Generalists, specialists and plasticity: evolution and environmental variation

- Stochastic environmental variation
  - Temporal
  - Geometric vs. arithmetic mean fitness
  - Spatial
  - Levins model
- Predictable environmental variation
  - Phenotypic plasticity

Evolution in varying environments

- Both temporal and spatial variability can maintain genetic polymorphism
- A consequence is that temporal and spatial variability cause chronic maladaptation

Adaptation to varying environments

- How does environmental variation influence adaptation, or the composition of genotypes in a population?

Stochastic temporal variation

- Fitness in a variable environment:
  \[ \lambda = \text{finite rate of increase} \]
  \[ N_t = N_0 \lambda^t \]
  \[ N_t = N_0 \lambda_1 \lambda_2 \cdots \lambda_t \]
- When \( \lambda \) varies temporally, what is fitness?

Stochastic spatial variation

- Maintains genetic variation (multiple niche polymorphism)
  - Chronic maladaptation
- Other solutions?

Stochastic temporal variation

- Imagine: \( \lambda \) varies 0-2.2
- Arithmetic mean:
  - Population expected to grow exponentially
- Simulate 10 populations
- Geometric mean
  - Provides better measure of fitness
  \[ \overline{\lambda}_g = 1.1 \]
- Traits that increase the arithmetic mean may not be selected

Summary for stochastic temporal variation:

- Traits are favored that maximize geometric mean fitness (not the arithmetic mean)
- Temporal variation favors “spreading the risk” or “Bet-hedging” -- the production of variation among offspring
  - Reduces variance in fitness across generations

Adaptation to stochastic spatial variation

- Genotypes in a population
  - Differ in their location on a niche axis -- specialists
  - Differ in their breadth -- generalists
- What is the composition of an adapted population?
Stochastic spatial variation: solutions

1. Specialist
2. Generalist
3. Diversity of specialists (Multiple niche polymorphism)
   - Does selection favors broadening ecological niche (generalist)?

Adaptation Stochastic Spatial variation

- Levins 1968: based on trade-offs
- Outcome depends on
  - Fine-grained or coarse grained
  - Frequency of each environment

A graphical model:
- Fitness set: the fitness of genotypes in alternative environments
- $a, b$: specialists
- $g$: generalist has the best fitness in both environments
- Adaptive function: the overall average fitness function
  $A = W_1 c_1 + W_2 c_2$
- Plotted as:
  $W_1 = A - W_2 c_2 / c_1$
  where relative frequencies of environments are $c_1, c_2$
- Optimal population composition: tangent point

A population of generalists:
- Convex fitness set: fitness of a generalist not much less than specialists
- Fine-grained environment: individual experience both habitats during lifetime in their relative frequencies, $c_1, c_2$
  $A = W_1 c_1 + W_2 c_2$
- Coarse-grained environment: individual experiences one habitat during lifetime
  $A = W_1 c_1 W_2 c_2$

A single specialist:
- Fine-grained environment
  $C_i >> C_j$
- Concave fitness set
  $W_i >> W_g$

A diversity of specialists (mix of $a, b$):
- Coarse-grained environment: individual experiences one habitat during lifetime
  $A = W_1 C_1 W_2 C_2$
- Concave fitness set
  $W_i >> W_g$

Summary for stochastic spatial variation

- Generalist can evolve, replace specialists
- Outcome depends on
  - Frequencies of habitats, $c_1, c_2$
  - How inferior is the generalist $g$
  - Whether environments are fine-grained or coarse-grained

Adaptation to stochastic variation:

Assumes
- No predictive cues about the environment
- Organisms cannot jointly satisfy multiple optima

Predictable environmental variation: Reliable cues

- Levins 1968
  - Phenotypic plasticity: Altering the phenotype to match each environmental state should be favored over canalization (specialist)
  - “Adaptation” within a generation

Bicyclus anynana
Wet season
Dry season
What is plasticity?

- Phenotypic expression of a genotype to different environments
- The property of genotypes
- Specific to traits and environments

Plasticity vs Adaptation

- Spatial variation in selection: if scale too small or gene flow too great, failure to adapt
- Temporal variation: if too fast, population will lag behind optimum
- In fact, why does not a perfectly plastic genotype replace non-plastic genotypes?

Visualizing plasticity

- Non-flat reaction norms indicate phenotypic plasticity
- Flat reaction norm: Environmental canalization, autonomous development

Phenotypic stability, plasticity

1. Some reaction norms show no plasticity.
2. Changes in scale, sensitivity
3. Changes in the rank order of genotypes changes across environments
   - Selection favors some genotypes in one environment and others in another.

Measuring reaction norms

- Labile traits: change rapidly within a lifetime (physiology or behavior)
  - Individuals can be measured in different environments
- Non-labile traits: phenotypic expression is fixed as some point during ontogeny (age at maturity, adult size, morphology)
  - Phenotypic expression in different environments is measured on different individuals of the same genotype

Types of reaction norms

- Phenotypic modulation, dependent development
- Developmental conversion (conditional strategies, polyphenism)
- Developmental conversion: Barnacle morphs
- Predator-induced defense
Evolution of plasticity: genetic control?

• Is plasticity under genetic control?
• 2 proposed mechanisms

![Diagram of genetic control of plasticity]

Genetic control of plasticity

1. Allelic sensitivity involves the response of a gene product from a particular locus to a change in conditions
   - E.g. enzymatic activity in response to temperature
   Underlies phenotypic modulation

2. Gene regulatory control
   • Environment-dependent activity of genes as a result of regulatory loci
   • Underlies developmental conversions

Evolution of plasticity: Genetic variation

• Genotype by environment interactions
• Genotypes differ in reaction norm slopes

![Graphs of reaction norms]

Responses to local environments

• Population decline, extinction
• Disperse, migrate
• Phenotype evolves in response to local selection: adaptive evolution
• Phenotype adjusts to increase fitness in local conditions: phenotypic plasticity

The evolution of reaction norms: a simple model

Why be plastic: results from models

• Assuming genetic variation for plasticity
• selection will favor adaptive plasticity when:
  (i) populations are exposed to variable environments, spatial or temporal
  (ii) environments produce reliable cues
  (iii) no single phenotype exhibits superior fitness across all environments: spatially variable selection

Why does phenotypic plasticity not always evolve?

1. Pure costs
   • Production costs
   • Trade-off costs
2. Limits to benefits
   • Cost of inaccurate environmental assessment
   • Lag-time: response to slow