Mechanisms that maintain diversity

Diversity: Species coexistence

Coexistence: Non-linear dynamics * Environmental heterogeneity

(density-dependence) (temporal, spatial)

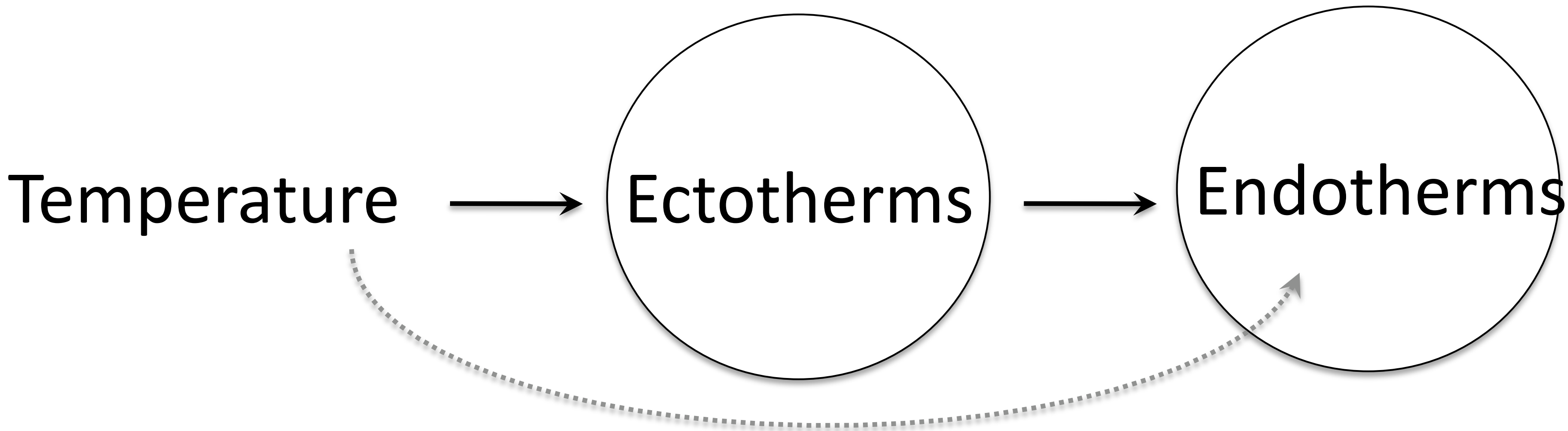
Coexistence via interplay between non-linearity and temporal heterogeneity

Spatial heterogeneity: population/community level responses

Temporal heterogeneity: trait responses ➔ population/ community dynamics

Temporal heterogeneity: biotic or abiotic

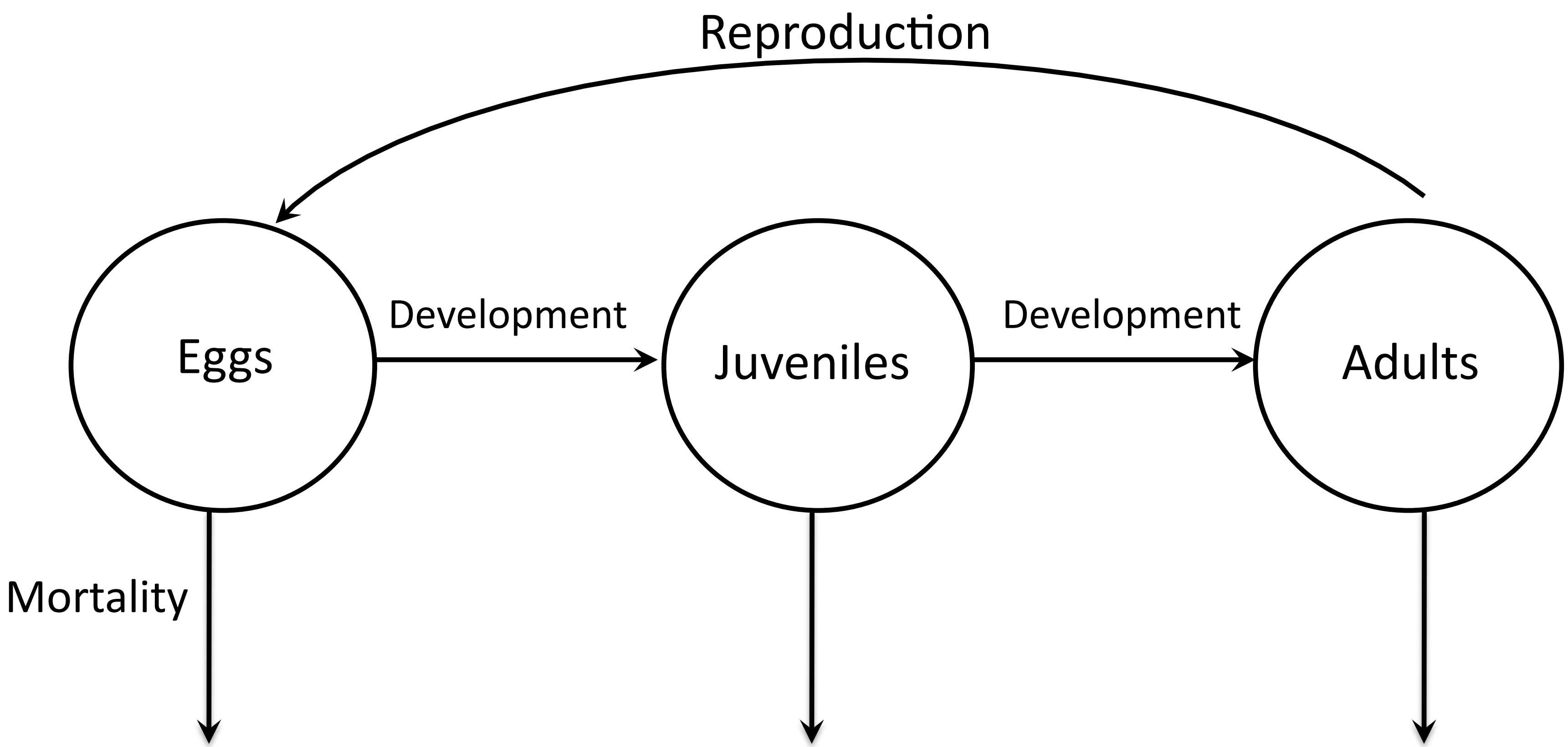
Abiotic environmental variation: **temperature**


Temperature
Ectotherms
Endotherms

1. Temperature affects all life stages of ectotherms

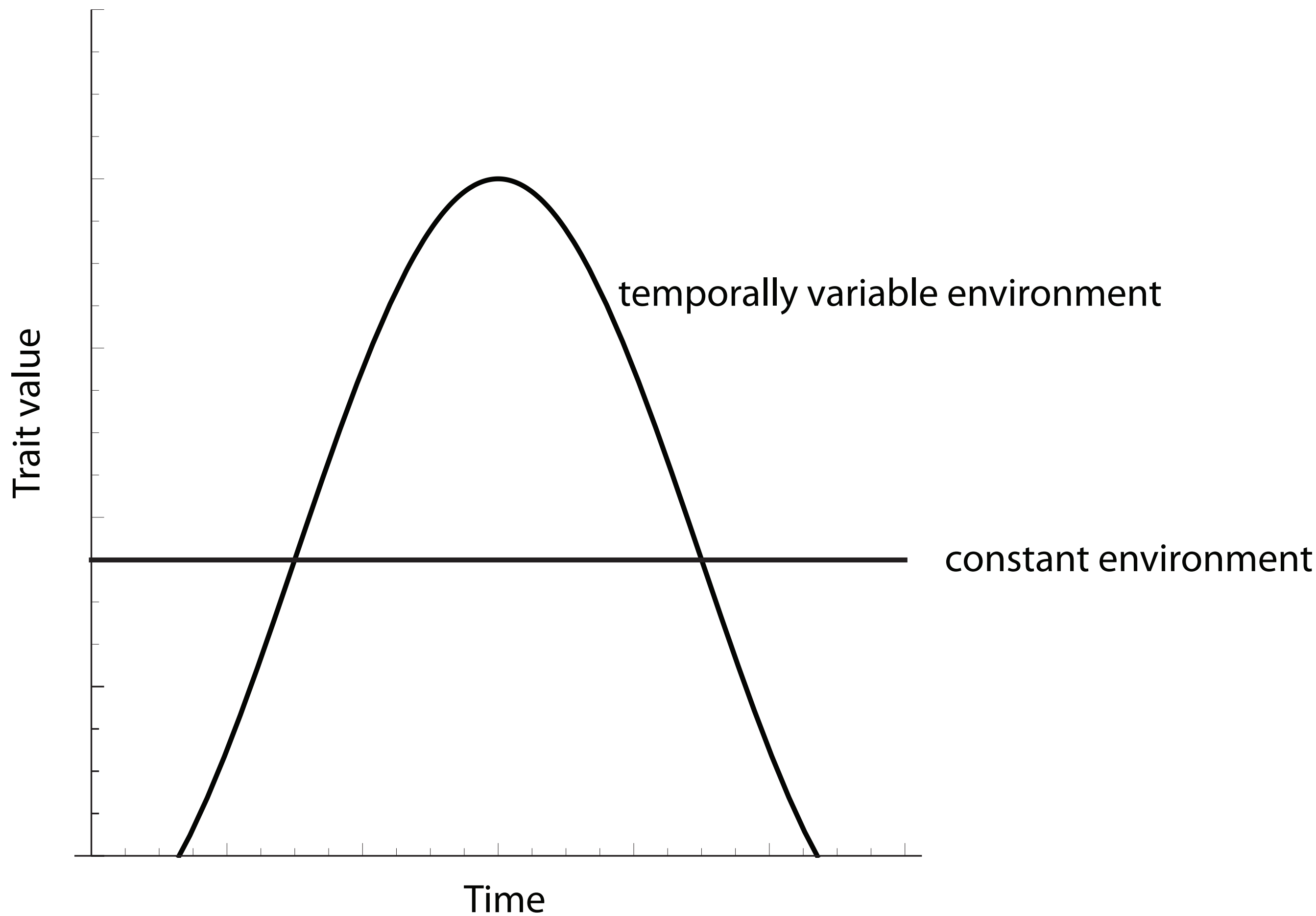
2. Life history and interaction traits temperature dependent

Temperature affects all life stages of ectotherms



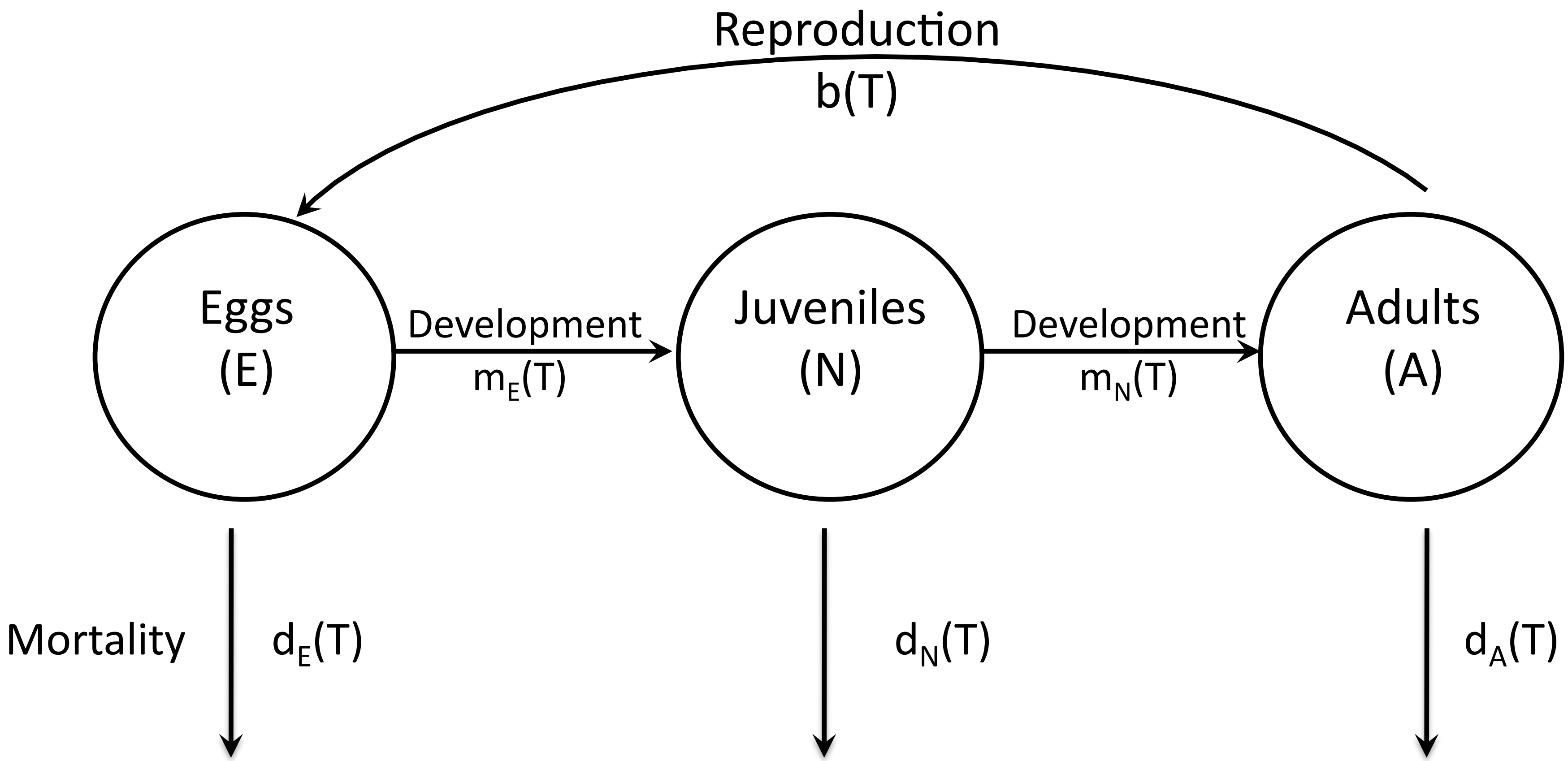
Stage-structured models

Traits are temperature dependent



Jensen's inequality: $f(\overline{T}) \neq \overline{f(T)}$

Temperature effects on population dynamics



Stage-structured population dynamics

Recruitment **Maturation** **Death**

$$\frac{dE}{dt} = \mathbf{b}(\mathbf{T},\mathbf{A})A - m_E(T)E - d_E(T)E$$ Egg

$$\frac{dN}{dt} = m_E(T)E - m_N(T)N - d_N(T)N - \mathbf{q_N}(\mathbf{T},\mathbf{N})N$$ Juvenile

$$\frac{dA}{dt} = m_N(T)N - d_A(T)A - \mathbf{q_A}(\mathbf{T},\mathbf{A})A$$ Adult

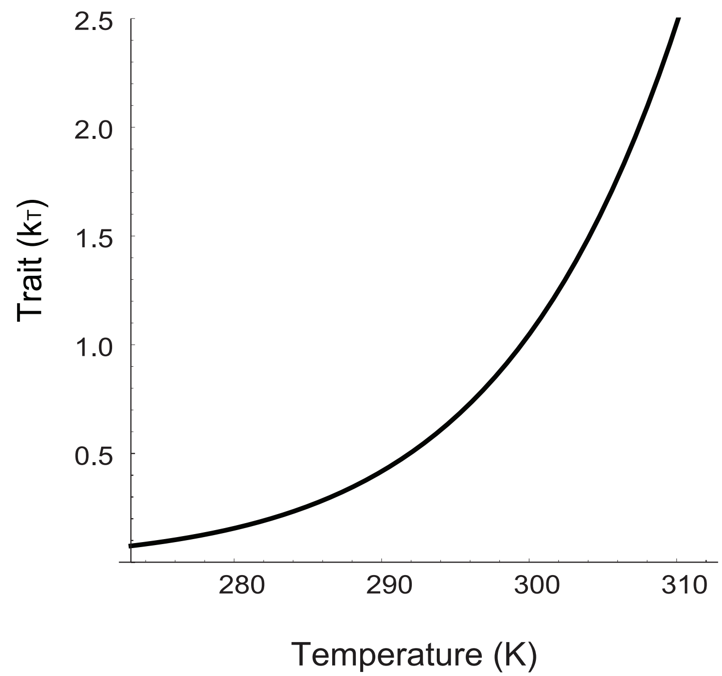
Density-dependence:

- Fecundity
- Juvenile mortality
- Adult mortality

Temperature responses of life history traits

Temperature responses of life history traits

Monotonic



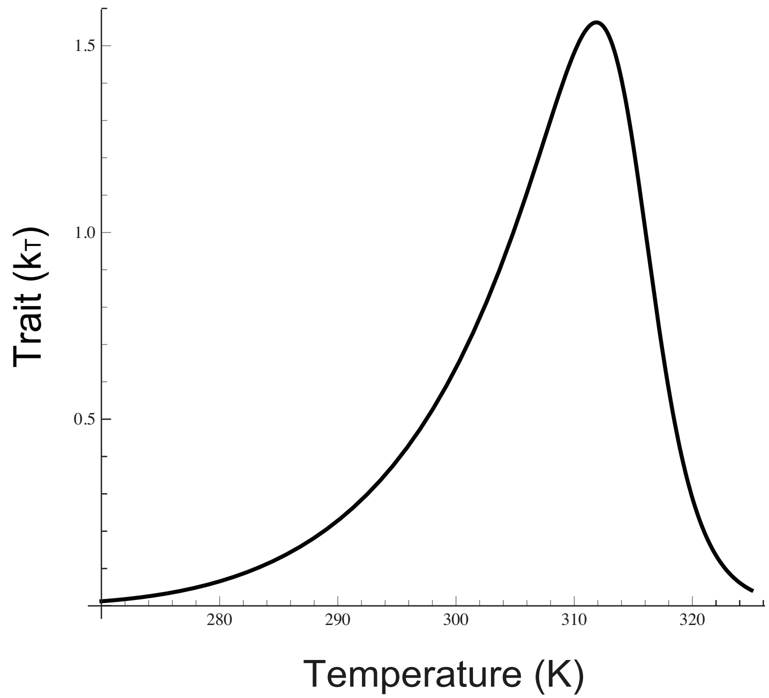
Mortality rate

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

Boltzmann-Arrhenius function

Temperature responses of life history traits

Left-skewed

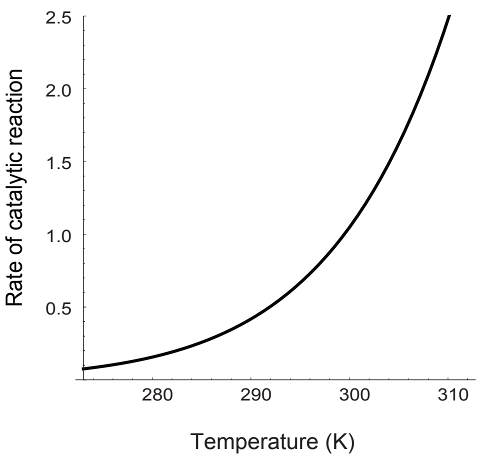


Development

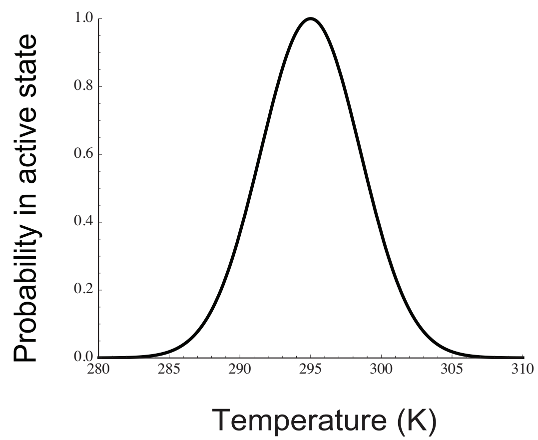
$$k_T = \frac{\frac{k_{T_R} T}{T_R} e^{A\left(\frac{1}{T_R} - \frac{1}{T}\right)}}{1 + e^{A_L\left(\frac{1}{T_{L/2}} - \frac{1}{T}\right)} + e^{A_H\left(\frac{1}{T_{H/2}} - \frac{1}{T}\right)}}$$

Sharpe-Schoolfield equation

Mechanistic basis of the temperature response of development



X



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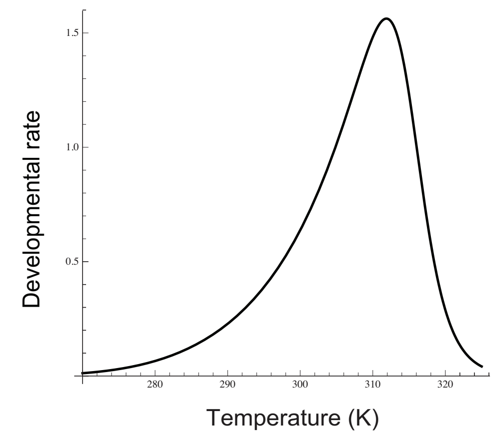


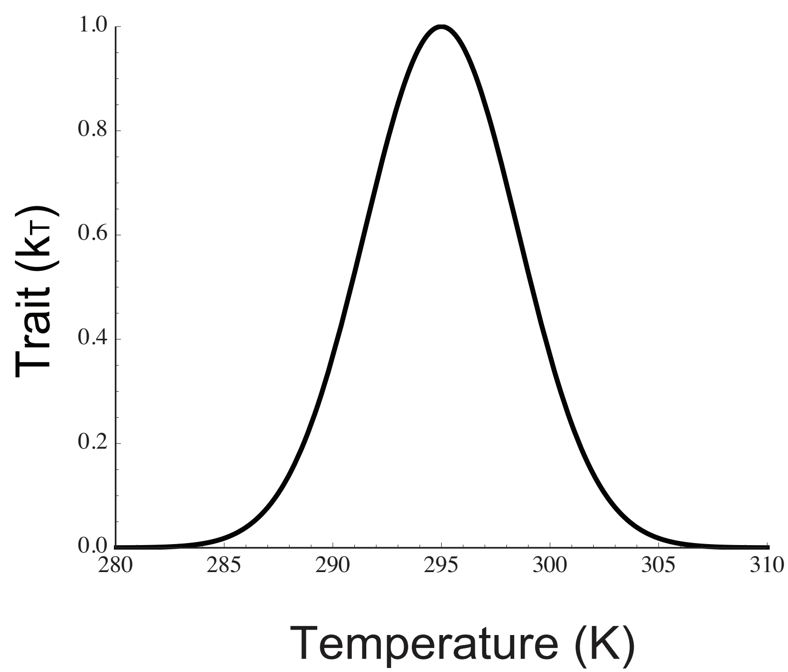
Rate of catalytic reaction

Probability being in active state

Overall Temperature response

Temperature responses of life history traits

Unimodal



Reproductive traits

$$k_T = k_{T_R} e^{-\frac{\left(T - T_{\text{opt}}\right)^2}{2s^2}}$$

Gaussian function

Stage-structured population dynamics

Recruitment **Maturation** **Death**

$$\frac{dE}{dt} = \mathbf{b}(\mathbf{T},\mathbf{A})A - m_E(T)E - d_E(T)E$$

Egg

$$\frac{dN}{dt} = m_E(T)E - m_N(T)N - d_N(T)N - \mathbf{q_N}(\mathbf{T},\mathbf{N})N$$

Juvenile

$$\frac{dA}{dt} = m_N(T)N - d_A(T)A - \mathbf{q_A}(\mathbf{T},\mathbf{A})A$$

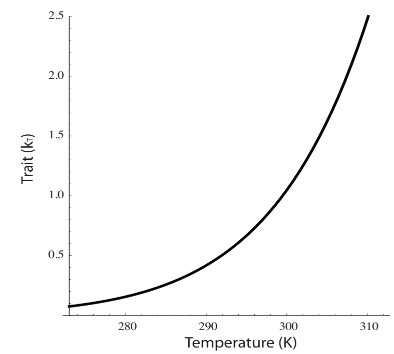
Adult

Density-dependence:

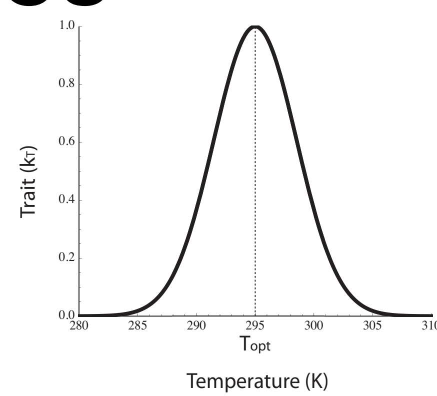
- Fecundity
- Juvenile mortality
- Adult mortality

Temperature response of intra-specific competition

1. Competition increases with temperature



2. Competition strongest at intermediate temperatures



Stage-structured population dynamics

Recruitment **Maturation** **Death**

$$\frac{dE}{dt} = \mathbf{b}(\mathbf{T},\mathbf{A})A - m_E(T)E - d_E(T)E$$

Egg

$$\frac{dN}{dt} = m_E(T)E - m_N(T)N - d_N(T)N - \mathbf{q_N}(\mathbf{T},\mathbf{N})N$$

Juvenile

$$\frac{dA}{dt} = m_N(T)N - d_A(T)A - \mathbf{q_A}(\mathbf{T},\mathbf{A})A$$

Adult

Stage-structured population dynamics

1. Constant temperature

2. Diurnal and/or seasonal variation in temperature

Stage-structured population dynamics

$$\frac{dE}{dt} = \mathbf{b}(\mathbf{T}, \mathbf{A})A - m_E(T)E - d_E(T)E$$

Egg

$$\frac{dN}{dt} = m_E(T)E - m_N(T)N - d_N(T)N - \mathbf{q_N}(\mathbf{T}, \mathbf{N})N$$

Juvenile

$$\frac{dA}{dt} = m_N(T)N - d_A(T)A - \mathbf{q_A}(\mathbf{T}, \mathbf{A})A$$

Adult

Stage-structured dynamics under constant temperatures

Conditions for population to increase from low density when vital rates are temperature-dependent.

Stage-structured dynamics under constant temperatures

Conditions for population to increase when rare: **intrinsic growth rate (r_m) > 0**

r_m = f(birth, **development**, death)

Temperature dependence of intrinsic growth rate

Age-structured population dynamics with temperature dependence of life history traits

Temperature dependence of intrinsic growth rate

$$\int_0^\infty e^{-r_m x}\; l_x b_x \;\mathrm{d}x = 1$$

Euler-Lotka equation

Temperature dependence of intrinsic growth rate

$$r_m(T) = -d(T) + \frac{1}{\alpha(T)} W\left(b(T)\alpha(T)e^{\left(d(T)-\bar{d}(T)\right)\alpha(T)} \right)$$

$b(T)$ temperature response of fecundity

$\bar{d}(T), d(T)$ temperature responses of juvenile and adult mortality

$\alpha(T)$ temperature response of development

(Amarasekare and Savage 2012)

Temperature dependence of r_m in terms of temperature responses of life history traits

Reproduction: Gaussian

Development: exponential

Mortality: exponential

Temperature dependence of intrinsic growth rate

$$r_m(T) \;\; = -d_{T_R} e^{A_d TD} + \frac{1}{\alpha_{T_R} e^{A_\alpha TD}} W\left(\bar{b}_{T_R} \alpha_{T_R} e^{A_\alpha TD - \frac{(T - T_{\mathrm{opt}_{\bar{b}}})^2}{2s^2} + \alpha_{T_R} e^{A_\alpha TD}\left(d_{T_R} e^{A_d TD} - \bar{d}_{T_R} e^{A_{\bar{d}} TD}\right)}\right)$$

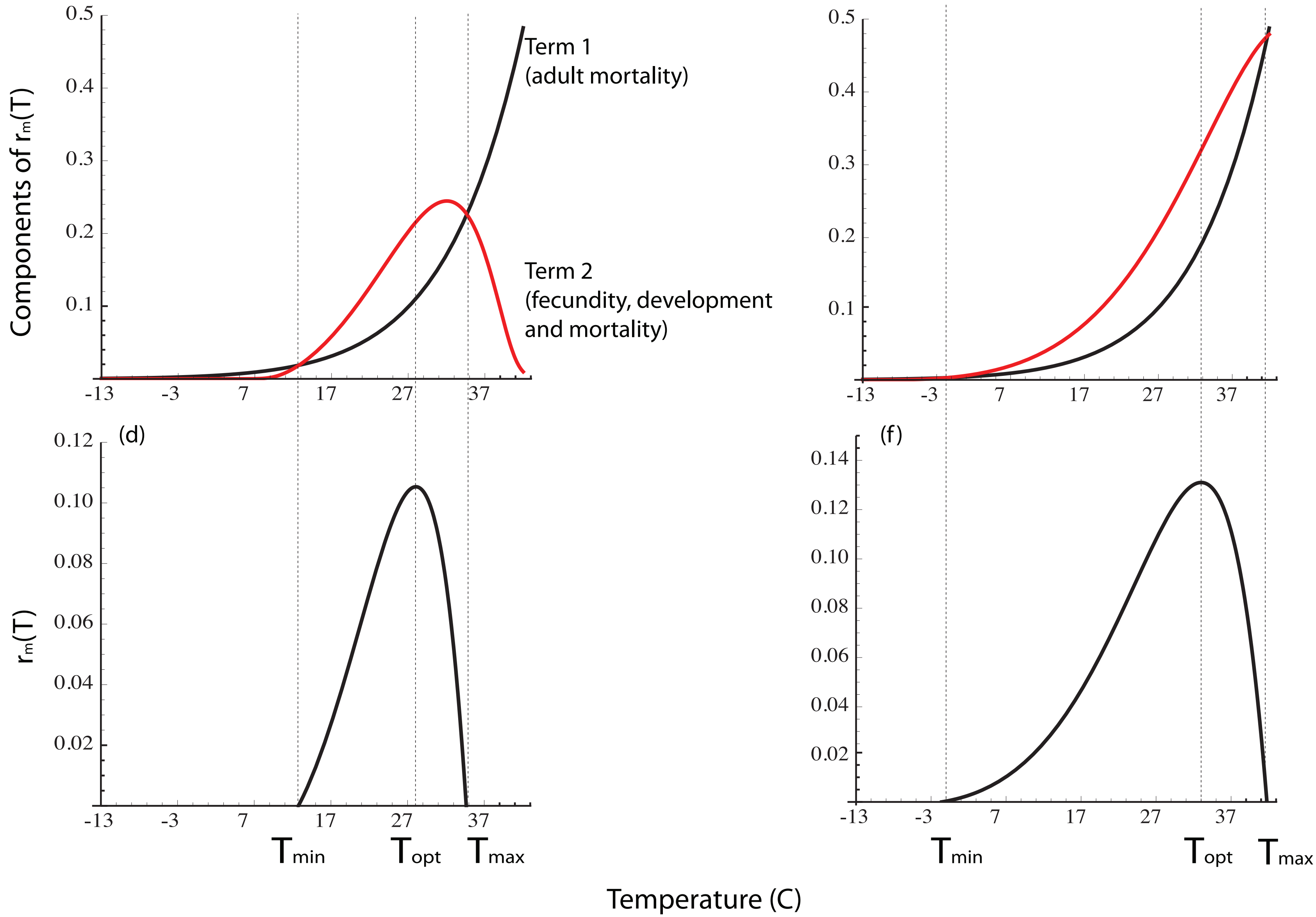
where

W=Lambert W function (product logarithm)

$$TD = \left(\frac{1}{T_R} - \frac{1}{T}\right)$$

(Amarasekare and Savage 2012)

Temperature dependence of r_m



Case studies: Tropical and temperate insects

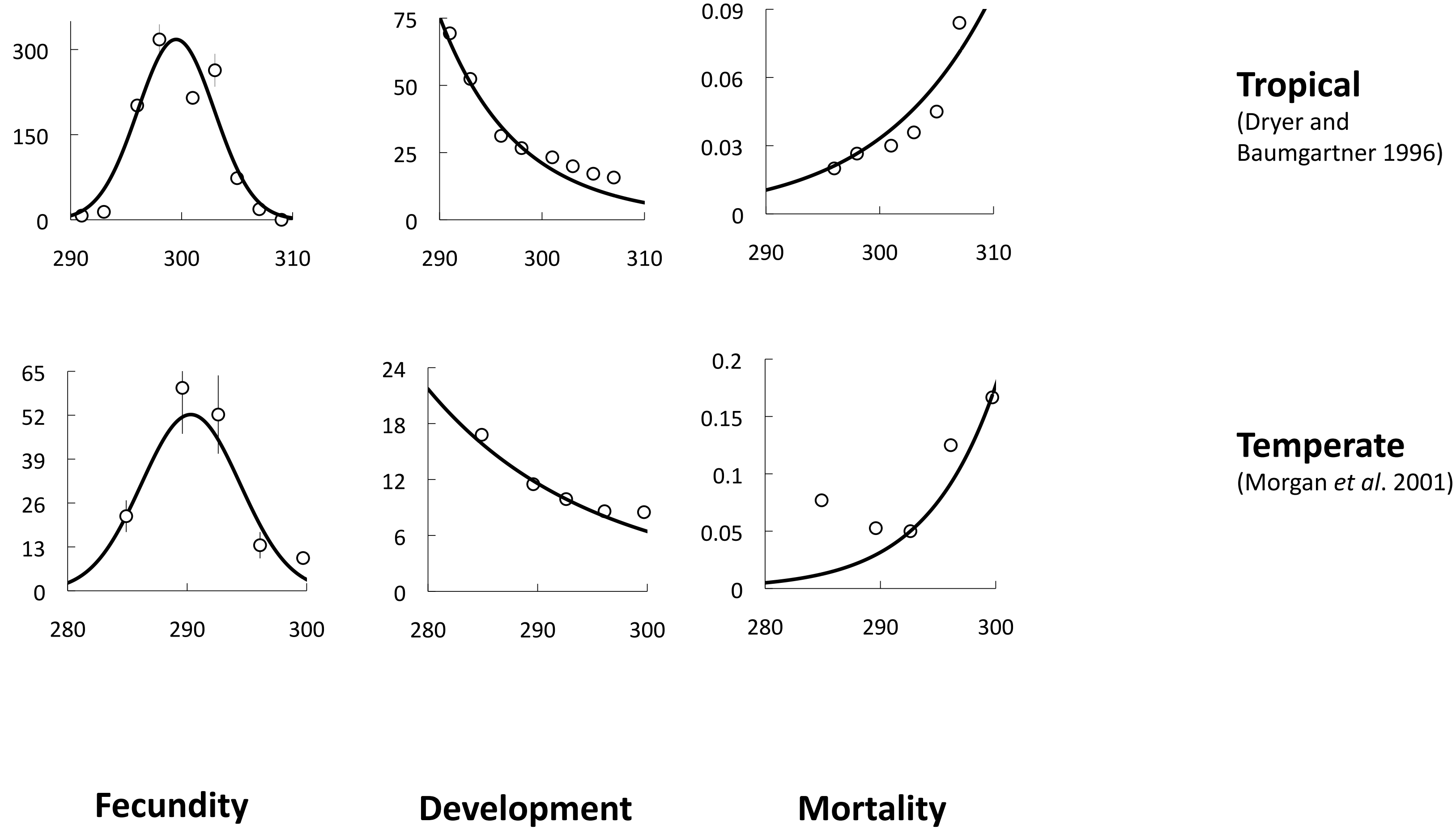
Tropical

Clavigralla shadabi
Benin, Africa
$8^{0}20'$N

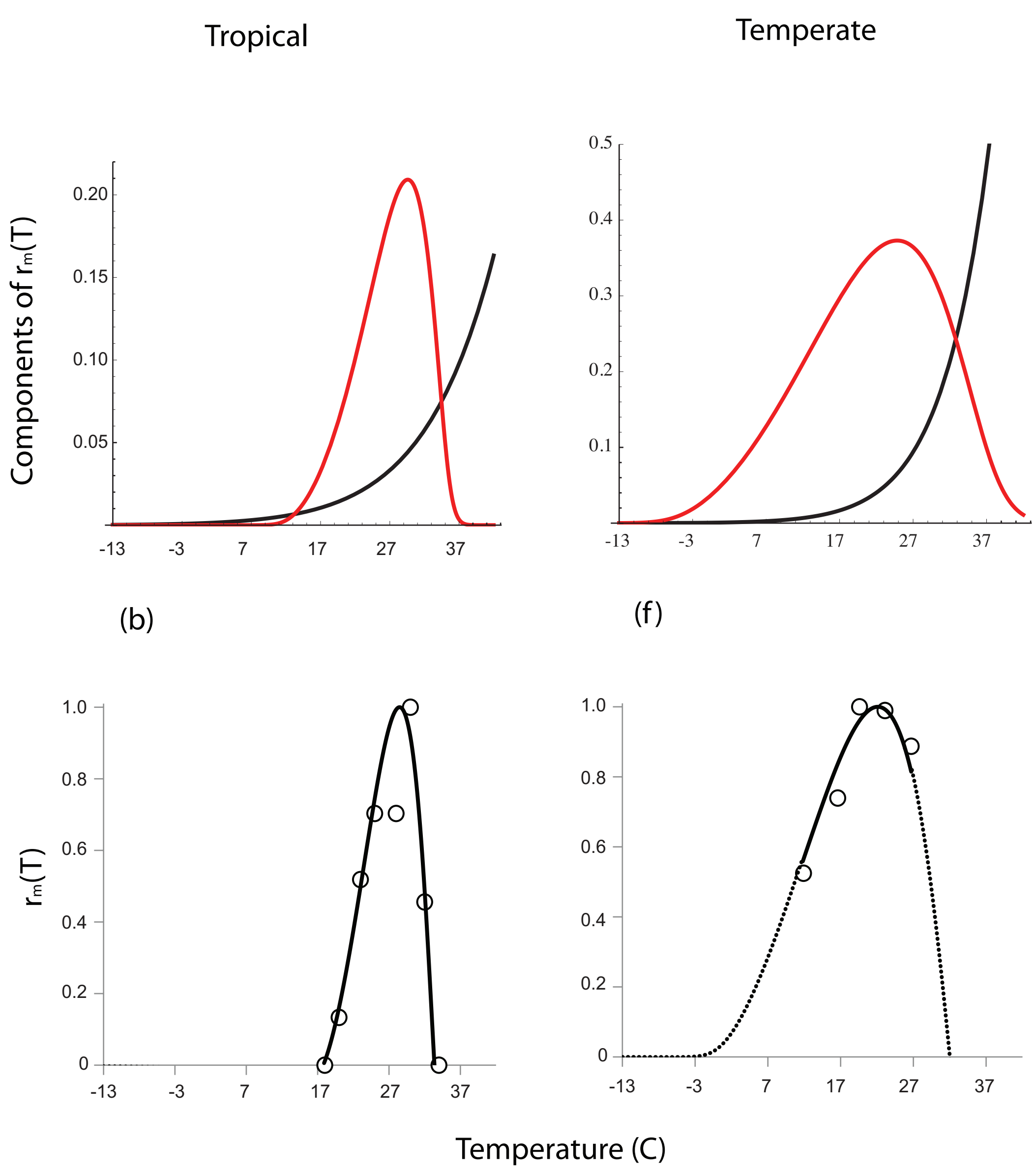
Temperate

Acyrthosiphon pisum York,
England $53^{0}57'$N

Temperature responses of life history traits



Tropical and temperate species



Temperature effects on population persistence

Density-independent population growth

$$\text{Fitness} = r_m(T) \begin{cases} > 0 \Rightarrow \text{Persistence} \\ < 0 \Rightarrow \text{Extinction} \end{cases}$$

$r_m(T)$: $f(b(T), a(T), d(T))$

Temperature effects on population persistence

Temp. responses of life history traits conserved across ectotherm taxa

Predict $r_m(T)$ for any species

$r_m(T)$: metric of extinction risk due to climate warming

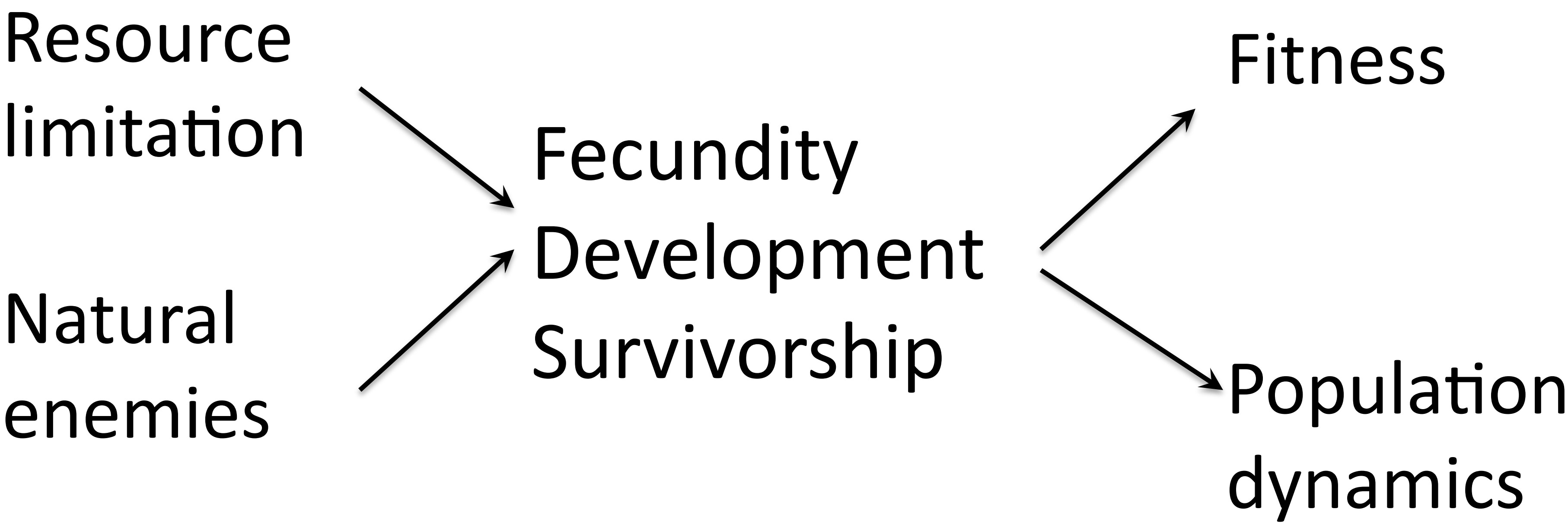
Temperature effects on population persistence

Density-independent population growth

Fitness = r_m $\begin{cases} > 0 \Rightarrow \text{Persistence} \\ < 0 \Rightarrow \text{Extinction} \end{cases}$

Density-dependent population growth (resources, natural enemies)

Fitness = f(density)



Density-dependent factors

Temperature responses of life history traits

Population viability

Stage-structured population dynamics

$$\frac{dE}{dt} = \mathbf{b}(\mathbf{T},\mathbf{A})A - m_E(T)E - d_E(T)E$$

Egg

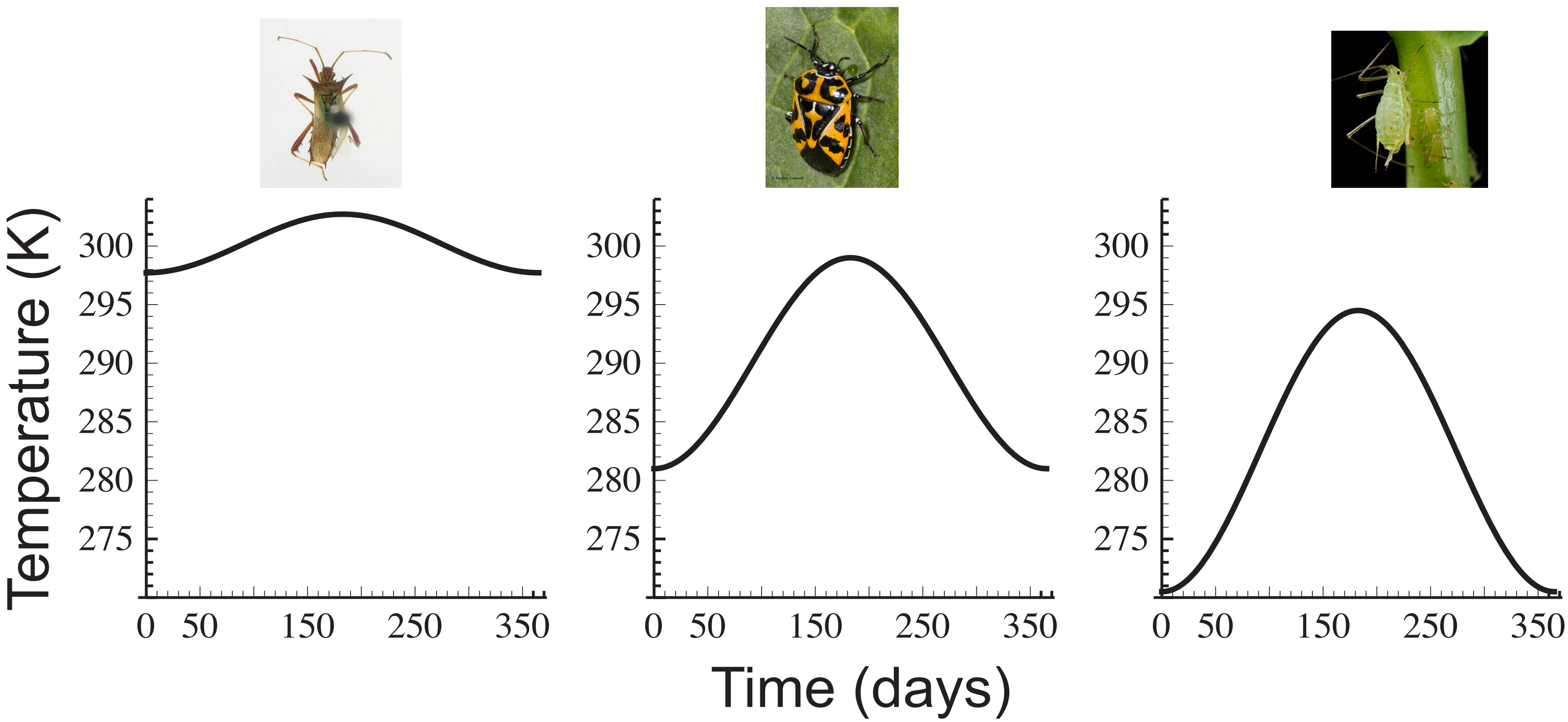
$$\frac{dN}{dt} = m_E(T)E - m_N(T)N - d_N(T)N - \mathbf{q_N}(\mathbf{T},\mathbf{N})N$$

Juvenile

$$\frac{dA}{dt} = m_N(T)N - d_A(T)A - \mathbf{q_A}(\mathbf{T},\mathbf{A})A$$

Adult

Thermal environment: seasonal variation in temperature



Clavigralla shadabi
Benin
$8^0$20’N

Murgantia histrionica
California, USA
$33^0$37’N

Acyrthosiphon pisum
York, England
$53^0$57’N

Incorporating seasonal variation into model

Let T=m(t)

where

T: temperature,

t: time (in days)

m(t): sinusoidal function describing seasonal variation

Incorporating seasonal variation into model

$$T(t) = meanT - amplT \cos\left(\frac{2\pi t}{year}\right)$$

meanT= mean annual temperature,
amplT = amplitude of temperature fluctuations (max-min)
year = 365.25

Stage-structured population dynamics

Recruitment **Maturation** **Death**

$$\frac{dE}{dt} = \mathrm{b}(\mathbf{T})(\mathbf{A})A - m_E(T)E - d_E(T)E$$

Egg

$$\frac{dN}{dt} = m_E(T)E - m_N(T)N - d_N(T)N - \mathbf{q_N}(\mathbf{T})(\mathbf{N})N$$

Juvenile

$$\frac{dA}{dt} = m_N(T)N - d_A(T)A - \mathbf{q_A}(\mathbf{T})(\mathbf{A})A$$

Adult

Case study: Mediterranean species

Harlequin bug
(*Murgantia histronica*)

Well-studied in the field

Temperature responses of traits quantified

Interplay between density-dependence and temperature variation

Case 1. Density-dependence at the earliest life stage (eggs)

Stage-structured population model

$$\frac{dE}{dt} = b(T)Ae^{-q(T)A} - m_E(T)E - d_E(T)E$$ Egg

$$\frac{dN}{dt} = m_E(T)E - m_N(T)N - d_N(T)N$$ Nymph

$$\frac{dA}{dt} = m_N(T)N - d_A(T)A$$ Adult

Temperature –dependent parameters

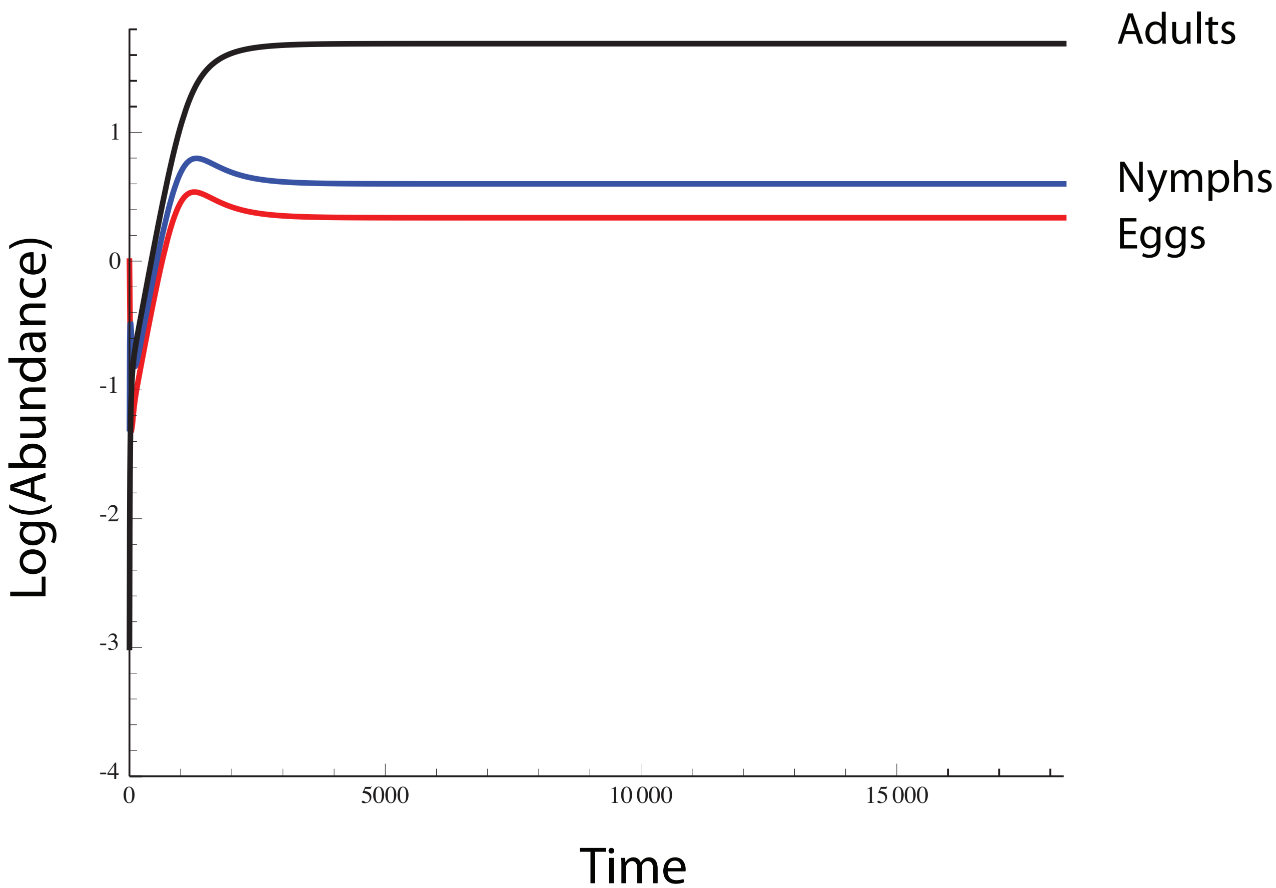
Density-dependent fecundity

Stage-structured population dynamics

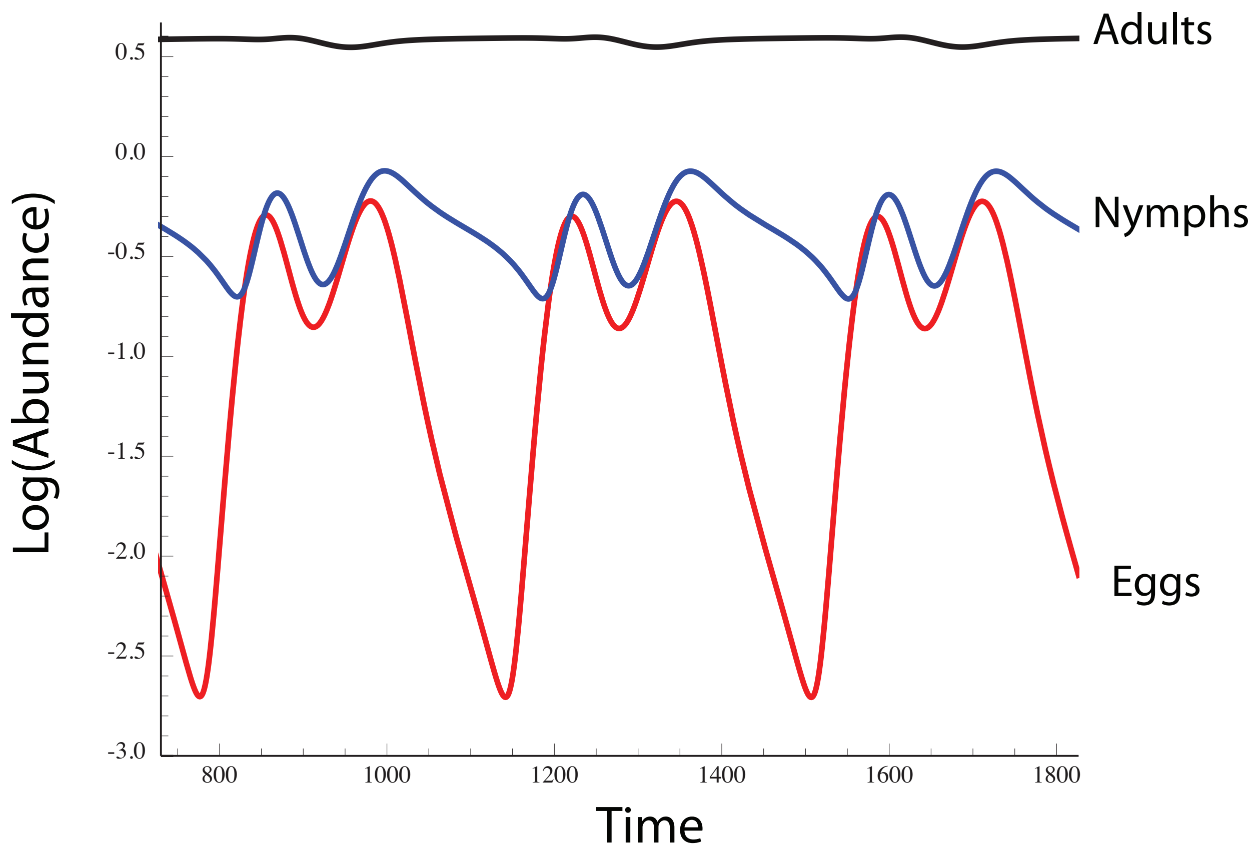
1. Constant temperature

2. Seasonal variation in temperature

Constant environment: density-dependent fecundity

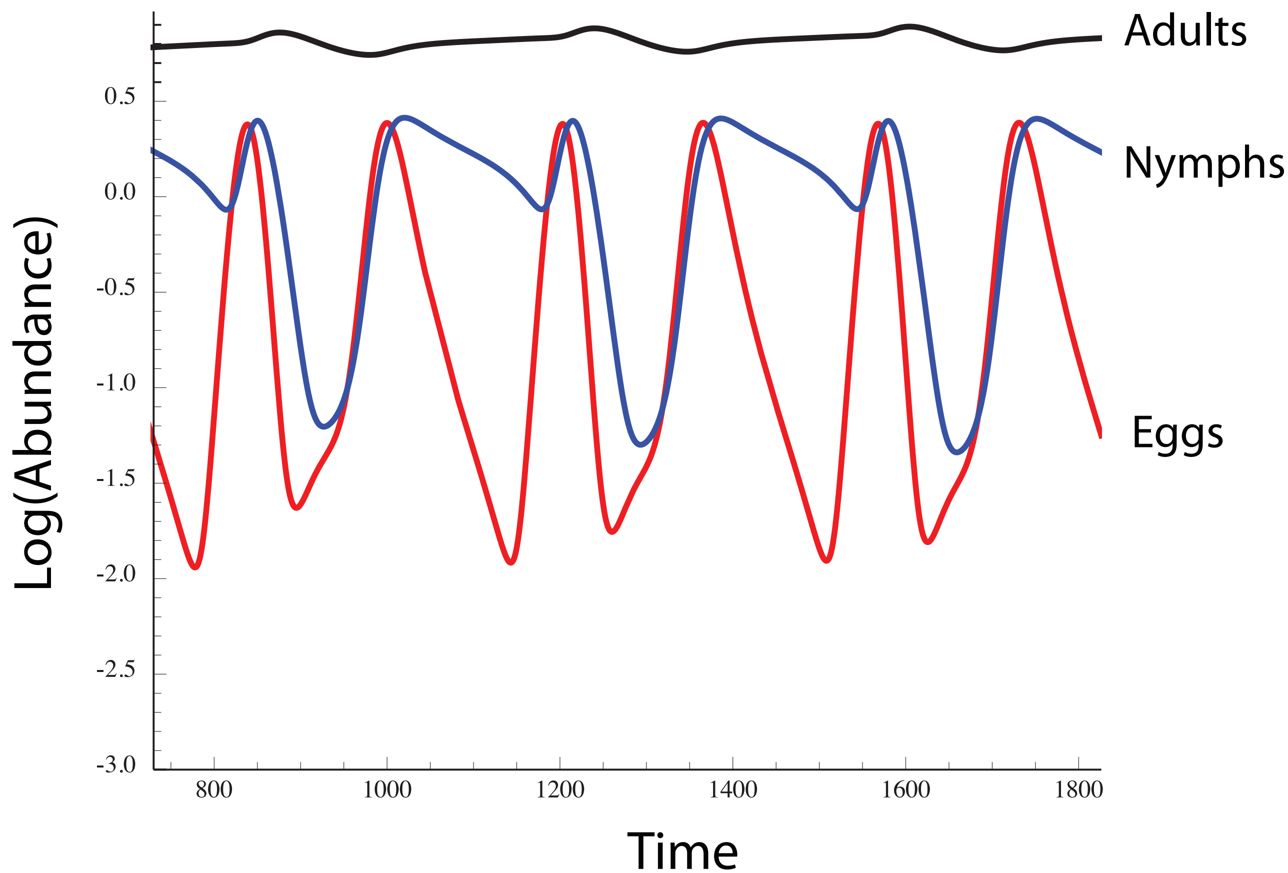


Stage-structured population dynamics in a seasonal environment



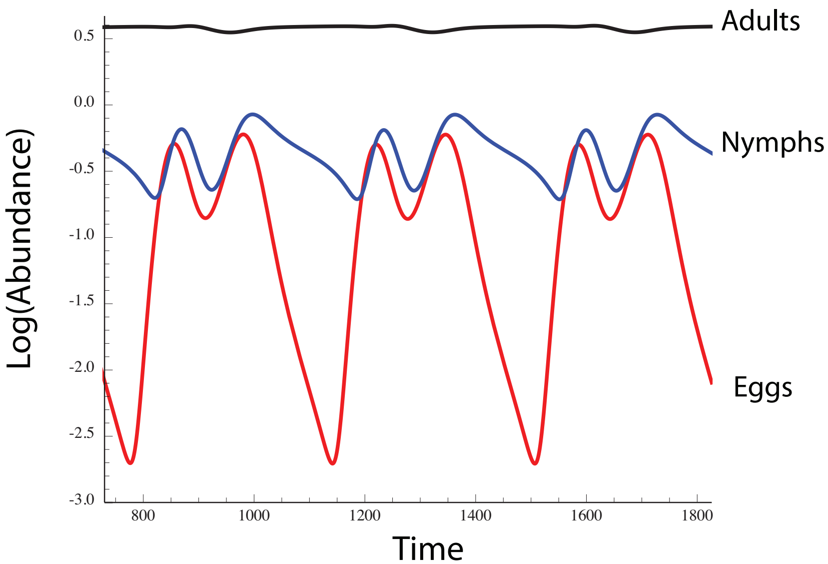
Competition increases with temperature

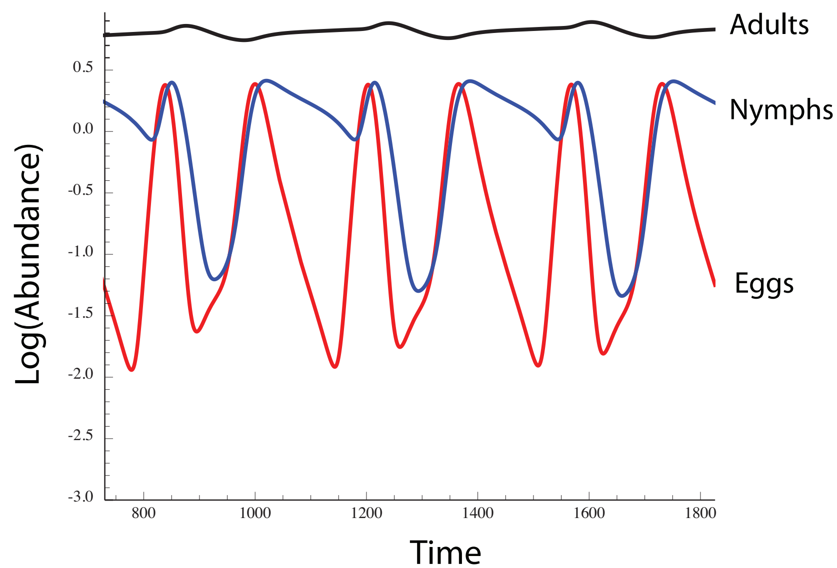
Stage-structured population dynamics in a seasonal environment



Competition strongest at intermediate temperatures

Density-dependence at egg stage





Competition increases with temperature

Competition strongest at intermediate temperatures

Interplay between density-dependent fecundity and temperature variation

Egg stage affected by competition and temperature

Nymphal stage tracks egg stage

Adult stage buffered from temperature variation

Interplay between density-dependence and temperature variation

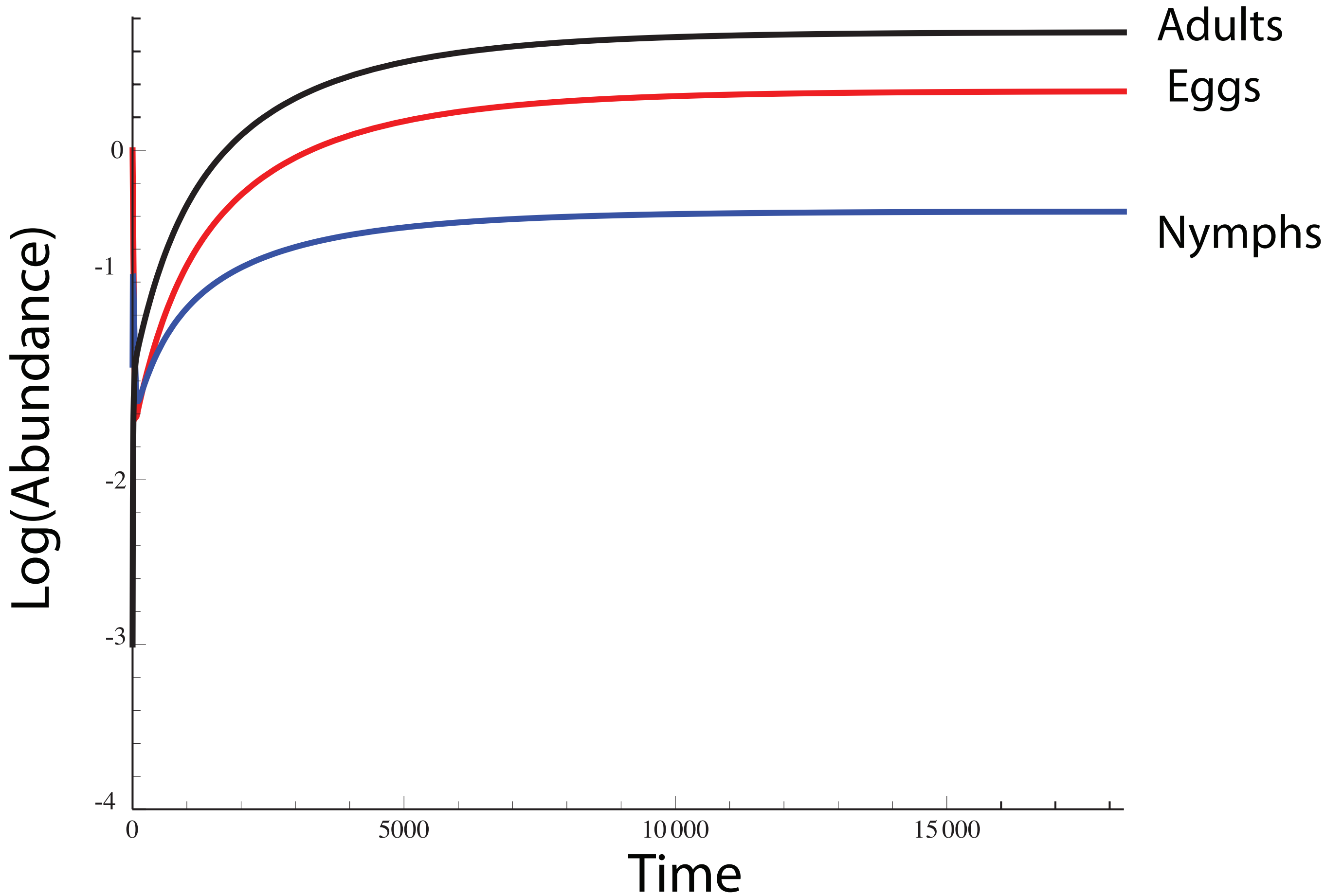
Case 2. Density-dependence at the intermediate life stage (nymphs/larvae)

Stage-structured population model

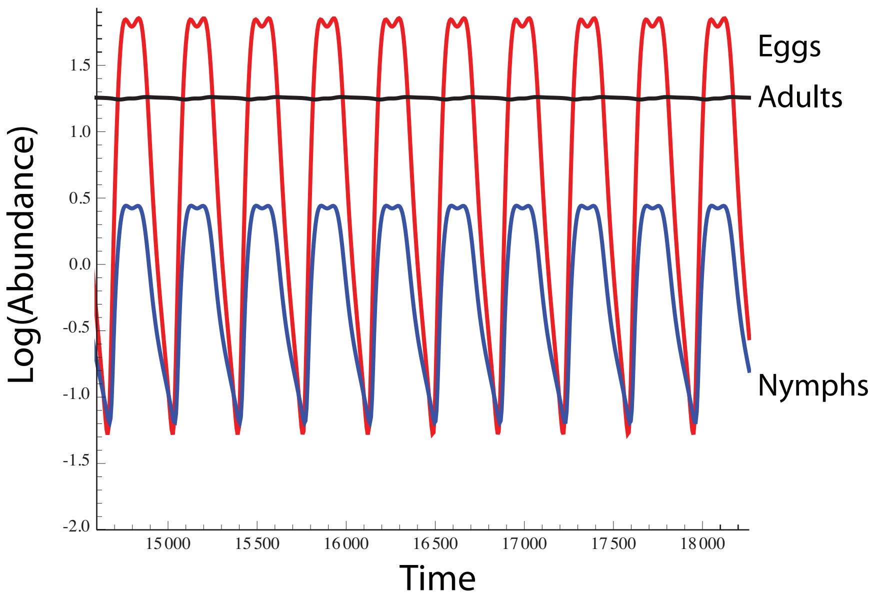
$$\frac{dE}{dt} = b(T)A - m_E(T)E - d_E(T)E$$
$$\frac{dN}{dt} = m_E(T)E - m_N(T)N - d_N(T)N - q(T)N^2$$
$$\frac{dA}{dt} = m_N(T)N - d_A(T)A$$

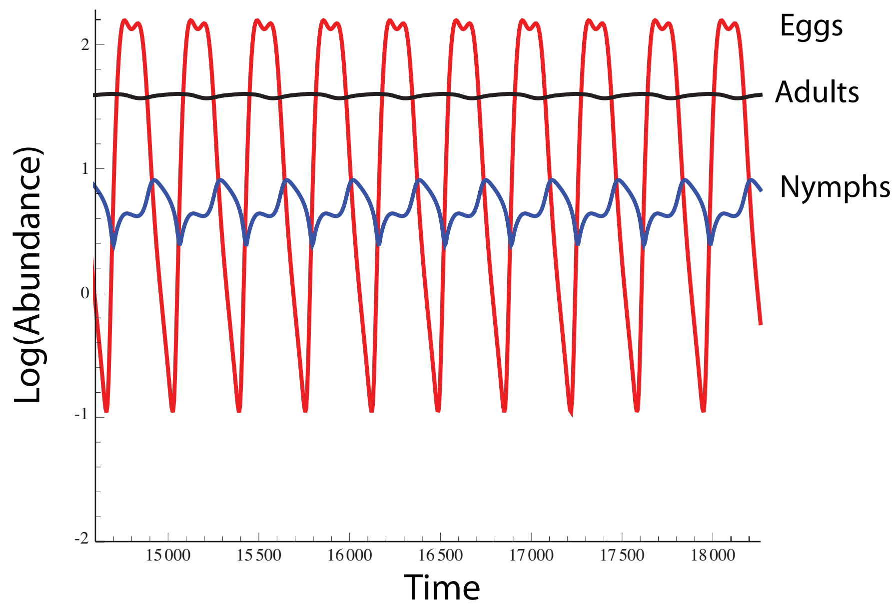
Density-dependent mortality at nymphal stage

Constant environment: density-dependent nymphal mortality



Density-dependence at nymphal stage





Competition increases with temperature

Competition strongest at intermediate temperatures

Interplay between density-dependent nymphal mortality and temperature variation

Egg stage affected by temperature only

Nymphal stage affected by temperature *and* competition

Adult stage buffered from temperature variation

Interplay between density-dependence and temperature variation

Case 3. Density-dependence at the adult stage

Stage-structured population model

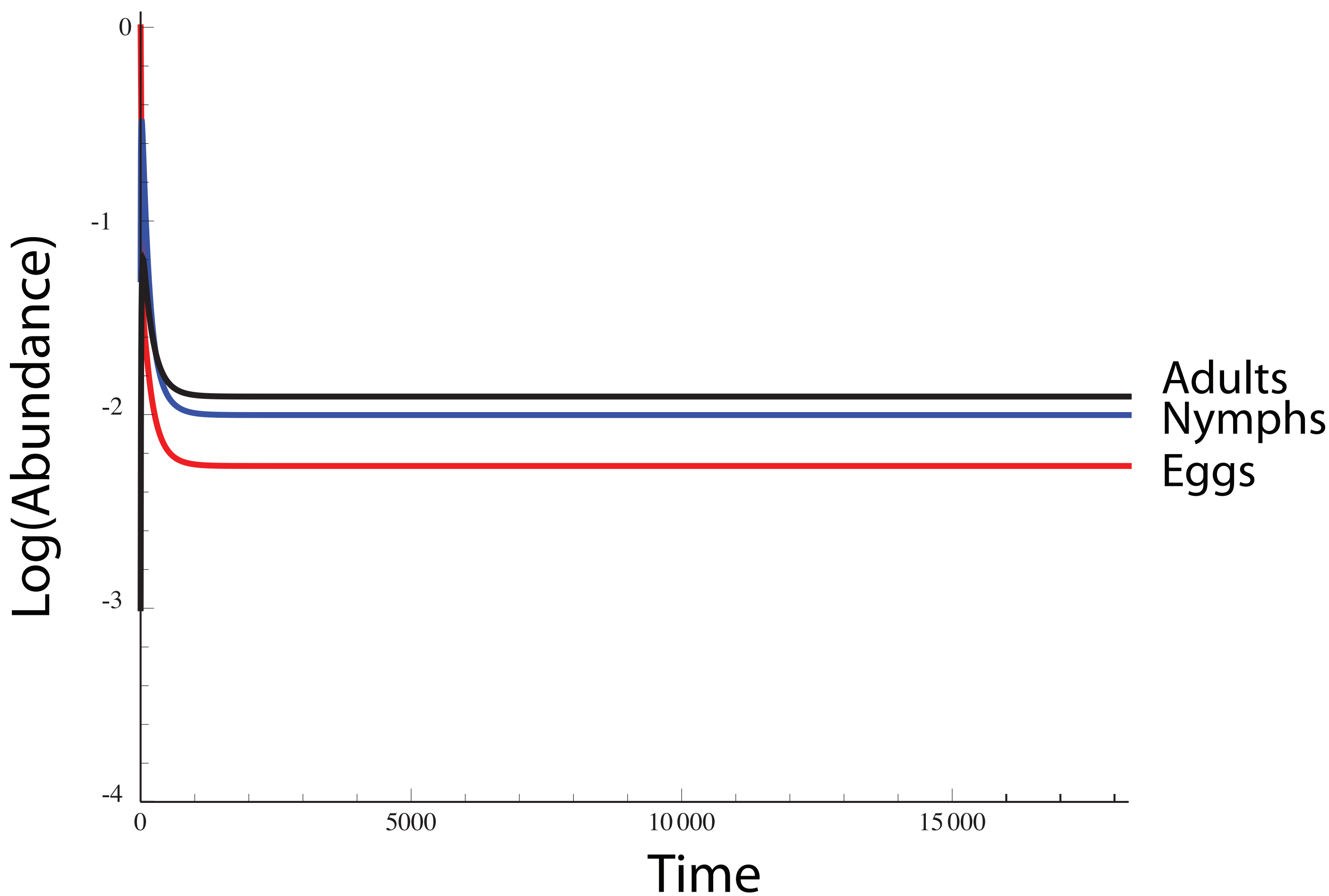
$$\frac{dE}{dt} = b(T)A - m_E(T)E - d_E(T)E$$

$$\frac{dN}{dt} = m_E(T)E - m_N(T)N - d_N(T)N$$

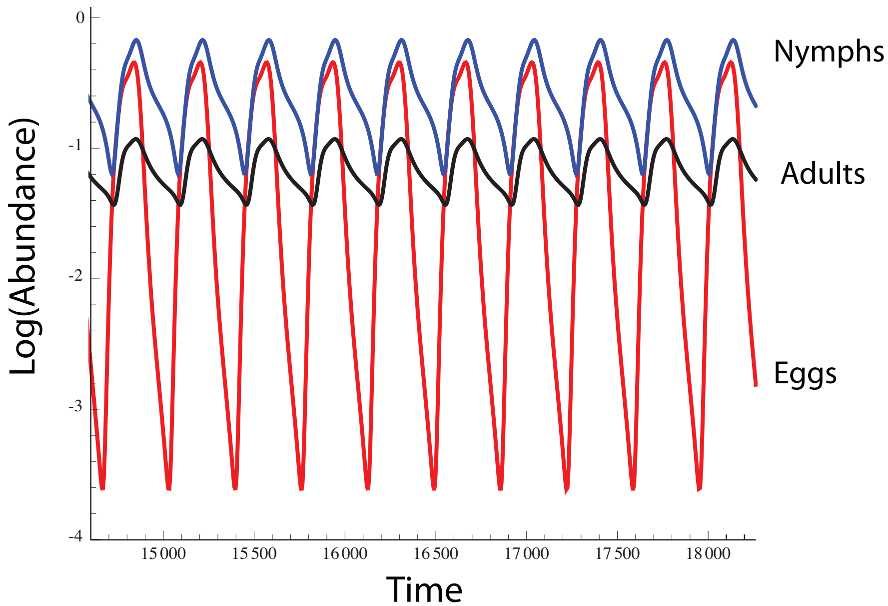
$$\frac{dA}{dt} = m_N(T)N - d_A(T)A - q(T)A^2$$

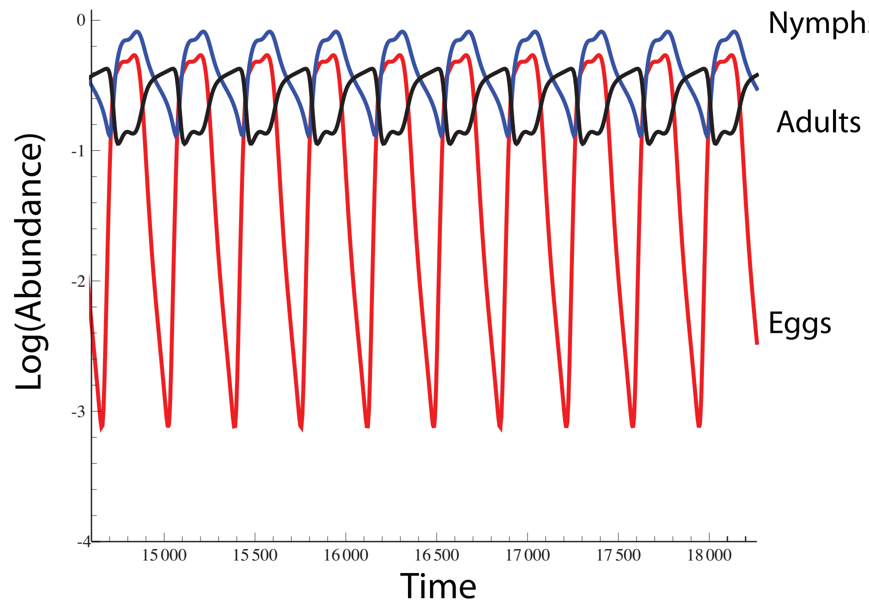
Density-dependent mortality at the adult stage

Constant environment: density-dependent adult mortality



Density-dependence at adult stage





Competition increases with temperature

Competition strongest at intermediate temperatures

Interplay between density-dependent adult mortality and temperature variation

Egg and nymphal stages affected by temperature only

Adult stage affected by temperature *and* competition

Adult stage exhibits fluctuations in abundance

Interplay between density-dependence and temperature variation

Egg stage exhibits the greatest fluctuations in abundance

DD fecundity*temperature variation – more complex dynamics

DD at adult stage – lowest overall abundance