Evolution as a Complex System

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Life and its evolution emerges through interaction among populations of agents

- Virtually all scientific models of the origin of life involves a growing network of interactions among chemicals resulting in a bounded metabolism
  - RNA world
  - Metabolism first
  - All organisms are self-organizing, open, energy-channeling, dissipative systems.
    - See Prigogine
- The biosphere as a whole is a self-organizing, open, energy-channeling, dissipative system.
  - Consider GAIA, or daisyworld
  - Consider niche theory and ecosystem thermodynamics (Schneider and Kay 1994)

Our Premises

- One key aspect of metabolic and evolutionary systems that makes them complex is the constraint of spatial configuration
- Most contemporary evolutionary theory is based on mathematical modeling of “well mixed” systems.
- When interaction is limited to local neighborhoods can lead to complex dynamics and internally driven pattern formation in all sorts of contexts.
- We aim to explore how the spatial context of biological populations might generally change evolutionary behavior relative to the “well-mixed” ideal of traditional theory using computational models.

- Spatial constraints on gene flow have long been considered to be important in the emergence of genetic diversity (types) within species
- (e.g., consider distributions of subspecies of *Peromyscus*)

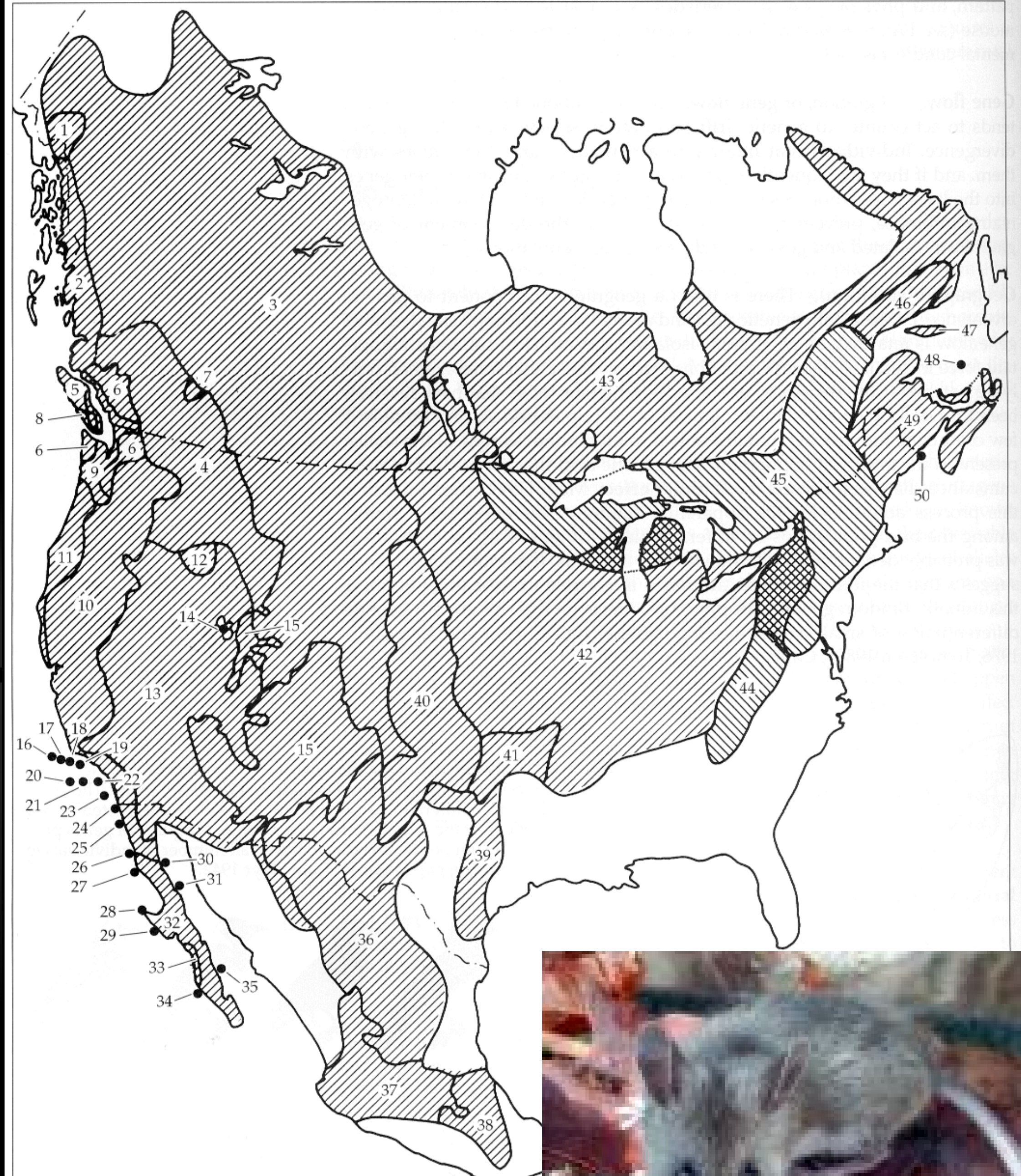
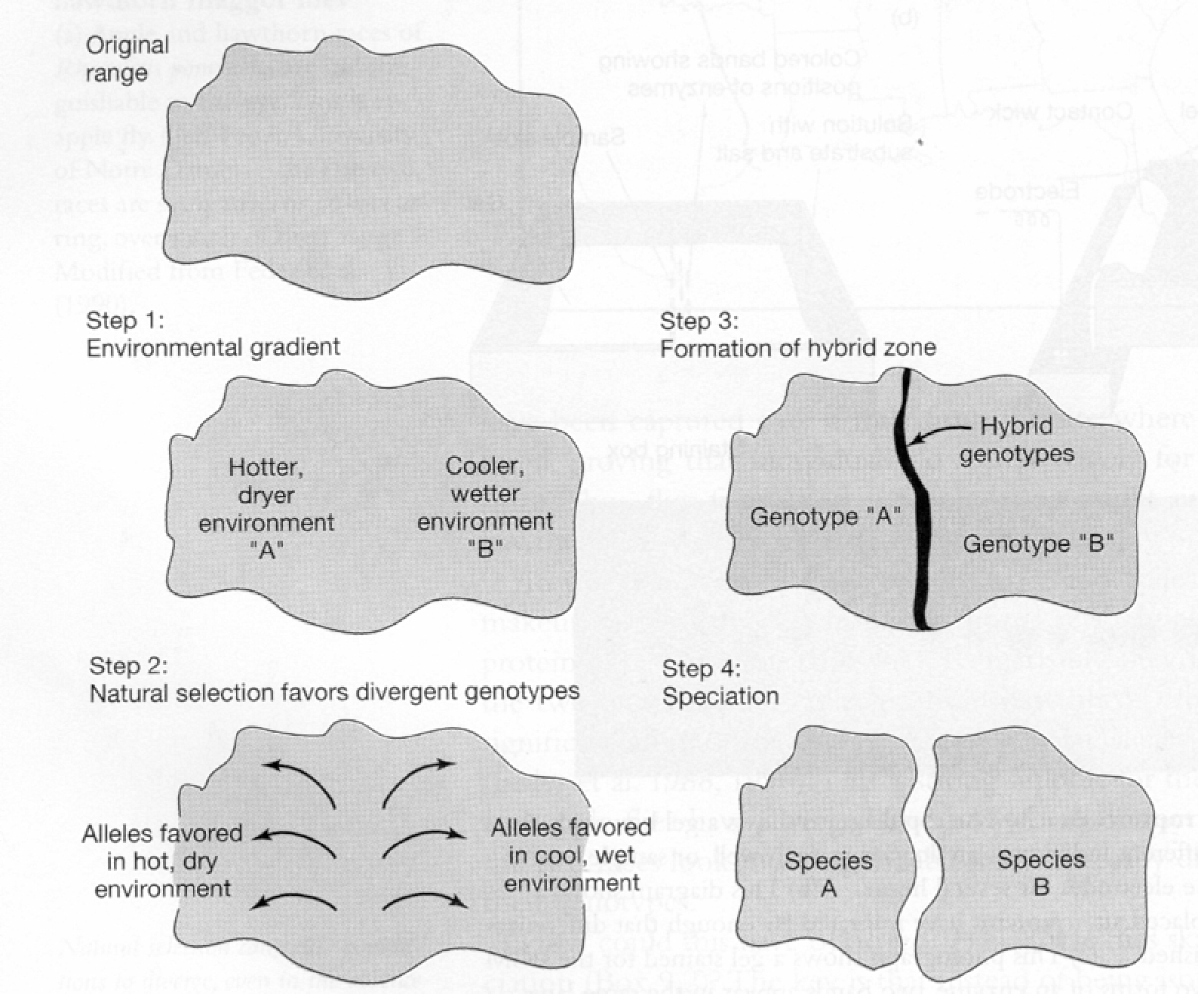


Figure 8.5 Geographic
cated by the subdivision
of these geographic races
which resembles backgro
length, which are related

Parapatric Population Subdivision and Speciation

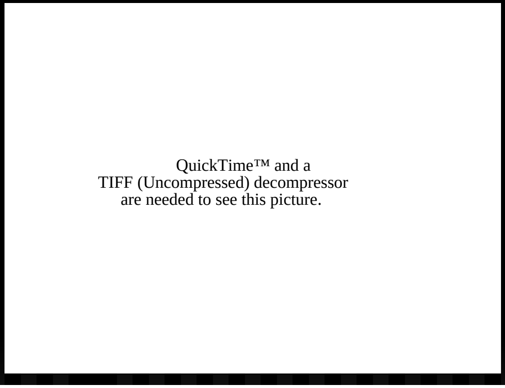
- Limitations of gene flow distance has also been suggested to contribute to speciation, driven by either selection or drift.



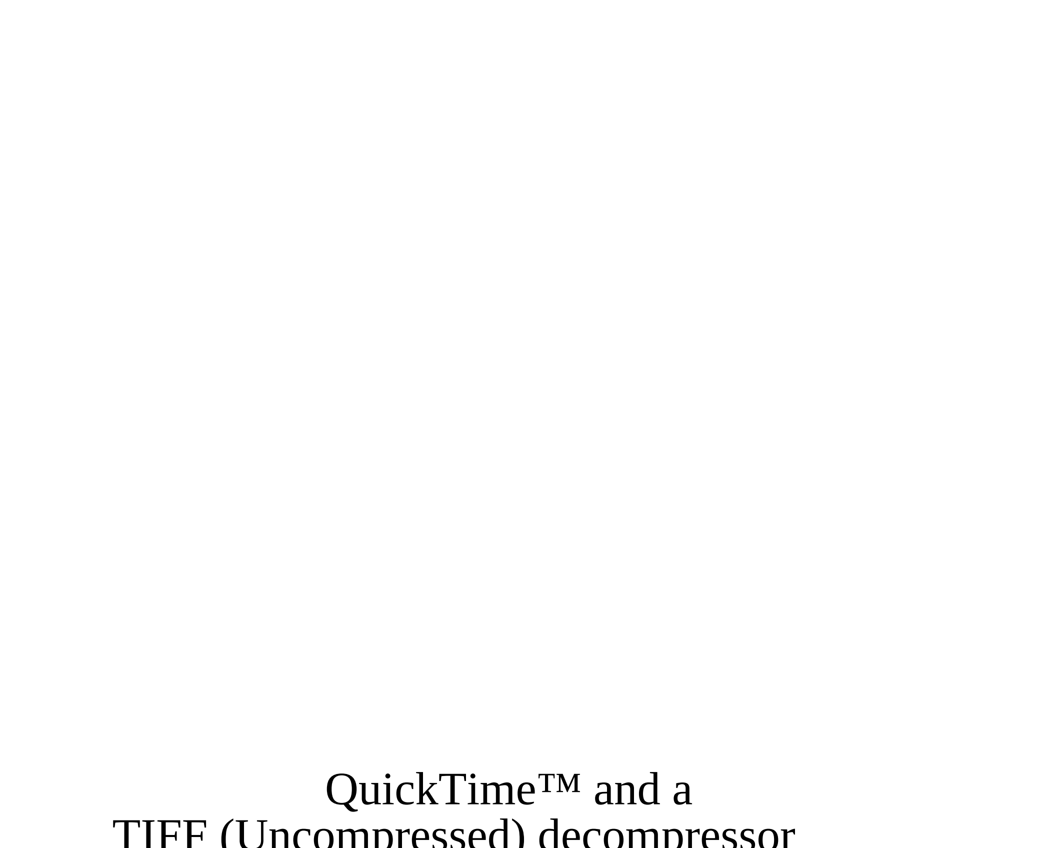
Turing Pattern Formation as an Analog of Parapatric Speciation

- Turing showed that dynamical systems characterized by localized interaction (isolation by distance) reinforced by inhibition of effects at a distance can yield self-organizing spatial pattern.
  - He applied these models to the formation of static color patterns on animal skins and pelage, but they can also describe dynamic patterns.

From Spatial Pattern to Speciation: an empirical example

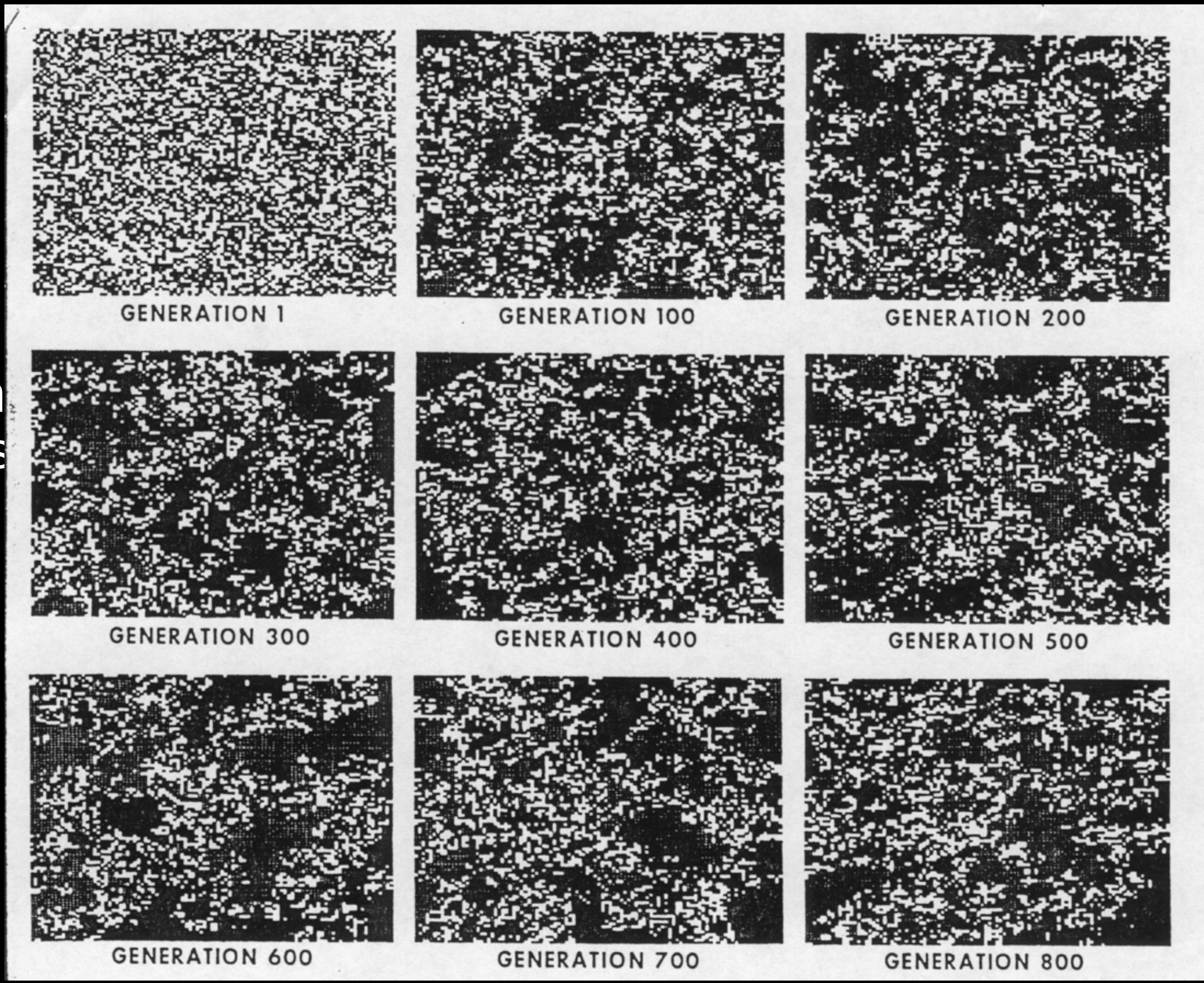


- “Speciation by Distance” in a broken-ring species, the greenish warbler (Irwin et al. 2002).
  - Did speciation occur if the ring didn’t break?



An example of spatial self-organization of a gene pool (Turner et al. 1982)

- Computational model of sexual plants
  - 2 alleles
  - Started with random distribution of alleles and genotypes in space
  - Random reproductive success and dispersal direction
  - Nearest neighbor mating



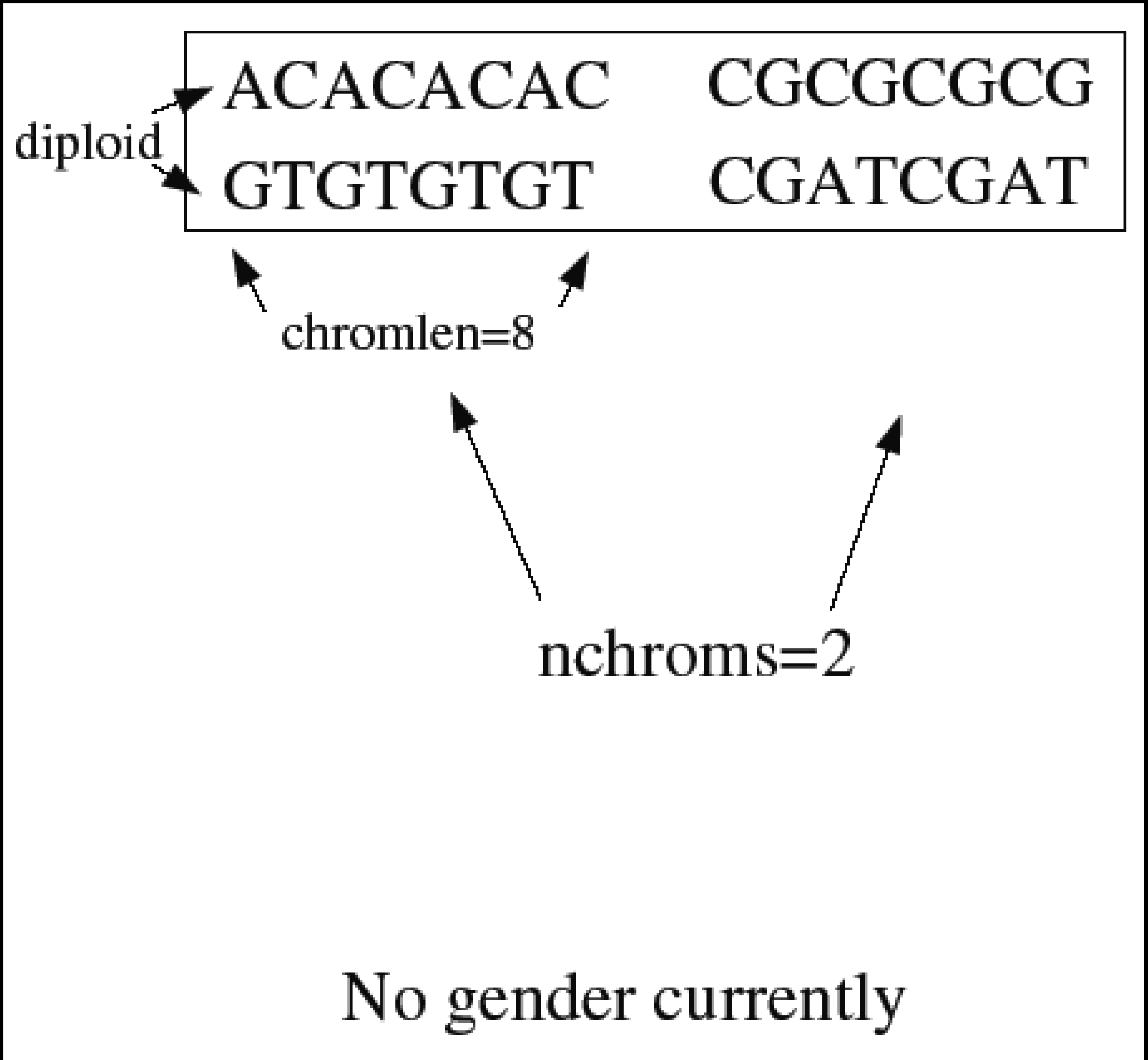
Modeling Neutral Parapatric Speciation

- Selection generated by environmental differences is a classic mechanism generating inhibition at a distance and spatial pattern formation matching the environmental template.
- Neutral models of this process have relied on outbreeding depression to generate inhibition at a distance.
  - Isolation by distance causes more distant neighborhoods to be genetically more different, on average.
  - To date these models have assumed an arbitrary degree of genetic difference beyond which mating is never successful and before which mating is always successful (see Gavrilets 1999, 2000).

Our model of Isolation by Distance

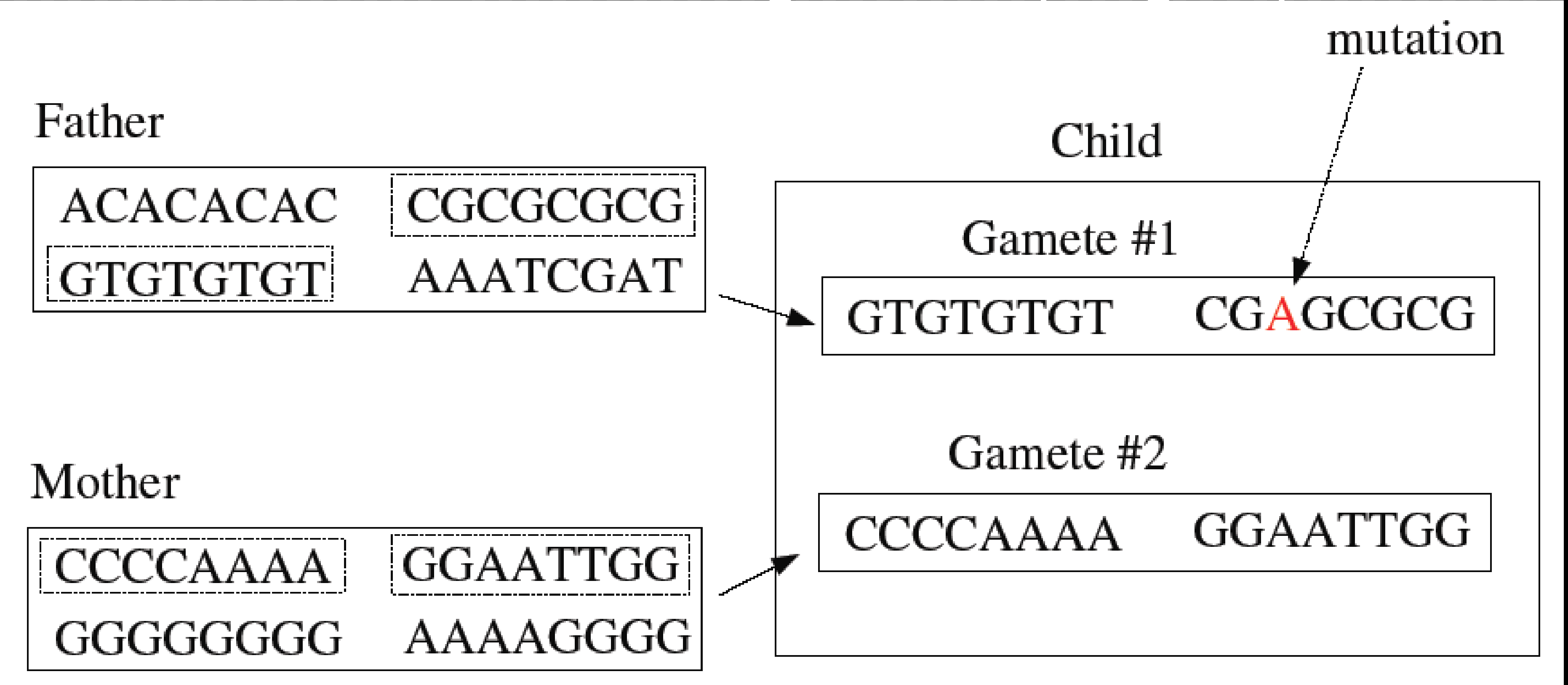
- We aim to explore spatial pattern formation in sexual populations
  - and ultimately the dynamics of parapatric speciation
- We represent space as a grid of adjustable size.
  - Individual grid cells can be occupied by one or more individuals. The occupancy limit is specified by the user.

Representing Genetic Individuals



Reproduction and Mutation

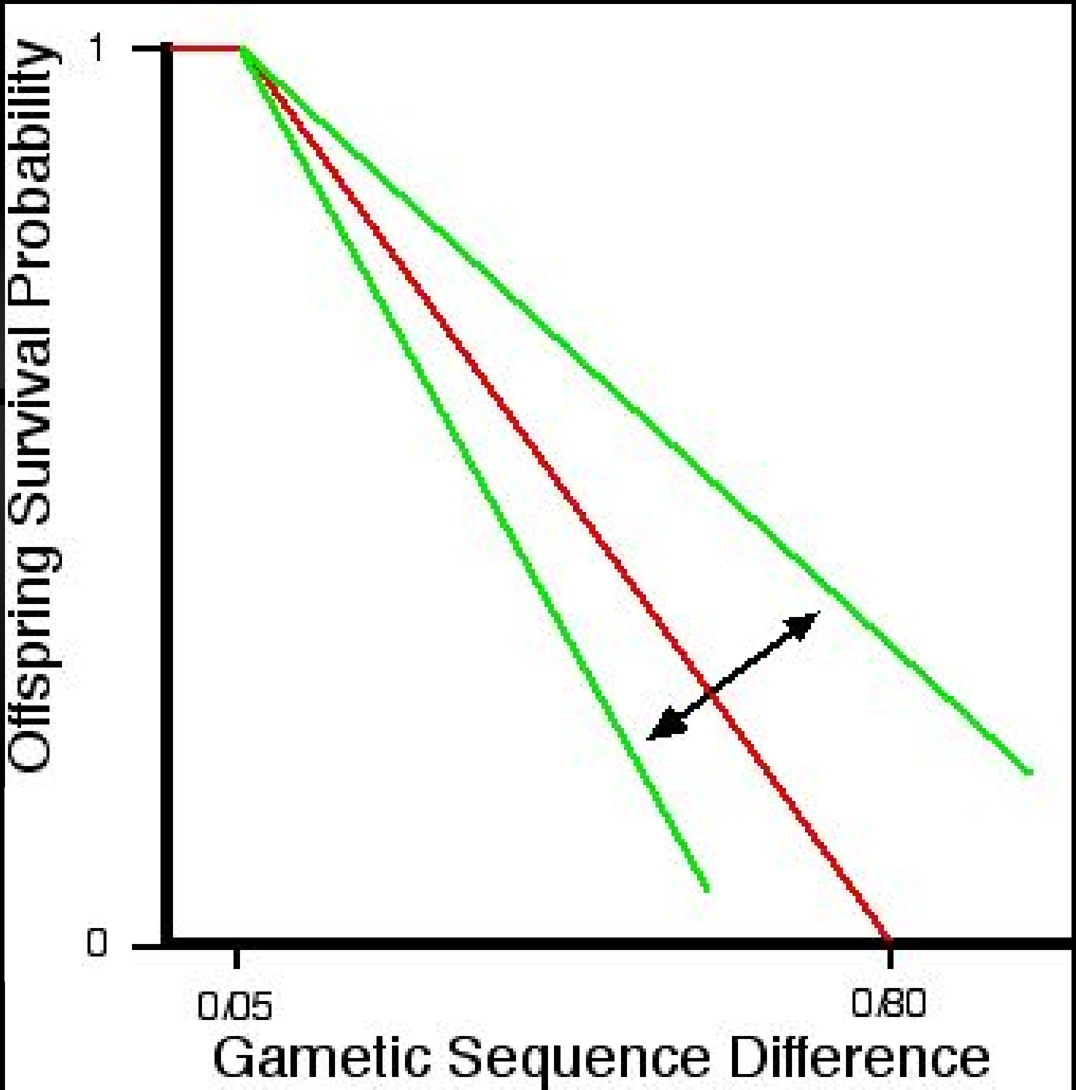
Mates are selected randomly from within the dispersal neighborhood, one of whom is randomly assigned to be the mother to anchor the origin of offspring dispersal.



Reproduction cont.

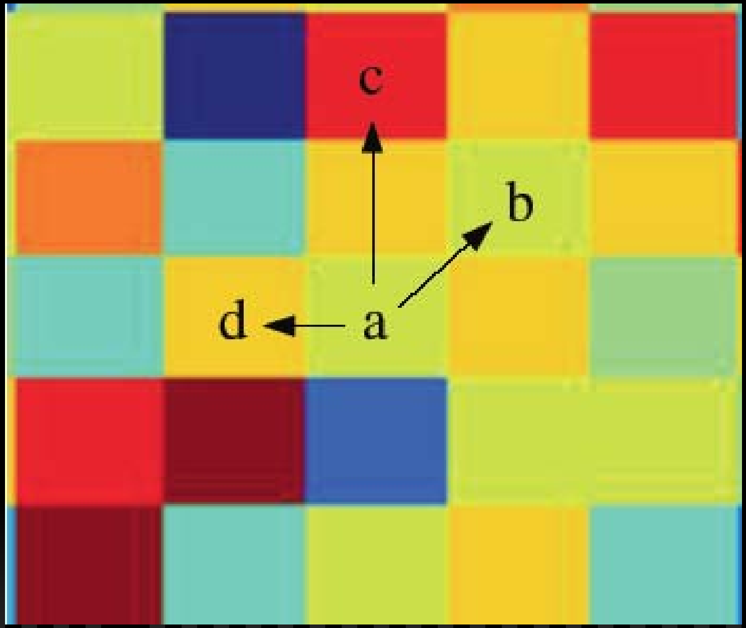
- Every individual is selected for a mating opportunity in the first pass each generation.
- Reproductive success is Poisson distributed with a mean of 1.
- Several factors can result in a shrinking population.
  - e.g., failure to place an offspring when there is no free space within the dispersal distance
  - Global population size is maintained by doing a second pass selecting individuals at random for additional mating opportunities
- Non-overlapping generations

Outbreeding Depression and Inhibition at a Distance



Dispersal

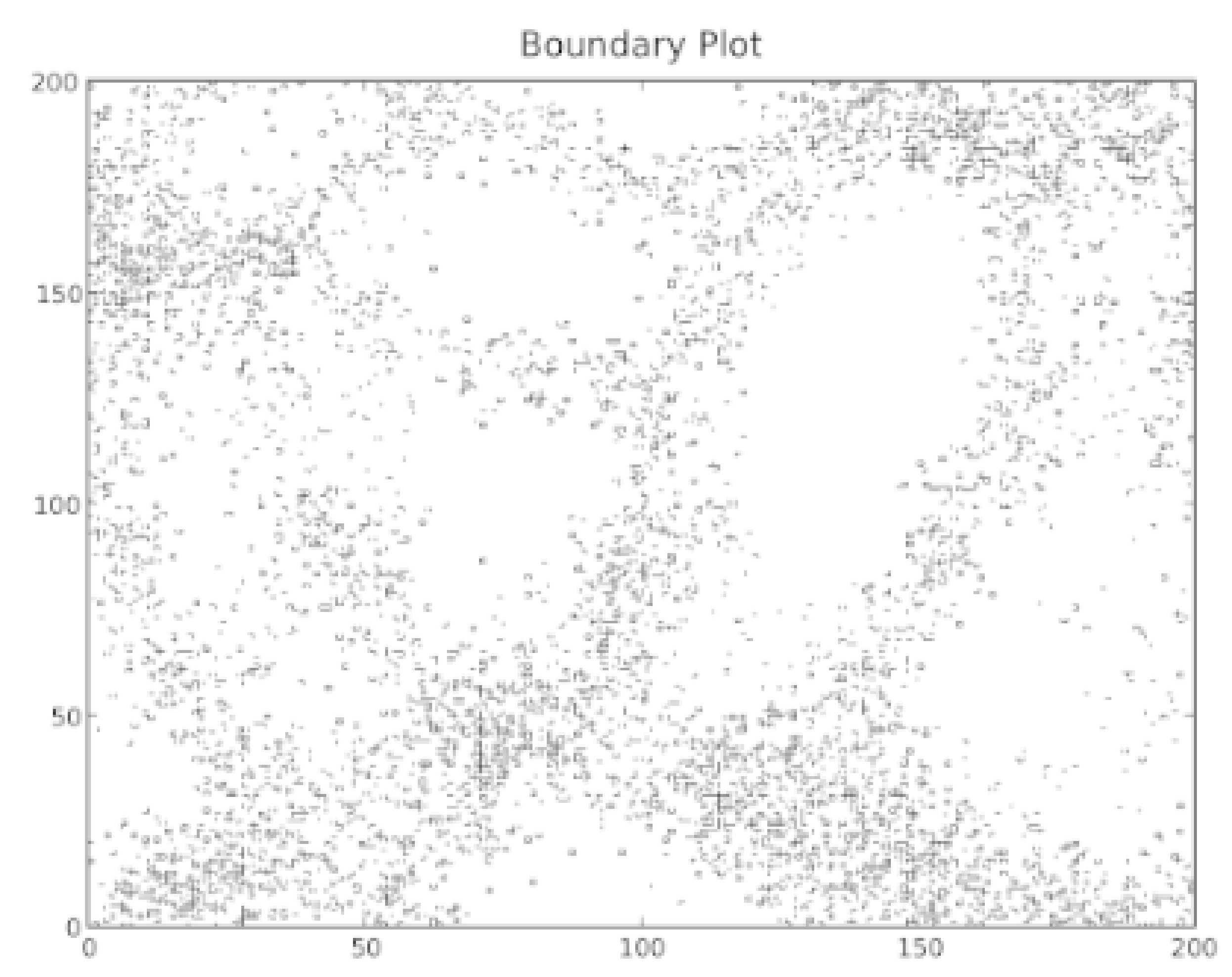
- Dispersal is random with regard to direction and distance, although the maximum distance is specified by the user.
- Distances measured as cell center-to-center, so a distance of 1.001 includes four neighbors, and a distance of 1.5 includes eight neighbors.

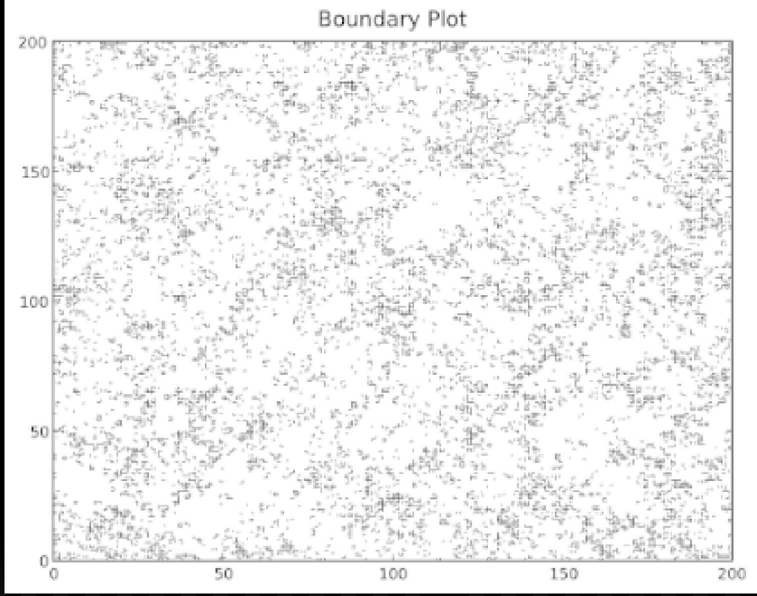


a to b: 1.41
a to d: 1
a to c: 2

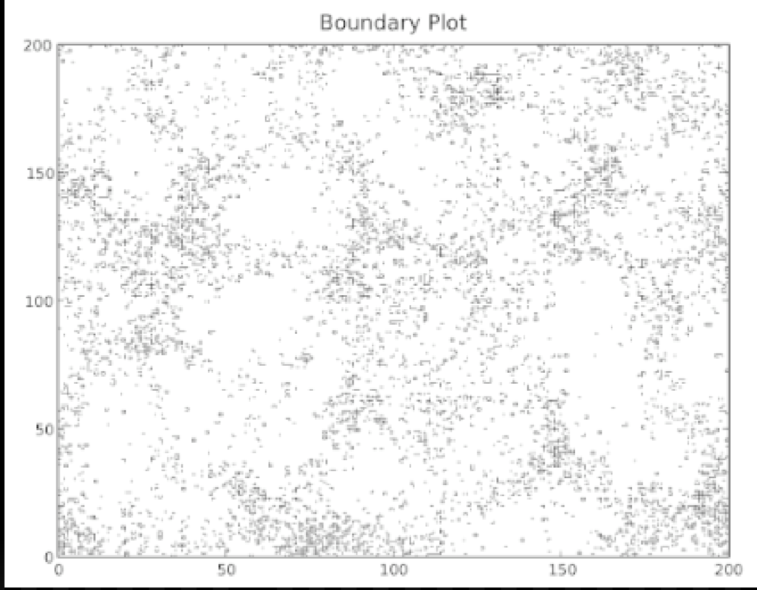
The Emergence of Homogeneous Clusters and Boundary Zones

- Lines were drawn between cells with genomic differences of 50% or more.
- Pop Size: 40000
- Grid Size: 200x200
- Disp Dist: 3
- Mut Rate: 0.002
- Num Chrom: 2
- Chrom Size: 1000
- Max Cell Occupancy: 1

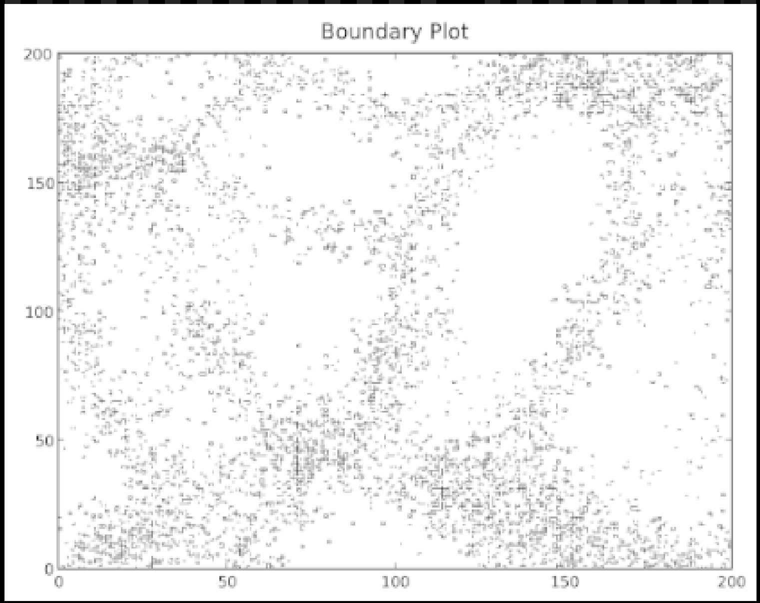




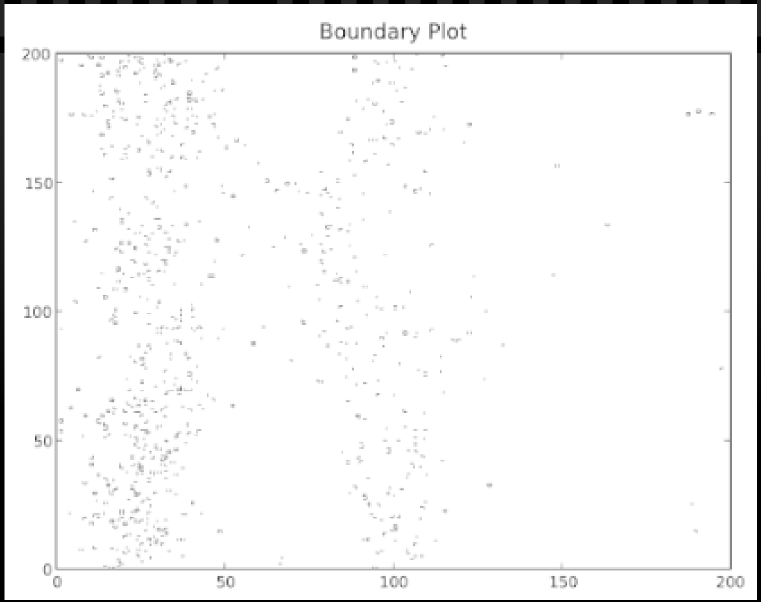
Dispersal Limit 1 Cell



Dispersal Limit 2 Cells



Dispersal Limit 3 Cells



Dispersal Limit 4 Cells

Sampling of Genetic Similarities Between Randomly Selected Pairs of Individuals

Gen 1000

QuickTime™ and a
TIFF (LZW) decompressor
are needed to see this picture.

Gen 2000

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TIFF (LZW) decompressor
are needed to see this picture.

Gen 3000

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Gen 6000

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Gen 7000

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Gen 8000

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Gen 9000

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Gen 10000

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Gen 11000

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Gen 12000

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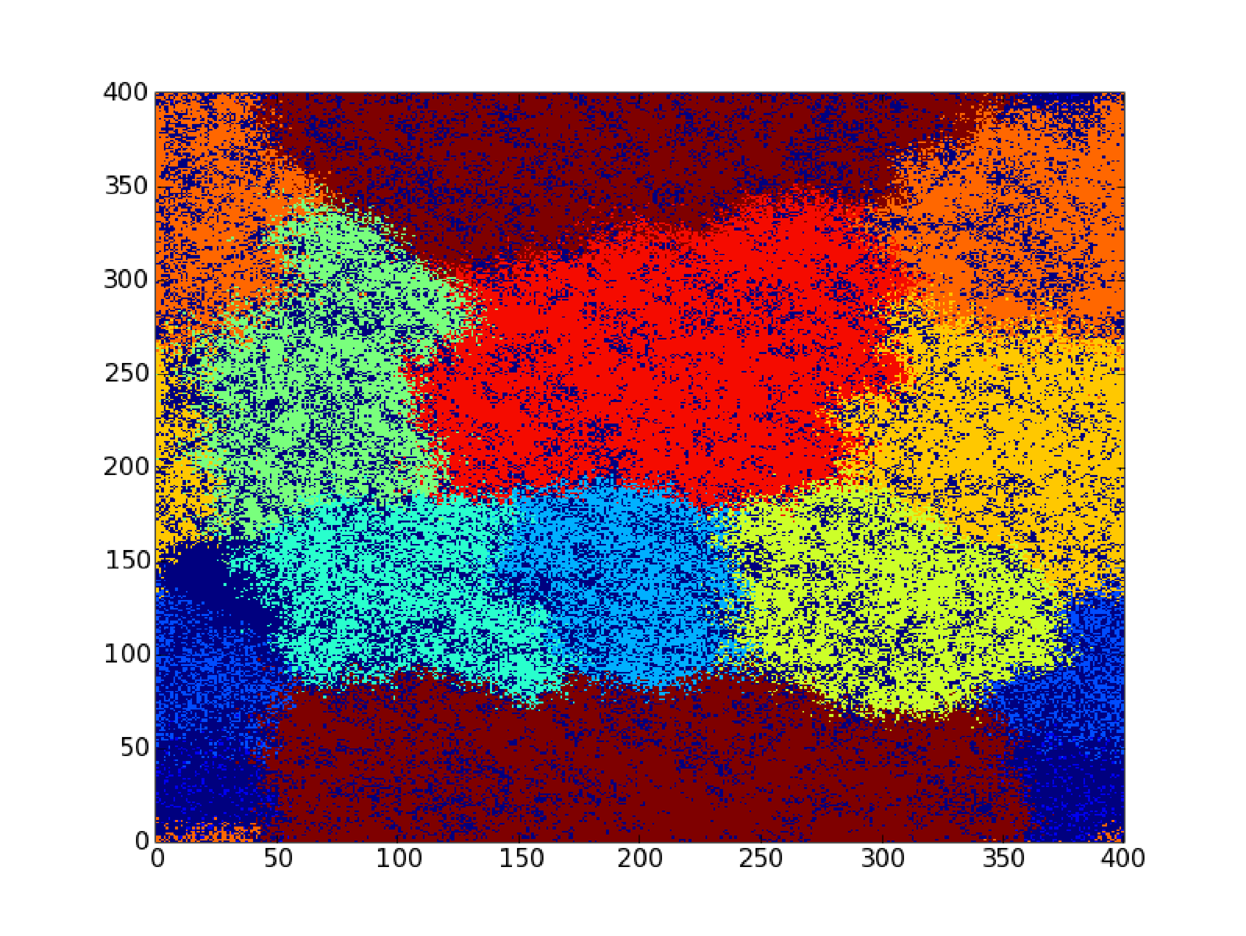
Temporal diversity waves and spatial configuration

- This is a snapshot of the landscape at a point when there were several peaks in the mismatch distribution (gen 100k), and multiple species. The set of types generating those peaks were spatially segregated.



Preliminary Conclusions and Future Directions

- Sexual populations can self-organize in space, with fuzzy boundaries separating diverged, homogeneous regions.
- Can we describe the conditions needed to complete parapatric speciation under this model?
- How does this process interact with extrinsic pattern-forming factors, such as local dispersal barriers and local selection differences?
- Can we successfully model the genetic evolution of a real species in a real environment to inform population/ecosystem management practices?

What about Natural Selection?

- Definition: a process that adaptively biases the evolution of a population so as to optimize the functional abilities of its components, given heritability of fitness differences.
- NS maximizes the rate of fitness increase
  - Maximization is a tendency to increase that generates optimizing processes
    - e.g. NS on organisms optimizes genomic architecture to maximize fitness
- NS requires processes of birth and death in a population of entities (e.g., individuals).
- If NS is to persistently drive evolution, it also requires a process of (creative) mutation.

Complex ADAPTIVE Systems

- Like NS, SO can be an optimizing process (Helbing and Vicsek. 1999. Optimal self-organization. arXiv:cond-mat)
  - Tornado in a bottle demo
  - Weather systems (vortexes and convection)
- SO leads to “autonomous adaptation to a changing environment.” (Heylighen. 1999. EOLSS online encyclopedia)

Natural selection is self-organization

- NS is an emergent process driven by the thermodynamic imperative.
- NS can cause elaborate co-evolutionary dynamics that optimize fitnesses, but the consequence of NS among lineages within a co-evolutionary system is to optimize the flow of energy through the system as a whole.
- It does not invalidate any of the science relating to NS done over the past 150 years.
- Ultimately, the theory of SO systems provides a more general context in which to understand NS.