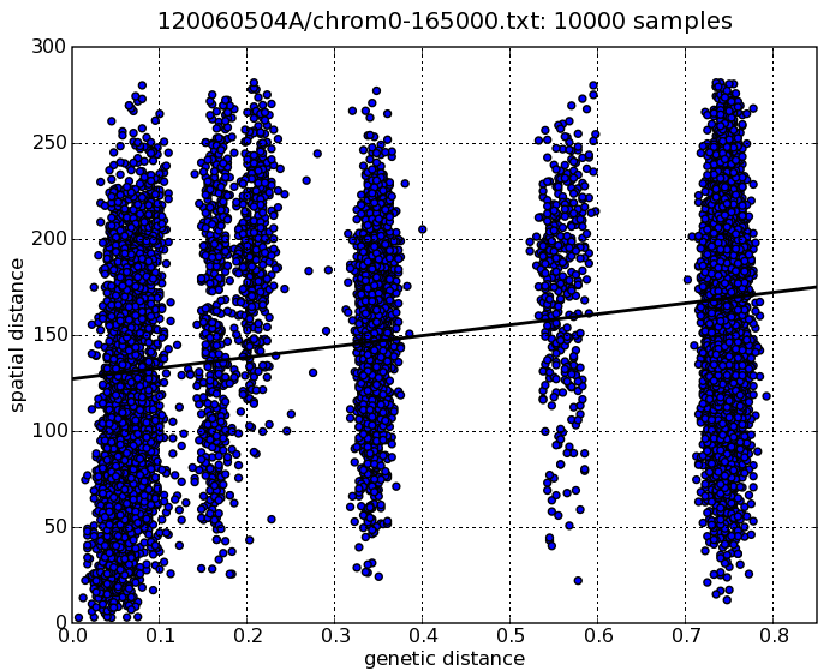
3. Results

➢ Isolation-by-Distance Scatter Plots

- ✓ plot of geographical distance vs. genetic distance
- ✓ same as mismatch distributions, with added spatial information



without outbreeding depression:
global randomization march to .75



with outbreeding depression:
→ *emergence of multimodality = subpopulations*

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4. Conclusion

➢ Concluding Points

- ✓ as in previous models, isolation by distance leads to the formation of localized subpopulations; gene flow is short compared to the system's size
- ✓ moreover, our model illustrates a process of parapatric speciation *in the absence* of environmental variation or species-level traits
- ✓ we invoked a selection process that is *endogenous* to the population dynamics, not due to the environment

→ *thus, this is a model of speciation through the spatial self-organization of the gene pool*

4. Conclusion

➢ Concluding Points (cont'd)

- ✓ in Gavrilets (2004), outbreeding depression is modeled as a step function — the population "stumbles upon" speciation
- ✓ in our model, reproductive incompatibility accrues by degree — speciation takes on a gradually increasing demographic cost
- ✓ while in a classical well-mixed model, gradual incompatibilities could not invade the population. . .
- ✓ . . . under isolation by distance, the demographic cost can be partially or completely avoided

→ *in a spatially extended gene pool, outbreeding depression serves as a mechanism of "inhibition at a distance" in a process of pattern formation a la Turing*

4. Conclusion

- Primary Conclusion
  - ✓ if the degree of outbreeding depression grows as gamete genomes become increasingly different, then:
    - the pattern of genetic and spatial population subdivision becomes far more well-defined
    - some subpopulations can diverge to the point where they complete a process of parapatric speciation

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