Phenotypic evolution in the Anthropocene

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1. Phenotypic traits constitute the interface between the organism and the environment

Macroscopic patterns (community properties, biogeographic patterns) arise from phenotypic trait responses to environmental variation

Environment: biotic (competition, predation), abiotic (temperature, rainfall)
2. Evolution of phenotypic traits results from the interplay between selection and constraints
3. Irreversible evolutionary end points result from constraints on phenotypic evolution
Challenge: incorporate mechanistic descriptions of constraints into models of eco-evolutionary dynamics
**Motivation:** predict whether species can adapt to perturbations in their biotic and abiotic environment (e.g., climate warming, species invasions)
Phenotypic evolution: interplay between selection and constraints

Selection: biotic and abiotic factors generate variance in fitness

Evolution: heritable variation

Variation: genetic constraint on phenotypic evolution
Energetic constraints

Trade-offs (negative correlations between traits)

Only certain evolutionary outcomes are possible (e.g., fecundity-longevity, fecundity-body size, semelparity-iteroparity)

Transitions between outcomes are difficult
Morphological constraints

Irreversible evolutionary endpoints
Morphological constraints

Upper limit to evolutionary trajectories (e.g., body size in insects)
Biochemical constraints

DNA replication, protein folding, metabolic pathways
Constraints on selection

Irreversible evolutionary end points

Upper limit to evolutionary trajectories
Phenotypic evolution in response to environmental perturbations
Data:

Rapid evolution in response to perturbations ==> species respond to novel selection pressures unimpeded by constraints

Failure to adapt to perturbations ==> constraints impede adaptation to new selection regimes
Phenotypic plasticity as a strategy to maximize fitness in variable environments

**Reaction norm**: range of phenotypic responses exhibited by a genotype in response to environmental variation.
Evolution of phenotypic plasticity

Selection and constraints

Constraints: genetic
energetic
biochemical
Temperature variation and thermal reaction norms

Do organisms have sufficient plasticity to respond to changing thermal environments (climate warming)?

Can plasticity evolve fast enough to keep pace with warming?

Role of biochemical constraints
Thermal reaction norms

Framework for characterizing thermal reaction norms

Data: qualitative nature of reaction norms conserved across taxa
Mechanistic descriptions of thermal reaction norms

**Mechanism at biochemical level**
- Rate-controlled (reaction kinetics and enzyme inactivation)
- Regulatory (neural and hormonal regulation)

**Trait response at phenotypic level**
- Monotonic
- Left-skewed
- Unimodal, symmetric

Graphs of:
- Per capita mortality rate vs. temperature
- Developmental rate vs. temperature
- Fecundity vs. temperature
Rate-controlled temperature responses

Monotonic

\[ k_T = k_{TR} e^{\frac{A_k}{T_R} - \frac{1}{T}} \]

Boltzmann-Arrhenius function
Rate-controlled temperature responses

Left-skewed

\[ k_T = \frac{k_{TR} T}{T_R} e^{A \left( \frac{1}{T_R} - \frac{1}{T} \right)} \frac{A_L \left( \frac{1}{T_L/2} - \frac{1}{T} \right)}{1 + e^{A_H \left( \frac{1}{T_{H/2}} - \frac{1}{T} \right)}} \]

Sharpe and DeMichele (1977), Schoolfield et al. (1981)
Regulatory responses

Symmetric, unimodal

\[ k_T = k_{T_{opt}} e^{-\frac{(T-T_{opt})^2}{2s^2}} \]

Gaussian function
Framework: characterize reaction norms based on temperature effects on biochemical processes

Prediction: if temperature effects on biochemical processes conserved across taxa, qualitatively similar reaction norms
Monotonic temperature responses: mortality

- Insect parasitoids
- Hemipteran herbivores
- Beetles
Left-skewed temperature responses: maturation

Drosophila species

Pine beetle

Insect parasitoids

Mite
Unimodal temperature responses: reproduction

Honeybees

Trissolcus murgantiae

Drosophila species

Trichogrammatidae

Ooencyrtus johnsonii
Unimodal temperature responses: attack and maximum uptake rates
Thermal reaction norms

Framework for characterizing reaction norms

Data: qualitative nature of reaction norms conserved across taxa
Constraints on thermal reaction norms
Regulatory responses: symmetric at extremes ==> similar constraints

Rate-controlled responses: asymmetric ==> different constraints
Reaction rates (e.g., metabolic, mortality) increase with temperature \( \Rightarrow \) biochemistry imposes fundamental constraint on longevity

\[
k_T = k_{TR} e^{A_k \left(\frac{1}{T_R} - \frac{1}{T}\right)}
\]

Monotonic reaction norms
Rate-controlled responses: faster decline at high temperatures than at low temperatures

=> different constraints

Left-skewed reaction norms

\[ k_T = \frac{k_{TR} T^A \left( \frac{1}{T_R} - \frac{1}{T} \right)}{1 + e^{A_L \left( \frac{1}{T_{L/2}} - \frac{1}{T} \right)} + e^{A_H \left( \frac{1}{T_{H/2}} - \frac{1}{T} \right)}} \]
Low-temperature decline: freezing of body fluids, slower response

High-temperature decline: protein denaturation, faster response

\[ k_T = \frac{k_{TR}^T e^{A_L \left( \frac{1}{T_R} - \frac{1}{T} \right)}}{1 + e^{A_L \left( \frac{1}{T_{L/2}} - \frac{1}{T} \right)}} \]
Hard limit at high temperatures: protein denaturation (irreversible process)

Softer limit at low temperatures: freezing of body fluids

Adaptations to avoid/minimize freezing of body fluids, not so for heat-induced protein denaturation
Biochemical constraints on thermal adaptation: slow down at low temperatures, drop dead at high temperatures
Climate warming ==> exposure to warmer thermal regimes ==> organisms more likely to encounter upper limit of phenotypic plasticity

Traits under strong biochemical control (e.g., development, mortality) more adversely affected
Thermal reaction norms of life history and interaction traits

- Attack rate
- Handling time
- Mortality
- Maturation
Temperature (K)

- Attack rate
- Handling time
- Maturation
- Mortality

**Typical seasonal**

**Warmer winters**

**Hotter summers**
Warming effects on trait responses

Rate-controlled responses (maturation and mortality) more adversely affected by warming than regulatory responses (attack rate, handling time)
Trait-level constraints and population/community-level consequences
Biochemical constraints --> demographic constraints prevent adaptation to novel thermal environments --> irreversible biogeographic pattern
Latitudinal directionality in invasion success

Tropical ectotherms more successful in invading temperate communities than vice versa
Evidence

1. Paleontological and biogeographic data
Diversity at higher latitudes

Geographic expansion of taxa originating in tropics (common)

Taxa originating at higher latitudes expanding to tropics (rare)

Re-invasion of tropics by higher-latitude taxa (rare)
Evidence

2. Contemporary invasion data
Most successful invaders of temperate habitats

Ectotherms of tropical origin

Cane toad, Asian tiger mosquito, Fire ant, scale insects, marine invertebrates
Most successful temperate invaders of tropical habitats

Endotherms

Passerine birds, rodents
Goal

Mechanistic underpinnings of directionality in invasion success
Latitudinal directionality in invasion success

Adaptation to novel environments

Tropical species better able to adapt to temperate habitats but not *vice versa*
Eco-evolutionary dynamics: quantitative genetic model of trait evolution, stage-structured model of population dynamics

Evolution of thermal reaction norm for reproduction

Amarasekare and Johnson (2017)
Tropical ectotherms invading temperate habitats (warmer to colder): reaction norm rapidly adapts to temperate thermal regime

Temperate ectotherms invading tropical habitats (colder to warmer): stochastic extinction during invasion phase precludes adaptation to tropical thermal regime
Temperate ectotherms invading tropical habitats

Thermal reaction norms for mortality and maturation reach upper limit of plasticity: increase in mortality and decrease in maturation --> low abundances during invasion phase --> extinction due to demographic stochasticity

Biochemical constraint imposes demographic constraint
Biochemical constraint on reaction norm evolution --> irreversible biogeographic pattern: latitudinal directionality in invasion success
Adaptation to climate warming

Evolution of upper thermal limit

Genetic variation in thermal reaction norms
Evolution of thermal reaction norms

Cryptic genetic variation: expressed in novel or extreme environments

(Waddington 1957; Gibson 2009; Masel & Siegal 2009)

Allow organisms to adapt to perturbations in typical environment
Uncovering cryptic genetic variation

Prediction:

Greater genetic variability in reaction norms in perturbed environments compared to typical environments
Harlequin bug

(Murgantia histrionica)

(Hemiptera: Pentatomidae)
Uncovering cryptic genetic variation

![Graphs showing developmental period and nymphal survivorship vs. temperature (C)]
Other empirical evidence

Rapid adaptation of low temperature threshold, no evidence for high temperature threshold
Data:

Rapid evolution in response to perturbations ==> species respond to novel selection pressures unimpeded by constraints

Failure to adapt to perturbations ==> constraints impede adaptation to new selection regimes
Hypotheses

Rapid evolution in response to environmental perturbations:

Genetic variation in reaction norms
Weak biochemical/energetic constraints

Failure of evolution:

Genetic and biochemical constraints
Life is driven by biochemistry

Biochemical constraints constitute strong impediments to evolution in response to changing environments
Things I do not understand

1. Irreversible processes in evolution
2. Constraints that cause regulatory responses to be symmetric at extremes
3. How to incorporate constraints into models of eco-evolutionary dynamics