Natural Selection in Variable Environments

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Snigdhadip Dey, Thiago Guzella, Stephen Proulx (UCSB)
NS in Variable Environments

- Temporal versus spatial variation
- Within- versus between-generation variation
- Continuous versus discrete variation
- Rates of environmental change versus environmental fluctuations

- Environmental dimensionality (information, cue reliability)

- Evolution by mutation accumulation
- Evolution from pre-existing genetic diversity
- Evolution from standing genetic variation
Caenorhabditis elegans

- bacteriofagous androdioecious nematode (ancestral dioecy)
- hermaphrodites can only mate with males: analogous to pollen discounting in angiosperms
- protandrous hermaphrodites (spermatogenesis is followed by oogenesis): self-sperm limited
- sex determination is chromosomal (X0 males; XX hermaphrodites)
- predominant selfing in ephemeral environments (boom and burst dynamics)
- 100 Mb genome size; 1 SNP/kb; recent "whole-genome" sweeps and background selection
C. elegans Experimental Evolution

- ancestor population with standing genetic diversity: hybrid from 16 wild isolates
- 4-day discrete non-overlapping generations, constant L1 to adult density of N=10^4
- ancestral and derived populations compared in “common garden” assays

review in Teotónio et al. Genetics (2017)
Domestication to the Lab Environment

Carvalho et al. BMC Evol Biology (2013a,b)
Poulet et al. Evolution (2016)
Domestication to the Lab Environment

• ~350 SNPs across 2 chromosomes, ~200k genotypes across 4 time points
• empty bars: expected binomial sampling; filled bars: observed
• 40% differentiated SNPs, 4% extinction_fixation

Chelo and Teotónio Evolution (2013)
Chelo et al. Heredity (2013)
Domestication to the Lab Environment

- dashed lines: expected Hi under genetic drift (numerical simulations with imposed/observed demography and expected genetic distances between SNPs; no mutation)

Chelo and Teotónio Evolution (2013)
Chelo et al. Heredity (2013)
Domestication to the Lab Environment

\[ \text{diploid viability} = 1 + \alpha \text{Hi}^k \]

Navarro and Barton (2002)

- “ABC” methods on He, Fis, Hi and CV(Hi) support balancing selection during lab domestication
- associative overdominance \[ w = (1-s)^x \times (1-hs)^y \] does not fit the data after 30 generations
Domestication to the Lab Environment

Domestication to the Lab Environment

- additive by additive (polygenic) epistasis,
  without main single locus additive effects

NS in Constant Environments

- head-to-head competitions between two inbred lines derived from the domesticated population
- right plots: not only polymorphism can be maintained, but the prob of extinction may increase

Population genetics and adaptation to changing environments

- population survival and adaptation depend on the order of mutation accumulation and time to “explore” the fitness landscape

see also Gorter et al. AmNat (2015)
Evolution From Pre-Existing Diversity: Fitness Reaction Norms

- genetic drift might lead to the loss of the best genotypes in the most extreme environment under slower environmental change

- adaptation can also be compromised the slower the environmental change because similarly fit genotypes can be maintained for longer
Experimental Evolution Design

- ancestor population with standing genetic diversity (lab adapted population)
- reproduction exclusively by selfing (genetically-modified to kill males)
- dashed vertical lines indicate sample points for individual genotyping
Experimental Population Genetic Dynamics

Guzella et al. (submitted)
Inference Model for Lineage ID and Frequency

Guzella et al. (submitted)
Expected Population Genetic Dynamics

Similar dynamics with linear and quadratic fitness reaction norms

Guzella et al. (submitted)
Identifying the two adaptive lineages

Noble et al. bioRxiv/Genetics (2017)
Expected Fitness Reaction Norms
Expected and Observed Fitness Reaction Norms

A. Graph showing the relationship between NaCl concentration (mM) and absolute fitness (log J).

B. Graph showing the relationship between NaCl concentration (mM) and absolute fitness (log J) for different lineages.

C. Graph showing the selection (S = log(J/J0)/log(P)/log(P)) for different NaCl concentrations.

D. Graph showing the selection (S = log(J/J0)/log(P)/log(P)) for different NaCl concentrations, with box plots indicating variability.
A Role for Genetic Drift and/or Maintenance of Polymorphism?
seven gradual populations at G35 revived and high salt evolution repeated
populations pool-genotyped at G35 and after 15 and 30 generations
Founder Effects and Selection Efficiency

Guzella et al. (submitted)
Founder Effects and Selection Efficiency

Guzella et al. (submitted)
• when individuals have information during development about the environment they will face at reproduction, one expects that the evolution of phenotypic plasticity underlies adaptation

• when this information about environmental change can only be provided by the mother then the selection for maternal effects should underlie adaptation
**Maternal Independent Effects**

offspring phenotypes do not depend on maternal environment

Consider two discrete phenotypes in two discrete environments; their geometric mean fitness across all possible environmental regimes can be described by:

\[
\log(\hat{w}_1) = (\alpha \log(c_{1s_{1,1}}) + (1 - \alpha) \log(c_{1s_{2,1}}))
\]

\[
\log(\hat{w}_2) = (\alpha \log(c_{2s_{1,2}}) + (1 - \alpha) \log(c_{2s_{2,2}}))
\]

\(\alpha\) is the frequency of environment 1
\(c\) is the fecundity of phenotype
\(s\) is the survivorship of phenotype

Proulx and Teotónio AmNat (2017)
Maternal Independent Effects

offspring phenotypes do not depend on maternal environment

For example, phenotype 2 is favored when:

$$\log(\hat{w}_2) - \log(\hat{w}_1) > 0$$

$$\rho_{2\rightarrow1} > -\frac{\rho_{2\rightarrow1} (\log(\delta_2) + \log(\zeta))}{\log(\delta_1) + \log(\zeta)}$$

$$\rho_{i\rightarrow j}$$ is the probability that environment changes from $i$ to $j$

$$\delta_i$$ is the relative survival of phenotype 2 in environment $i$

$$\zeta$$ is the relative fecundity of phenotype 2

Proulx and Teotónio AmNat (2017)
Deterministic Maternal Effects

offspring phenotypes depend on maternal environment in a consistent manner

$$\log(\hat{w}_{\text{aDME}}) = \left( (1 - \rho_{1\rightarrow2})\alpha \log(c_{2}s_{1,2}) + \rho_{1\rightarrow2}\alpha \log(c_{2}s_{2,2}) + \ldots \right)$$

$$\log(\hat{w}_{\text{DME}}) - \log(\hat{w}_{\text{MIE}}) > 0$$

$\alpha$ is the frequency of environment 1

$\rho_{i\rightarrow j}$ is the probability that environment changes from $i$ to $j$
Randomizing Maternal Effects

Mothers randomize offspring phenotypes, but the probability of producing a given phenotype does not depend on maternal environment.

\[ \log(\hat{w}_{\text{RME}}) = \alpha \log(\gamma c_{1,s_{1,1}} + (1 - \gamma)c_{2,s_{1,2}}) + ... \]

\[ \log(\hat{w}_{\text{RME}}) - \log(\hat{w}_{\text{MIE}}) > 0 \]

\[ \rho_{i \rightarrow j} \] is the probability that environment changes from \( i \) to \( j \)

\( \gamma \) is the probability of producing phenotype 1

Proulx and Teotónio AmNat (2017)
Deterministic and Randomizing ME Relative Fitness Difference to Maternal Independent Effects

Proulx and Teotónio AmNat (2017)
Selection for Maternal Effects in Fluctuating Environments

Plotted: Fitness difference between maternal effects and maternal independent effects larger than $10^{-3}$

hDME: “hybrid deterministic maternal effects”, when the probability of randomizing offspring phenotypes depends on the maternal environment

Proulx and Teotónio AmNat (2017)
Adaptive Sugar Provisioning Controls Survival of *C. elegans* Embryos in Adverse Environments

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2Basic Science Division
Fred Hutchinson Cancer Research Center
Seattle, WA 98109
USA

embryos are not generally sure to hyperosmotic con
the salt in a way that max
We next tested daf-2(e6)
which carry a hypomorph
insulin-like growth factor
engage in OPC and found
adapt their embryos to s
No embryos from OPC e

Maternal Effects in *C. elegans*

Hermaphrodites challenged with high NaCl concentrations since larval
stages have broods with poor survivorship in anoxia

Dey et al. (not published)
Maternal Effects in *C. elegans*

Adaptive Sugar Provisioning Controls Survival of *C. elegans* Embryos in Adverse Environments

Hermaphrodites trade-off glycerol production necessary for their survival in high salt conditions with glycogen provisioning of their embryos.
Adaptation to High Salt Conditions

Fitness response ($\Delta w_t \pm SE$)

KEGG analysis:
- ↑ reg
- ↓ reg
- no change

Theologidis et al. BMC Biology (2014)
Guzella et al. (not published)
**Ancestral Adaptive State**

Life-cycle and high salt adapted population

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Dey et al. Plos Biology (2016)
Ancestral Adaptive State
life-cycle and high salt adapted population

Dey et al. Plos Biology (2016)
Experimental Evolution in Correlated Environments

- **Predictable**: probability of changing environments of 0.95 across 60 generations
- **Constant**: probability of changing environments of 0.02 across 60 generations
- **Both regimes**: frequency of anoxia generations of 50%
Adaptation to Predictably Alternating Environments

Dey et al. Plos Biology (2016)
Evolution of Deterministic Maternal Effects

Dey et al. Plos Biology (2016)
Adaptation to (Predictably) Constant Environments

Dey et al. Plos Biology (2016)
Adaptation to Constant Environments

Dey et al. Plos Biology (2016)
Evolution in Uncorrelated Environments

Unpredictable: probability of changing environments of 0.45 across 60 generations as in the other regimes: frequency of anoxia generations of 50%
Evolution of Maternal Effects

A

Fecundity response (± SE)

-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5

anoxia
normoxia

Maternal hatching

Hatchability response (± SE)

-0.8
-0.4
0.0
0.4
0.8
1.2
1.6

Maternal

Offspring

anoxia
normoxia
anoxia
normoxia
anoxia
normoxia

Dey et al. Plos Biology (2016)
Expected Evolution of Randomizing Maternal Effects

Ancestral adaptive state

Wright-Fisher numerical simulations under the unpredictable environmental sequences

Dey et al. Plos Biology (2016)
Correlated Environmental Sequences

[Graphs showing autocorrelation and cumulative periodogram for different unpredictable sequences over generations.]
Information and Transgenerational Effects

Unpredictable Reliable: light cue reliably given to mothers during oogenesis whenever their offspring will face anoxia
Grandmothers exposed to anoxia prepare their offspring to perceive the cue in order for them to provision in turn their offspring.

Dey et al. (not published)
Adaptation to Unpredictably Fluctuating Environments?

Growth rate response (± SE)

-0.8  -0.4  0.0  0.4  0.8

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Dey et al. (not published)
Adaptation to Unpredictably Fluctuating Environments?

Growth rate response (± SE)

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**Collaborators:** Christian Braendle (CNRS-Nice), Patrick Phillips (UOregon), Luke Noble and Matt Rockman (NYU), Denis Roze (CNRS-Roscoff), Boris Shraiman (KITP)

**Lab Support:**

Bruno Afonso, Sara Carvalho, Ivo Chelo, Anna Crist, Hervé Gendrot, Christine Goy, Pablo Ibáñez, Sofia Nunes, Veronica Pereira, Ania Pino, Sara Santos

**Funding:**

[Logos of funding institutions]
Epigenetic Inheritance Model

\[ B_i = \begin{bmatrix} 1 & 2 \\ 1 - \beta_{i,1} & \beta_{i,1} \\ \beta_{i,2} & 1 - \beta_{i,2} \end{bmatrix} \]

Matrix determining probability that offspring have phenotype 1 or 2

\[ S_i = \begin{bmatrix} 1 & 2 \\ s_{i,1} & 0 \\ 0 & s_{i,2} \end{bmatrix} \]

Offspring survivorship in environment \( i \)

One generation iteration is:

\[ N_1 = N_0 S_J B_A \]
Long-run growth of population

For constant reproductive factor:  \[ \lambda = \exp \left[ \frac{1}{T} \left( T \log [\lambda_{\text{fixed}}] \right) \right] \]

If per generation multiplier is a random variable then —

\[ \lambda = \exp \left[ \frac{1}{T} \left( \sum_t \log [\lambda_t] \right) \right] = \exp \left[ \sum_i p_i \log [\lambda_i] \right] \]
Long-run growth of population: non-scalar

For constant reproductive factor:

\[ \lambda = \exp \left[ \frac{1}{T} \left( T \log [\lambda_{\text{fixed}}] \right) \right] \]

\[ \lambda = \exp \left[ \frac{1}{T} \left( \log \left[ \begin{bmatrix} n_{1,0} & n_{2,0} \end{bmatrix} (B_{E_1} S_{E_1} B_{E_2} S_{E_2} B_{E_3} \ldots) \cdot (1, 1) \right] \right) \right] \]

For a specific “genotype” that has a pair of B matrices. We can calculate the growth by multiplying together the matrices over time. The lambda that is equivalent to the fixed multiplier is the Lyapunov exponent.