Genetics and ecology of adaptation to stochastic environments

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Environments vary randomly

- Virtually all natural environments exhibit noisy, random fluctuations.

- Faster than trends: major challenge for organisms in the wild
Environments vary randomly

- Stochastic fluctuations are **random**, but can be **predicted probabilistically**
- Time scale of predictability depends on **temporal autocorrelation** $\rho$

\[\rho = 0.1\]

\[\rho = 0.9\]

- Climate change is altering not only mean environments (= trend), but also their (auto)correlation structure
Stochastic environments affect ecology and evolution

- Fluctuating demographic vital rates $\rightarrow$ Fluctuating population size/density\(^1\)

- Affects all individuals at all population sizes\(^1\)
  $\rightarrow$ Strong source of stochasticity and extinction risk.

Stochastic environments affect ecology and evolution

- Source of fluctuating selection

**Darwin’s finches**
Grant & Grant 2002 Science

**Great tit (breeding time)**
Reed et al 2013 Science

**Sticklebacks (spine number)**
Reimchen & Nosil 2002 Evolution

- Negative mismatch years
- Positive mismatch years

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Stochastic environments affect ecology and evolution

• Source of fluctuating selection

• Can cause the evolution of specific response mechanisms: bet hedging, or phenotypic plasticity

• Major source of chance in evolution: Environmental stochasticity increases variance among replicate instances of evolution, similar to drift (causing fixations, etc...)
Predictability of population responses

- How do random fluctuations in the environment translate into fluctuations at all levels of population biology? With what predictability at each level?

(A) Phenotypic plasticity
(B) Fluctuating selection
(C) Stochastic demography

Figures from Grant & Grant (2002 Science, 2014 PUP)
Predictability of population responses

- How do random fluctuations in the environment translate into fluctuations at all levels of population biology? With what predictability at each level?

- Investigating stochasticity requires a high level of replication, to account for randomness in the process.

- An approach combining experimental evolution with theory can help shed light on patterns from natural populations.
I – Experimental evolution in stochastic environments

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Experimental evolution with *Dunaliella salina*

- **Halotolerant micro-algae** (freshwater to NaCl saturation). Shallow water (lagoons): *salinity fluctuates* with precipitation, wind, sunlight
- Short generation time ~ 1 day
- Extremophile: few ecological interactions → Niche easily mimicked in the lab
- **Physiological traits respond plastically to salinity**: metabolite content. Glycerol: osmotic stress Carotene: Protection against light, oxidative stress.

http://www.lesalindeguruissan.fr/
Experimental evolution
under randomly fluctuating salinity

• Salinity changed at each transfer (every 3-4 generations),
  using a liquid-handling robot: - High replication
    - Complex fluctuation pattern
Experimental evolution under randomly fluctuating salinity

- Autocorrelation as the treatment: $\rho = -0.5, 0, 0.5, 0.9$

- >35 independent time series per autocorrelation

- Applied to 3 collection strains, single vs pair mixes
  = high vs low genetic variance

- Population size at each transfer estimated using flow cytometry + absorbance + fluorescence.
Stochastic population dynamics

- Combined time series and treatments
  Population size rapidly reaches **stationary distribution**, at a balance between randomly fluctuating growth and density-dependent regulation.
Extinction rate

- Population survival curve: fraction of populations persist up to $t$ days

- Faster extinction under smaller environmental autocorrelation
- No clear effect of genetic variance (mixtures vs single strains) overall

$\rho = 0.9$
$0.5$
$0$
$-0.5$
Distribution of population size

- Stationary distribution of lnN well described by a reverse gamma, more skewed in more autocorrelated environments ...

... as predicted by theory of fluctuating optimum\(^1\)

1: Chevin, Cotto & Ashander (2017 Am Nat)
Trans-generational tolerance curves

- Measure **tolerance curve with environmental memory, mediated by transgenerational plasticity**

![Graph showing trans-generational tolerance curves](image)

- **Acclimation salinity** (before previous transfer, ~ 3 generations earlier)
- Measurement salinity

- **Lowest** $r$ in shifts from low to high salinity.
Trans-generational tolerance curves

- Combined with pattern of experimental fluctuations, this predicts well the effects of salinity on population growth

\[ \rho = -0.5 \quad \rho = 0 \quad \rho = 0.5 \quad \rho = 0.9 \]

Environmental autocorrelation
Evolutionary responses

- These tolerance curves have evolved in response to our stochastic treatments.
- Little to no effect on current tolerance breadth \( \sigma \), but effect on interaction \( K \) between past and current environment.

\[
\rho \quad \rho^2
\]

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Evolutionary responses

• Currently investigating **salinity reaction norms of underlying traits**:
  - Cell morphology and content (Glycerol, carotene...)
  - Gene expression
  - Epigenetic marks
  - Recombination rate
  - ...

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Tracking genetic change

• Populations were stored at multiple time points in all surviving replicates, and DNA extracted.

• Sequencing markers (ITS) and candidate genes to track population genetic change in this experiment

→ Measure mean and variance of allele frequency change
  - over unit time step (~infinitesimal diffusion parameters)
  - on longer run.
Fluctuating selection:
from phenotype to genotype

• In such experiments with randomly changing environments, what kind of genetic change do we expect to observe?

• How does this depend on the genetic basis of adaptation to environmental stress:
  Polygenic vs oligogenic response?
  Gene affecting the trait or its plasticity?
II – Theory: Genetic basis of adaptation to stochastic environment

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Selection at QTL

• Covered here:
What are the properties of **selective sweeps in randomly fluctuating environment**, for genes affecting phenotypic trait, possibly with background polygenic variation? How does this depend on pattern of environmental fluctuations (variance, autocorrelation...)?

• Not covered here:
Adaptive maintenance of genetic/phenotypic variance for a trait
Maintenance of polymorphism in models with no explicit phenotype
Distribution of fitness effects in fluctuating environment
...

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2: Dempster (1955), Gillespie (1991),...
3: Connallon & Clark (2015):
Moving optimum model

• Changing environment assumed to cause moving optimum phenotype for an ecologically important trait

• Optimum follows Gaussian autoregressive process, with mean \( \bar{\theta} \), variance \( \sigma_{\theta}^2 \) and autocorrelation \( \rho \) (over 1 generation).

Classic evolutionary assumption\(^1\) ... ... with some empirical support\(^2\)

\[
W(z) = W_{\text{max}} \exp \left( - \frac{(z - \theta_t)^2}{2\omega^2} \right)
\]

1: Reviewed by Kopp & Matuszewski (2014 Evol Appl)
2: Chevin, Visser & Tufto (2015 Evolution)
“Major” QTL and polygenes

• Genetic model\(^1\)
  - **Haploid sexual** population (easily extended to diploid)
  - **Major quantitative trait locus**: Bi-allelic A\( \mid \)a, frequencies \( p \mid q \)
    
    Additive effect \( a \) on mean trait
  - **Polygenic background**: Unlinked variation at many unlinked loci causes normally distributed breeding values in background.
    
    Background mean \( m \) and genetic variance \( G \)

Assume linkage equilibrium, and background variance at equilibrium between stabilizing selection and mutation + recombination.

- Residual component of phenotypic variation with variance \( V_e \).
  
  Total phenotypic variance \( P = G + V_e \)

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\(^1\): modified from Lande (1983 Heredity)
“Major” QTL and polygenes

• Response to selection\(^1\):

Frequency at major gene: \( \Delta p = pq \frac{\partial \ln \bar{W}}{\partial p} \)

Mean phenotype in the background: \( \Delta m = G \frac{\partial \ln \bar{W}}{\partial m} \)

• Mean fitness is mixture of Gaussians

\[
\bar{W} = W_{\text{max}} \sqrt{S \omega^2} \left[ p \exp \left( -\frac{S}{2} (m + a - \theta)^2 \right) + q \exp \left( -\frac{S}{2} (m - \theta)^2 \right) \right]
\]

\( S = \frac{1}{\omega^2 + P} \) is the strength of stabilizing selection

1: modified from Lande (1983 Heredity)
“Major” QTL and polygenes

- Alternative description of selection:
  \[
  \frac{p'}{q'} = \frac{p W_A}{q W_a} = \frac{p}{q} \exp \left\{ -\frac{S}{2} [a^2 + 2a(m - \theta)] \right\}
  \]

  \[\rightarrow\text{Genomic fitness epistasis}:\] selection at focal locus depends on background mean phenotype \(m\), which may evolve in time because of all other polymorphic loci.

- Mutation favored if allows approaching optimum, \(0 < a < -2(m - \theta)\) (for \(m \leq \theta\))
  \[\rightarrow\text{Necessarily deleterious when background at optimum} (m = \theta)\]

- In the long run:
  \[
  \frac{p_t}{q_t} = \frac{p_0}{q_0} \exp \left\{ -\frac{S}{2} [a^2 t + 2a \sum_{i=0}^{t-1} (m_i - \theta_i)] \right\}
  \]
  \[\rightarrow\text{Cumulative influence of epistasis depends on summed background mismatch with optimum}\]
Single locus dynamics
(no background genetic variance)

- First assume background $m$ cannot evolve
- Then $\ln(p/q)$ is Gaussian, with mean:
  $$E\left\{\ln\left(\frac{p}{q}\right)\right\} = \ln\left(\frac{p_0}{q_0}\right) - \frac{S}{2}\left[a^2 + 2a (m - \bar{\theta})\right]t = \ln\left(\frac{p_0}{q_0}\right) + E(s)t$$

  ➔ Expected selection coefficient $E(s)$ is constant, and unaffected by environmental fluctuations

- The variance of $\ln(p/q)$ is:
  $$\text{var}\left(\ln\left(\frac{p}{q}\right)\right) = (Sa)^2 \text{var}(\sum_{i=0}^{t} \theta_i) \approx (Sa\sigma_\theta)^2 \left[\frac{1+\rho}{1-\rho} t - 2 \left(\frac{\rho}{1-\rho}\right)^2\right]$$

  ➔ Variance increases close to linearly with time, more rapidly with larger environmental autocorrelation
Single locus dynamics
(no background genetic variance)

- Small autocorrelation of optimum ($\rho = 0.1$)

- Large autocorrelation of optimum ($\rho = 0.9$)
Evolving mean background trait

• Selection gradient on mean phenotype:
\[ \beta = \frac{\partial \ln \bar{W}}{\partial m} = -S(m + p' a - \theta) \rightarrow \text{mismatch of overall mean trait} \]

Dynamics of mean background \( m \) and frequency \( p \) at major locus are coupled.

• In constant environment:
  One **unstable polymorphic equilibrium**:
  \[ p = \frac{1}{2}, \quad m = \theta - \frac{a}{2} \]

  Two **stable monomorphic equilibria**:
  \[ p = 0, \quad m = \theta \quad \rightarrow \text{Loss of mutation} \]
  \[ p = 1, \quad m = \theta - a \quad \rightarrow \text{Fixation of mutation} \]
Evolving mean background trait

- Close to unstable equilibrium, a slight change in initial conditions or parameter values affects which stable equilibrium is reached:

\[ m - \theta \]

\[ p_0 = 2 \times 10^{-3} \]

\[ p_0 = 10^{-3} \]

Dynamics of p

Adapted from Lande (1983 Heredity), Chevin & Hospital (2008 Genetics)
Bistability in stochastic environment

• If optimum fluctuates randomly, then higher environmental autocorrelation causes larger $\text{var}(p)$, and more bistable genetic basis of adaptation.

\[ \rho = 0.2 \quad \rho = 0.8 \]

\[ p \quad m - \theta \quad \text{time} \]
Weak effect approximation

- **Weak mutation effect:** \( \beta = -S(m + p'a - \theta) \approx -S(m - \theta) \)

  → Evolution of mean background can be analyzed first, then plugged into dynamics of QTL.

- In a constant environment, approach of mean background to optimum produces geometric decline of selection coefficient at major gene\(^1\)

- This also applies to expected trajectory in fluctuating environment.

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\(^1\) Chevin & Hospital (2008 Genetics)
Weak effect approximation

- **Applied to stochastic component of selection:**
  Neglect influence of frequency fluctuations at QTL on fluctuating selection on mean background trait.

- Stochastic distribution of mismatch $x$ with optimum known from previous theory\(^1\):

$$\text{var}(m + p'a - \theta) \approx \sigma_x^2 = \frac{\sigma_\theta^2}{1 - SG/\ln(\rho)}$$

$\rightarrow$ Smaller mismatch with higher genetic variance and autocorrelation, because better adaptive tracking of optimum

$$\text{Autocorr}(m + p'a - \theta) \approx \rho_x \approx \rho(1 - SG)$$

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1: Lande & Shannon (1996 Evolution); Chevin & Haller (2014 Evolution)
Weak effect approximation

• With background genetic variance, the variance of $\ln(p/q)$ becomes

$$\text{var} \left( \ln \left( \frac{p}{q} \right) \right) = \frac{(Sa\sigma_x)^2}{SG} \frac{1 + \rho_x}{1 - \rho_x} [1 - \exp(-SGt)]$$

• Variance does not increase indefinitely, it plateaus at:

$$\text{var}_{\text{max}} \left( \ln \left( \frac{p}{q} \right) \right) = \frac{(Sa\sigma_\theta)^2}{SG} \frac{1 + \rho_x}{1 - \rho_x}$$

→ Higher background genetic variance $G$ causes:
  - Smaller maximum variance of allelic frequencies
  - Faster approach to this maximum variance.

1: Lande & Shannon (1996 Evolution); Chevin & Haller (2014 Evolution)
Background variance buffers fluctuations at major gene

- Small autocorrelation of optimum ($\rho = 0.1$)

- Large autocorrelation of optimum ($\rho = 0.9$)
Background variance buffers fluctuations at major gene

- Small genetic variance \((G = 0.1)\)

- Large genetic variance \((G = 1)\)
Plasticity QTL
QTL for phenotypic plasticity

• Allelic effect with environment-dependent component: $a + b \varepsilon_d$
  Slope $b$ quantifies effect on phenotypic plasticity.

• Environment of development $\varepsilon_d$ partially predicts environment of selection $\varepsilon_s$ affecting optimum: $\theta = B\varepsilon_s$ (with $E(\theta) = E(\varepsilon_d) = E(\varepsilon_s) = 0$)
  Regression of $\varepsilon_s$ on $\varepsilon_d$ has slope $\kappa = \text{predictability of selection}$

• Focus on stationary fluctuations, no major shift in optimum.
  $\Rightarrow$ Plasticity only selected through its influence on the stochastic variance of phenotypic mismatch.
Pure plasticity gene
- No background variation -

• Assume mutation at QTL has no net phenotypic effect when averaged across environments: $a = 0, b \neq 0$.
Also no background genetic variance for the trait.

• **Expected frequency change:**

$$E \left\{ \ln \left( \frac{p'q}{q'p} \right) \right\} = -\frac{S\sigma^2_\varepsilon}{2} b(b - 2B\kappa)$$

The expected selection coefficient depends on **predictability** $\kappa$ between development and selection

$\rightarrow$ Plasticity with slope $0 \leq b \leq 2B\kappa$ is favored.
Selection is maximal for $b = \tilde{b} = B\kappa$.

• Autocorrelation $\rho$ of environment across generations has no effect *per se* on mean selection coefficient, only predictability of selection $\kappa$ matters
Pure plasticity gene
- No background variation -

- Variance of allelic frequency

\[
\text{var}\left\{ \ln \left( \frac{p'q}{q'p} \right) \right\} = \frac{S^2 b^2 \sigma_\epsilon^4}{4} \left[ 4B^2 (1 + \kappa^2) + 2b(b - 4B\kappa) \right]
\]

- Among values of plasticity that are adaptive on average \((0 \leq b \leq 2B\kappa)\), larger ones cause larger variance of frequency change, even if same effect on expected selection coefficient.
Pure plasticity gene
- No background variation -

- Example with predictability of selection $\kappa = 0.7$

$b = 0.25\bar{b}$ (undershoot)  
$b = \bar{b}$  
$b = 1.75\bar{b}$ (overshoot)

Same expected trajectory, different stochastic variances
Pure plasticity gene
- WITH background genetic variation -

• Adaptive tracking of the optimum by the mean background phenotype reduces strength of selection on plasticity$^1$:

New optimum plasticity $\tilde{b} \approx B \left( \kappa - \frac{SG}{SG - \ln(\rho)} \right)$

Regression slope of mean background on environment of development

Logit allelic frequency

$$b = \tilde{b}$$

Expected $s$ without background variance

Expected $s$ with background variance

1: Michel, Chevin & Knouft (2014 Evolution)
Tufto (2015 Evolution)
Plasticity gene with pleiotropic effect

• Mutation at QTL biases the phenotype in all environments: \( a \neq 0, b \neq 0 \)
• Expected selection coefficient has an additional term, which is deleterious in stationary environment, as it displaces mean phenotype from average optimum.
• Still spreads if advantage of plasticity overcomes pleiotropic cost, \( c = -\frac{S}{2}a^2 \).

Expected background compensates by evolving away from average optimum.
Ongoing/future extensions

• Evolving plasticity in the background
  → Competition between major and minor genes towards optimal plasticity

• Include genetic drift: additional source of stochasticity

• Contrast to individual-based simulations, notably for genetic variance in autocorrelated env\(^1\)

• More explicit model relating selection to tolerance curves to match our experiment
Summary

**Experiments**
- Models with moving optimum phenotype/environment correctly predict population fluctuations in stochastic environment
- Experimental evolution of transgenerational acclimation, but not tolerance breadth to current environment

**Theory**
- Temporal autocorrelation increases variance of allelic frequency
- Background genetic variance limits fluctuations at focal QTL
- QTL for plasticity can sweep despite pleiotropic cost in average environment.
Thanks!
Realized environmental time series

Autocorrelation

Variance

Mean

Truncation reduces variance in highly correlated environment

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Stochastic population dynamics

- **Individual time series**
  Combination of 3 measurement types allows precise estimates of $N$

\[
\begin{align*}
\text{Strain C, } & \rho = 0.9 \\
\text{Strain B, } & \rho = 0 \\
\text{Strain A, } & \rho = -0.5
\end{align*}
\]
Experimental evolution of trans-generational tolerance curves

- These tolerance curves have evolved in response to our stochastic treatments.
- Little to no effect on tolerance breadth $\sigma$, but effect on interaction $K$ between past and current environment.
Experimental evolution of trans-generational tolerance curves

Slope = 1/K

$\mu_{acc}$

$\sigma_{acc}$

Experimental evolution of trans-generational tolerance curves
Plasticity, evolution and demography

- Phenotypic plasticity of traits under selection underlies environmental tolerance\(^1\)

- Fluctuating environments alter plastic responses, phenotype-fitness relationship (selection), and rates of evolution

- This largely drives populations dynamic fluctuations in a randomly changing environment

Lande (2014 JEB)
Weak effect approximation

- **Weak mutation effect:** \[ \beta = -S(m + p'a - \theta) \approx -S(m - \theta) \]
- Relates to curvature of fitness landscape: \[ \frac{\partial \beta}{\partial p} = 0 \iff \frac{\partial^2 \ln \bar{W}}{\partial m \partial p} = 0 \]

Small \(a = -m_0/5\)

Large \(a = -m_0/2\)