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

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Heaving Toward Speciation

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   - Different Geographical Modes of 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”)
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.
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
  
  \[ \text{the conventional wisdom is that it is the environment that tears species apart} \]
  
  - the dogma of relaxation toward a well-mixed equilibrium is reminiscent of pre-oscillatory chemistry: disbelief in the possibility of spontaneous, \textit{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
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   - Representing Space and Spatial Constraints
   - Genomics and Sexual Reproduction
   - Offspring Viability Under Outbreeding Depression
   - Model Mechanics, Reproduction, Stabilization

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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 within a distance $d$, drawn from a Gaussian distribution with mean and standard deviation $\delta$
  - we call it the $\delta$-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 $\delta$-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 $\delta$-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
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   - Spatial Self-Organization: The Essence of Parapatric Speciation
   - Distribution of Empty Space
   - Mismatch Distribution Histograms
   - Isolation-by-Distance Scatter Plots

4. Conclusion
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 0.75

- 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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- 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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