Non-linearity * Variability ⟶ Diversity

Interplay between non-linearity and variability

Spatial ✓

Temporal

Interplay between non-linearity (local dynamics) and temporal variation

Local dynamics

Competition

Consumer-resource interactions (predation, parasitism)

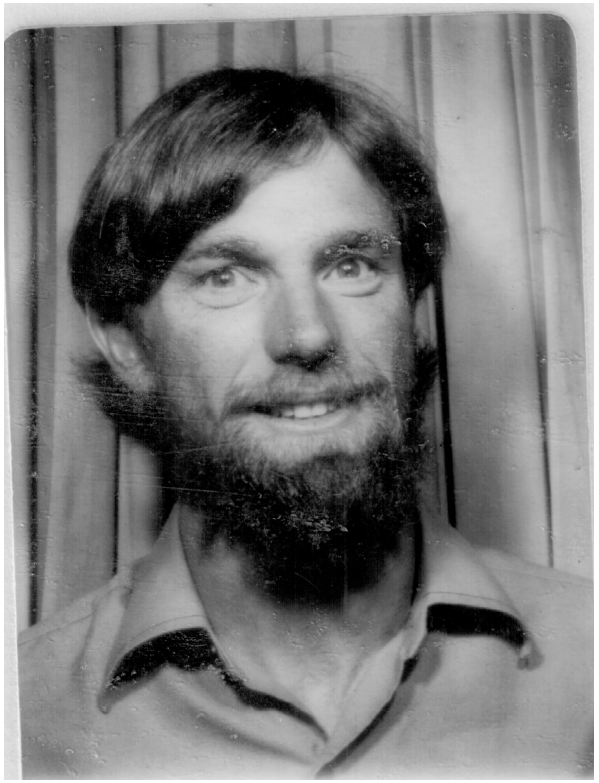
Temporal variation

Abiotic environment

- Temperature variation
- Climate warming

The storage effect

Peter Chesson (1985, 1994, …, 2019)



What does storage mean?

The gain in reproduction during favorable periods is stored in some way (e.g., through adult longevity in species with overlapping generations, or dormant seeds in annual plants) so that the population can survive the losses it suffers during unfavorable periods.

Storage effect

Species experience little or no inter-specific interactions (e.g., competition, predation) when rare, and experience mostly self-limitation (e.g., intra-specific competition) when abundant.

Components of the storage effect

1. Species-specific responses to environmental variation

2. Negative or no correlation between favorability of the environment and strength of inter-specific competition

3. Buffered population growth

1. Species specific responses to environmental variation

Environmental variation mostly abiotic (e.g., temperature, rainfall)

1. Species-specific responses to environmental variation

The environment that maximizes fitness is not the same for all species (e.g., colder vs. warmer periods of the year, serpentine vs. non-serpentine soil)

Species differ in the way they respond to abiotic environmental variation (e.g., temperature, rainfall)

e.g., some do better at warmer temperatures, others do better at cooler temperatures

Species-specific responses ==> **an environment favorable to one species is unfavorable to its competitors**

==>mostly encounter conspecifics

==> strong intra-specific competition and little or no inter-specific competition

Components of the storage effect

1. Species-specific responses to environmental variation ✓

2. Correlation between environmental favorability and strength of competition

3. Buffered population growth

An environment favorable to one species is unfavorable to its competitors

==> little or no inter-specific competition during unfavorable periods for competitor

==> strong intra-specific competition during favorable periods for focal species

2. Correlation between environmental favorability and strength of competition

Negative or zero correlation between favorability of the environment and strength of inter-specific competition

Components of the storage effect

1. Species-specific responses to environmental variation ✓

2. Correlation between environmental favorability and strength of competition ✓

3. Buffered population growth

3. **Buffered population growth**

Species have a mechanism to survive unfavorable environments in space or time (e.g., dormancy, dispersal, high adult longevity)

Components of the storage effect

1. Species-specific responses to environmental variation

2. Zero or Negative correlation between favorability of the environment and strength of inter-specific competition

3. Buffered population growth

Spatial/temporal niche partitioning via the storage effect

Storage effect

A mechanism for temporal niche partitioning framed in terms of species' responses to abiotic environmental variation

A hierarchy of mechanisms

Mechanism for temporal niche partitioning: **Storage effect**

Mechanism of the **Storage effect**:

Interplay between environment variation and competition increases intra-specific interactions relative to inter-specific interactions

Mechanistic basis of the storage effect

Temperature as the axis of abiotic variation

Temperature as the axis of abiotic variation

1. Ubiquitous (diurnal, seasonal)
2. Direct (ectotherms) and indirect (endotherms) effects
3. Perturbations (climate warming)

Challenge

Non-linearities due to density dependence

Non-linearity in species' responses to abiotic (temperature) variation

Interplay between non-linearities

Community level: temporal niche partitioning

Species level: storage effect

Individual level: phenotypic traits

Goal

Predict outcomes of temporal niche partitioning via the storage effect based on how temperature variation affects the underlying life history and consumption traits

Characterizing temperature responses of phenotypic traits

Life history:

Birth, maturation and mortality rates

Consumption:

Attack rate, handling time

Mechanistic basis of trait responses to temperature

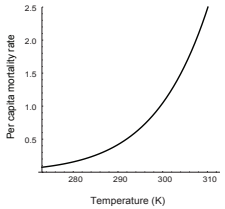
Mechanism at biochemical level

Rate-controlled
(reaction kinetics and enzyme inactivation)

Regulatory
(negative feedback)

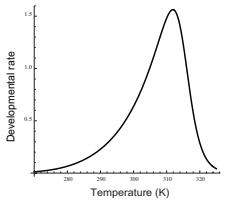
Trait response at phenotypic level

Monotonic



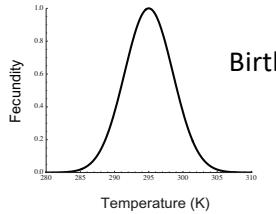
Mortality

Left-skewed



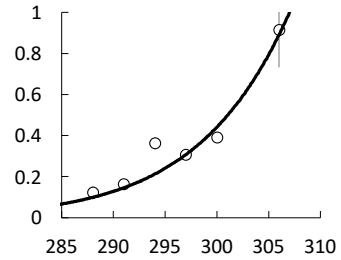
Maturation

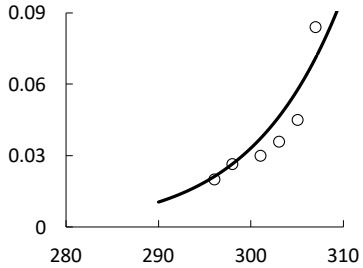
Unimodal, symmetric

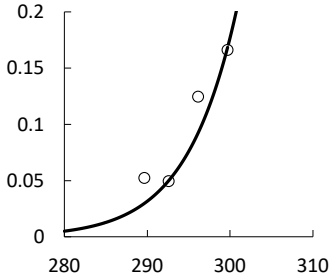


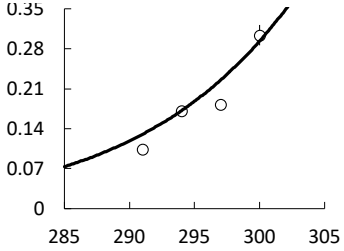
Birth, attack

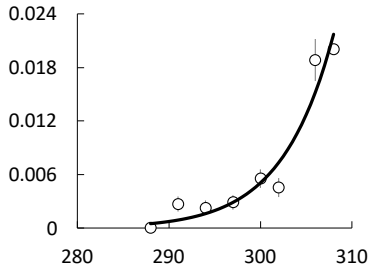
Monotonic temperature responses: mortality

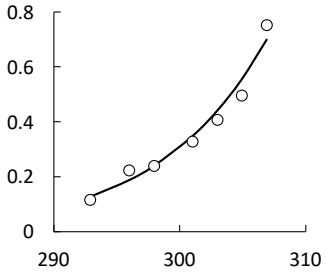




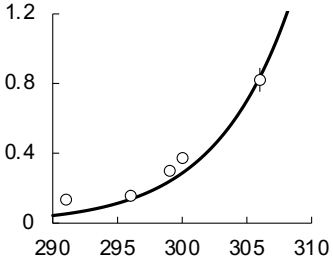




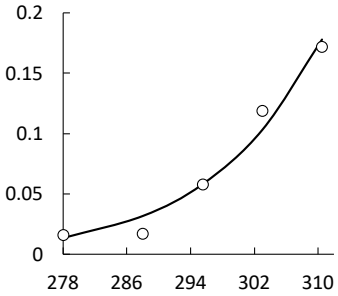




Hemipteran herbivores

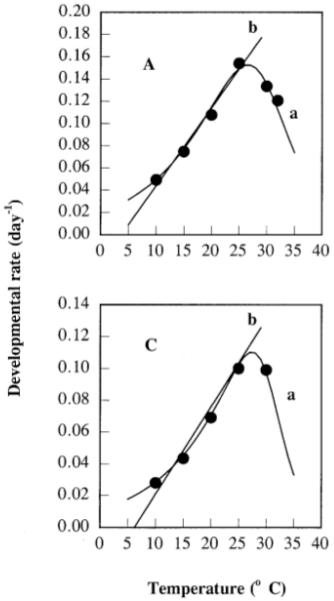


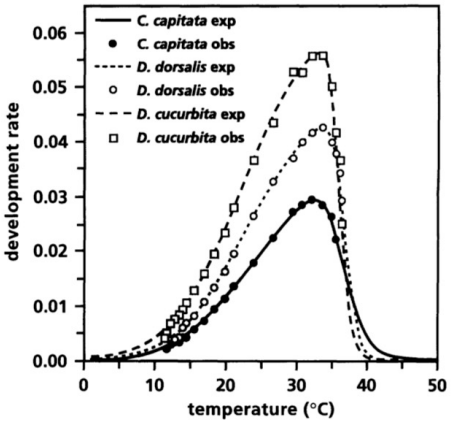
Insect parasitoids



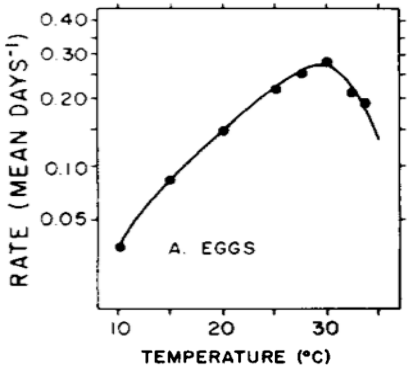
Beetles

Left-skewed temperature responses: maturation

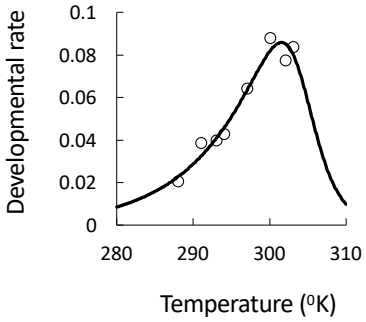


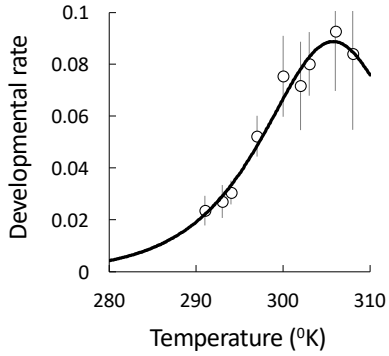


Drosophila species

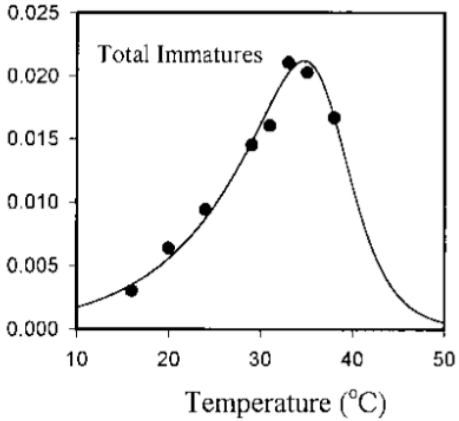


Pine beetle



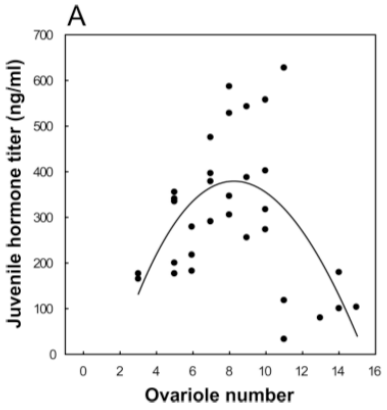


Insect parasitoids

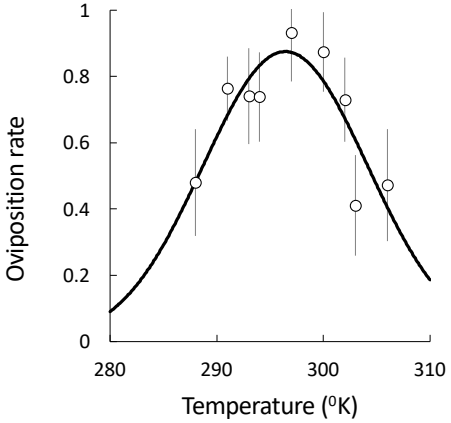


Mite

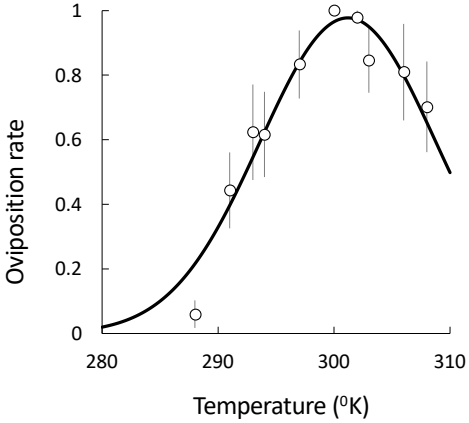
Unimodal temperature responses: reproduction

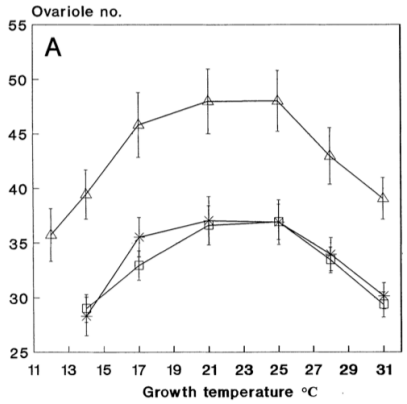


Honeybees

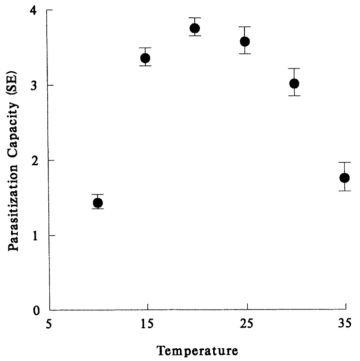


Trissolcus murgantiae

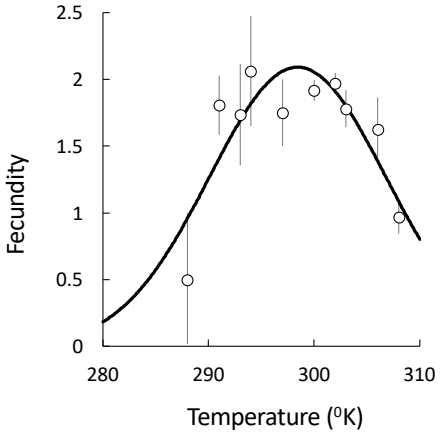




Drosophila species

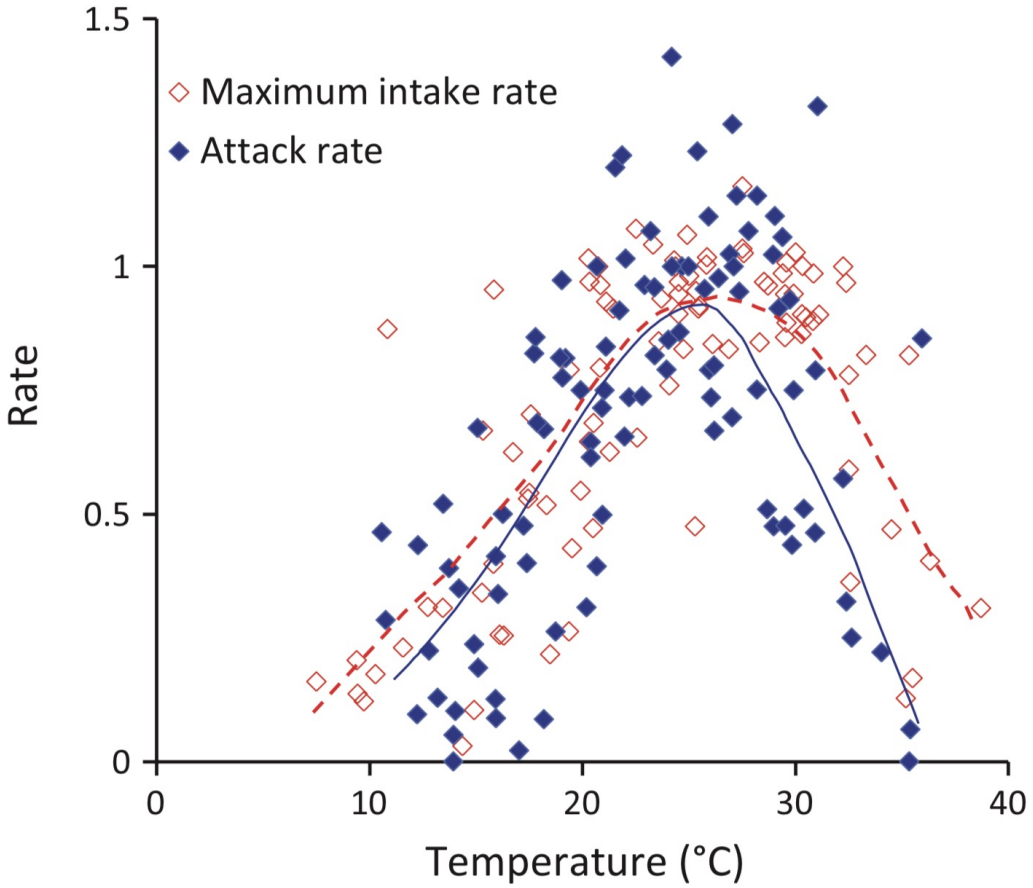


Trichogrammatidae



Ooencyrtus johnsonii

Unimodal temperature responses: attack and maximum uptake rates



Attack rate: unimodal

Handling time=1/max uptake rate: U-shaped

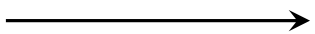
Englund *et al.* (2011)

Temperature effects on life history and consumption traits

Data: trait responses conserved across ectotherm taxa

$\Rightarrow$ Trait-based framework that applies broadly

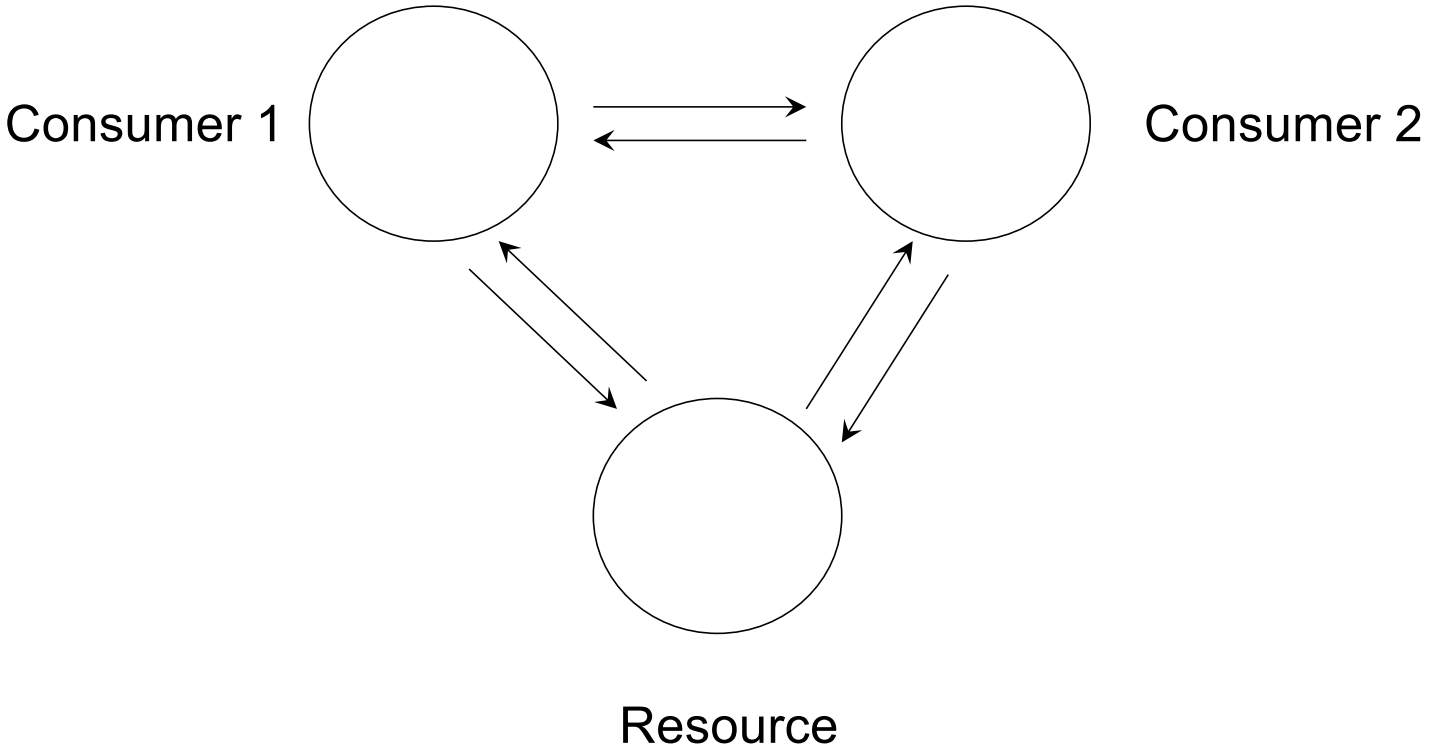
Temperature effects on phenotypic traits



Dynamics of species interactions

Trait-based models of species interactions

Exploitative competition



Exploitative competition in constant environment

$$\frac{dR}{dt} = R\left(r\left(1 - \frac{R}{K}\right) - a_1 C_1 - a_2 C_2\right)$$ Resource

$$\frac{dC_1}{dt} = C_1\left(e_1 a_1 R - d_1\right)$$ Consumer 1

$$\frac{dC_2}{dt} = C_2\left(e_2 a_2 R - d_2\right)$$ Consumer 2

R* rule: competitive exclusion

Exploitative competition in seasonally varying environments

Trait-based consumer-resource model

Resource growth

Resource exploitation

$$\frac{dR(t)}{dt} = r(T(t))R(t)\big(1 - q(T(t))R(t)\big) - a_R(T(t))R(t)C_R(t) - a_I(T(t))R(t)C_I(t)$$

$$\frac{dC_R(t)}{dt} = e_R a_R(T(t))R(t)C_R(t) - d_R(T(t))C_R(t)$$

Consumer 1 (resident)

$$\frac{dC_I(t)}{dt} = e_I a_I(T(t))R(t)C_I(t) - d_I(T(t))C_I(t)$$

Consumer mortality

Consumer 2 (invader)

Mechanistic trait responses

Seasonal temperature variation

Mutual invasibility criteria in seasonally varying environments

Mutual invasibility criteria

$$\frac{1}{\tau}\int_0^{\tau}\frac{1}{C_i(t)}\frac{dC_i(t)}{dt}\,\mathrm{d}t > 0$$

$$\mathrm{i}=1,\,2$$

Time-averaged per capita growth rate when rare

Mutual invasibility criteria

$$\frac{1}{\tau}\int_0^\tau \frac{dC_i}{dt}\frac{1}{C_i} = \frac{1}{\tau}\int_0^\tau e_i a_i(T(t))R_{C_j}(T(t)) - d_i(T(t))\ \mathrm{d}t > 0$$
$$i, j = 1, 2, i \neq j \tag{1}$$

$R_{C_j}(T(t))$: instantaneous resource availability set by the resident consumer in a seasonally varying environment (time-varying $R^\star$)

When the consumers exhibit linear functional responses and temperature variation is predictable (i.e., mean temperature and the amplitude of seasonal fluctuations remain approximately constant over time), the instantaneous resource availability set by the resident consumer is given by:

$$R_{C_j}(T(t)) = \frac{d_j(T(t))}{e_j a_j(T(t))}.$$

Mutual invisibility criteria in seasonal environments

$$\frac{1}{\tau}\int_0^\tau \frac{dC_i}{dt}\frac{1}{C_i} = \frac{1}{\tau}\int_0^\tau e_i a_i(T(t))\frac{d_j(T(t))}{e_j a_j(T(t))} - d_i(T(t))\ \mathrm{d}t > 0$$

$$i, j = 1, 2, i \neq j$$

Mutual invasibility criteria in seasonal environments

$$\frac{\int_0^\tau \frac{e_i a_i(T(t))}{e_j a_j(T(t))} d_j(T(t))\ \mathrm{d}t}{\int_0^\tau d_i(T(t))\ \mathrm{d}t} > 1.$$

Consumer *i*'s lifetime reproductive success in a seasonal environment

After separating the temperature-independent components and doing some algebra, we can derive the **sufficient** condition for mutual invasibility.

Sufficient condition for mutual invasibility

$$\frac{\int_0^\tau d'_2(T(t))\mathrm{d}t}{\int_0^\tau a'_2(T(t))\frac{d'_1(T(t))}{a'_1(T(t))}\mathrm{d}t} < \frac{R_{1T_{\mathrm{opt}}}}{R_{2T_{\mathrm{opt}}}} < \frac{\int_0^\tau a'_1(T(t))\frac{d'_2(T(t))}{a'_2(T(t))}\mathrm{d}t}{\int_0^\tau d'_1(T(t))\mathrm{d}t} \tag{1}$$

where

$R_{iT_{\mathrm{opt}}} = \frac{d_{iT_R}}{e_i a_{iT_{\mathrm{opt}}}}$ $i, j = 1, 2, i \neq j$, and,

$d'_i(T(t))$ and $a'_i(T(t))$ are the temperature-dependent mortality and consumption rates.

Necessary condition for mutual invasibility

$$\frac{\int_0^\tau d_2(T(t))\mathrm{d}t}{\int_0^\tau a_2(T(t))\frac{d_1(T(t))}{a_1(T(t))}\mathrm{d}t} < \frac{\int_0^\tau a_1(T(t))\frac{d_2(T(t))}{a_2(T(t))}\mathrm{d}t}{\int_0^\tau d_1(T(t))\mathrm{d}t} \qquad (1)$$

Note: hats have been dropped for convenience.

Necessary condition for mutual invasibility

$$\left(\frac{\int_0^\tau d_1(T(t))\mathrm{d}t}{\int_0^\tau a_2(T(t))\frac{d_1(T(t))}{a_1(T(t))}\mathrm{d}t}\right)\left(\frac{\int_0^\tau d_2(T(t))\mathrm{d}t}{\int_0^\tau a_1(T(t))\frac{d_2(T(t))}{a_2(T(t))}\mathrm{d}t}\right) < 1 \qquad (1)$$

Criteria for coexistence in seasonal environments

Necessary and sufficient ==> species limit themselves more than they do others ==> **stable coexistence**

Necessary only ==> one species excludes the other ==> **competitive dominance**

Neither necessary nor sufficient ==> outcome depends on initial conditions ==> **priority effects**

The necessary condition from the consumer-resource model:

$$\left(\frac{\int_0^\tau d_1(T(t))\mathrm{d}t}{\int_0^\tau a_2(T(t))\frac{d_1(T(t))}{a_1(T(t))}\mathrm{d}t}\right)\left(\frac{\int_0^\tau d_2(T(t))\mathrm{d}t}{\int_0^\tau a_1(T(t))\frac{d_2(T(t))}{a_2(T(t))}\mathrm{d}t}\right) < 1 \tag{1}$$

is equivalent to the necessary condition for for mutual invasibility in the Lotka-Volterra framework:

$$\left(\frac{\alpha_{21}}{\alpha_{11}}\right)\left(\frac{\alpha_{12}}{\alpha_{22}}\right) < 1 \tag{2}$$

with

$$\alpha_{ii} = \frac{1}{\int_0^\tau d_i(T(t))\mathrm{d}t}$$

Intra-specific
competition coefficient

$$\alpha_{ji} = \frac{1}{\int_0^\tau a_j(T(t))\frac{a_i(T(t))}{d_i(T(t))}\mathrm{d}t}$$

$$i, j = 1, 2, i \neq j$$

Inter-specific
competition coefficient

$$\alpha_{ii} = \frac{1}{\int_0^\tau d_i(T(t))\mathrm{d}t}$$

Mechanistic derivation of competition coefficients based on species' consumption and mortality rates

$$\alpha_{ji} = \frac{1}{\int_0^\tau a_j(T(t))\frac{a_i(T(t))}{d_i(T(t))}\mathrm{d}t}$$

$$i, j = 1, 2, i \neq j$$

Intra-specific competition

$$\alpha_{ii} = \frac{1}{\frac{1}{\tau}\int_0^{\tau} d_i(T(t))\mathrm{d}t}$$

Intra-specific competition coefficient proportional to the consumer's time-averaged mortality rate

$$\mathrm{i}=1,\ 2$$

Smith and Amarasekare, (2018)

Inter-specific competition

$$\alpha_{ji} = \frac{1}{\int_0^{\tau} a_j(T(t)) \frac{a_i(T(t))}{d_i(T(t))} \mathrm{d}t}$$

Invader's consumption rate

Resource availability set by resident consumer

Smith and Amarasekare, (2018)

Mutual invasibility

1. Intra-specific competition
   (Invader's mortality rate)
2. Inter-specific competition

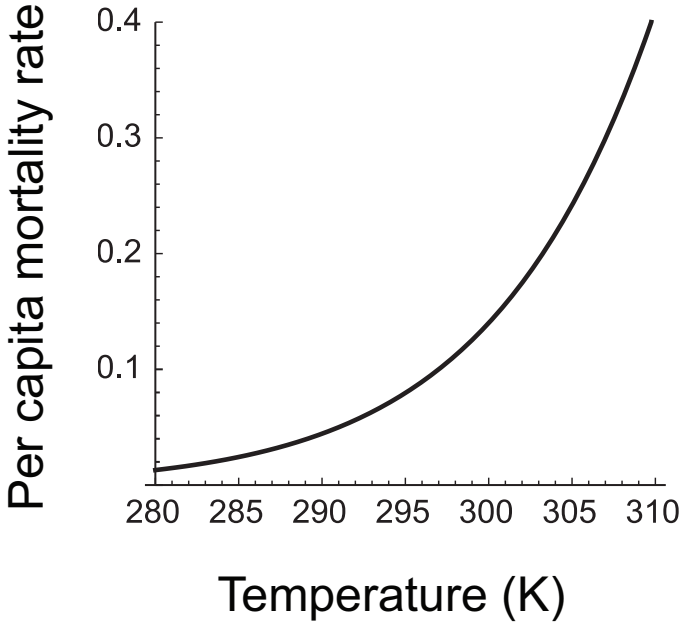
   2.1 Resource availability set by resident
   (Resident's consumption and mortality rates)

   2.2 Invader's resource acquisition ability
   (Invader's consumption rate)

Temperature effects on determinants of invasion success

- Resource availability
- Resource consumption
- Mortality

Temperature response of mortality rate

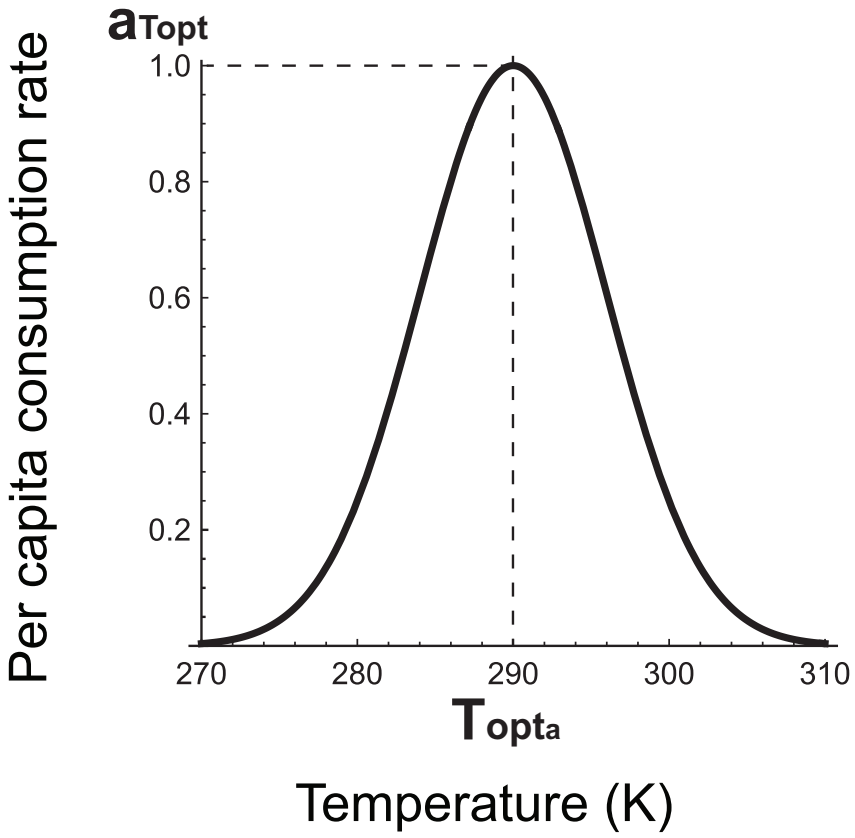


$$d(T) = d_{T_R} e^{A_d \left(\frac{1}{T_R} - \frac{1}{T} \right)}$$

Boltzmann-
Arrhenius function

A_d determines temperature sensitivity of mortality

Temperature response of consumption rate



$$a(T) = a_{T_{\mathrm{opt}}} e^{-\frac{(T - T_{\mathrm{opt_a}})^2}{2{s_a}^2}}$$

Gaussian function

Relative strengths of intra- and inter-specific competition depends on the nature of thermal adaptation

Thermal adaptation driven by latitudinal variation in seasonal temperature regimes

Latitudinal variation in seasonal thermal regimes

Tropical climates: high mean temperature, low-amplitude seasonal fluctuations

Temperate climates: low mean temperature, high-amplitude seasonal fluctuations

Nature of thermal adaptation

Higher-latitude species cold adapted: lower thermal optima, active at lower temperatures

Lower-latitude species warm-adapted: species: higher thermal optima, active at higher temperature

Nature of thermal adaptation

Lower-latitude species thermal specialists: narrower response breadths, active during narrow temperature range

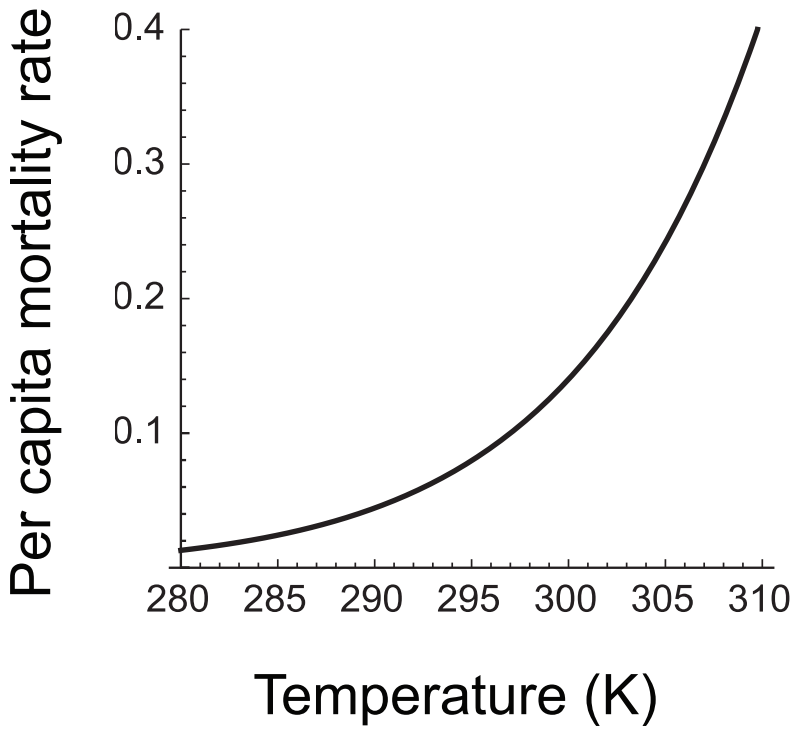
Higher-latitude species, thermal generalists: wider response breadths, active during wider temperature range

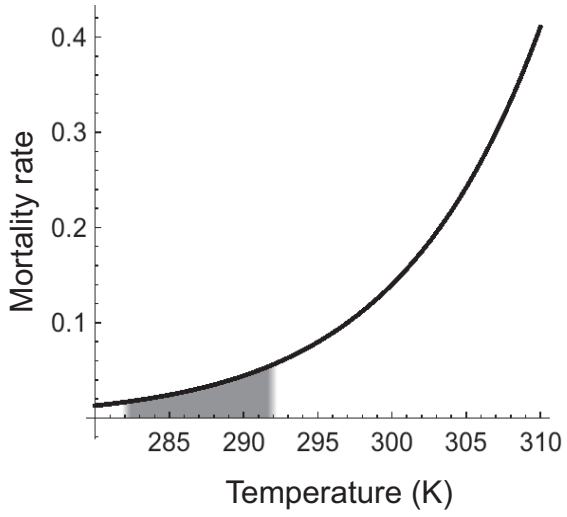
Intra-specific competition (self-limitation) depends on thermal adaptation

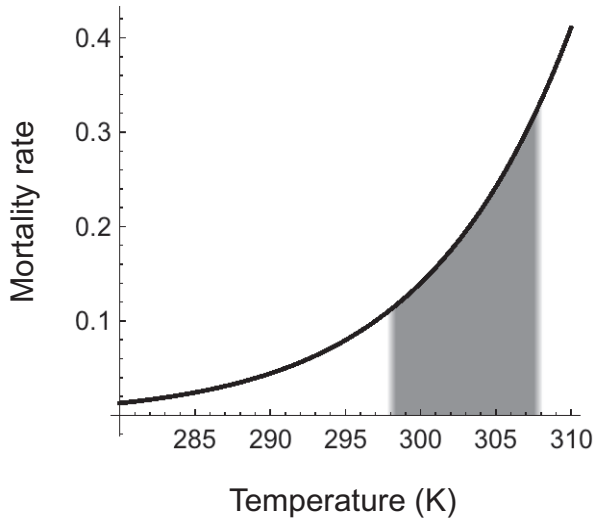
$$\alpha_{ii} = \frac{1}{\frac{1}{\tau}\int_0^\tau d_i(T(t))\mathrm{d}t}$$

Time-averaged mortality rate

Self-limitation strength inversely proportional to average mortality rate







Cold-adapted
Lower average mortality
Stronger self-limitation

Warm-adapted
Higher average mortality
Weaker self-limitation

Cold-adapted species experience stronger self-limitation than warm-adapted species

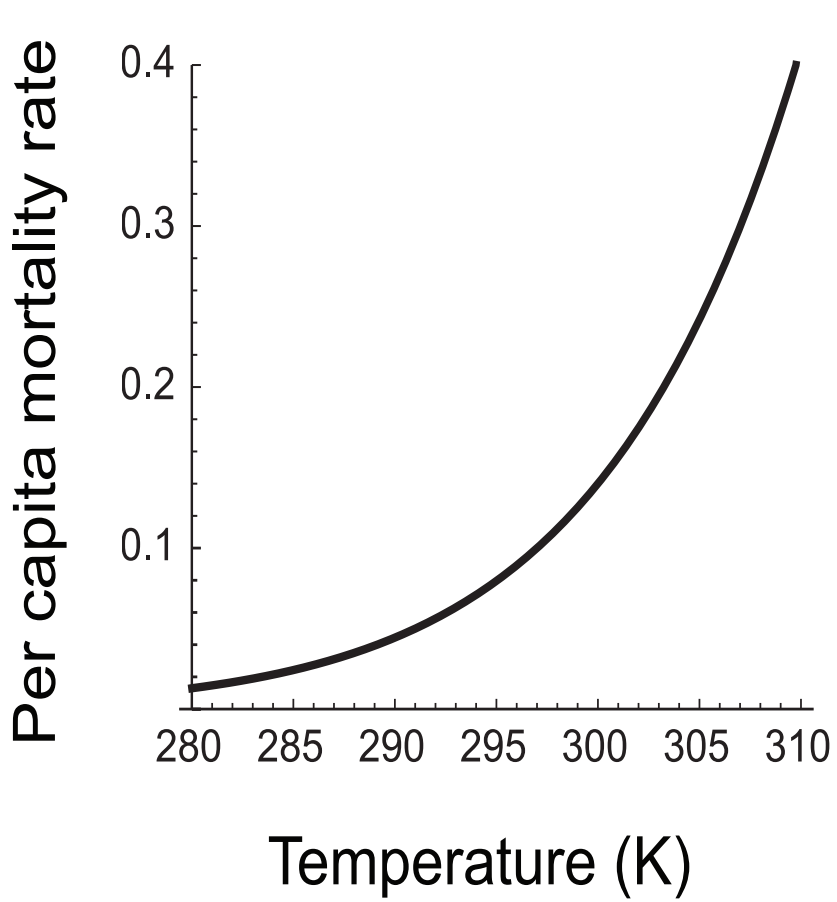
Inter-specific competition

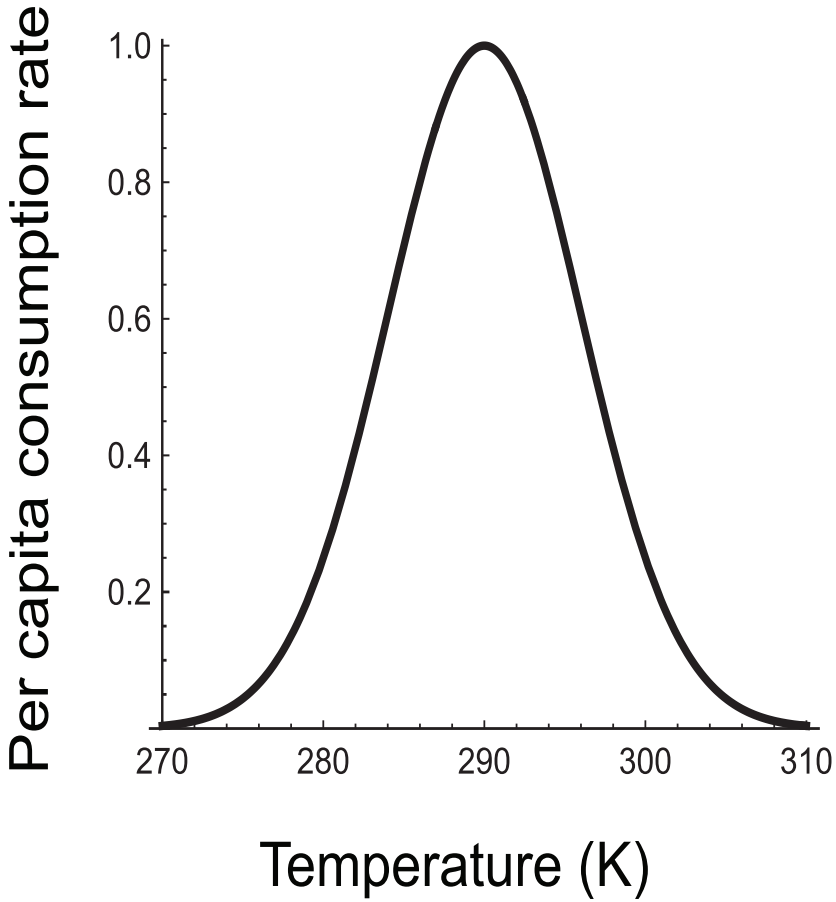
Resource availability set by resident [$\mathbf{R^*(T(t))}$]
(Resident's consumption and mortality rates)

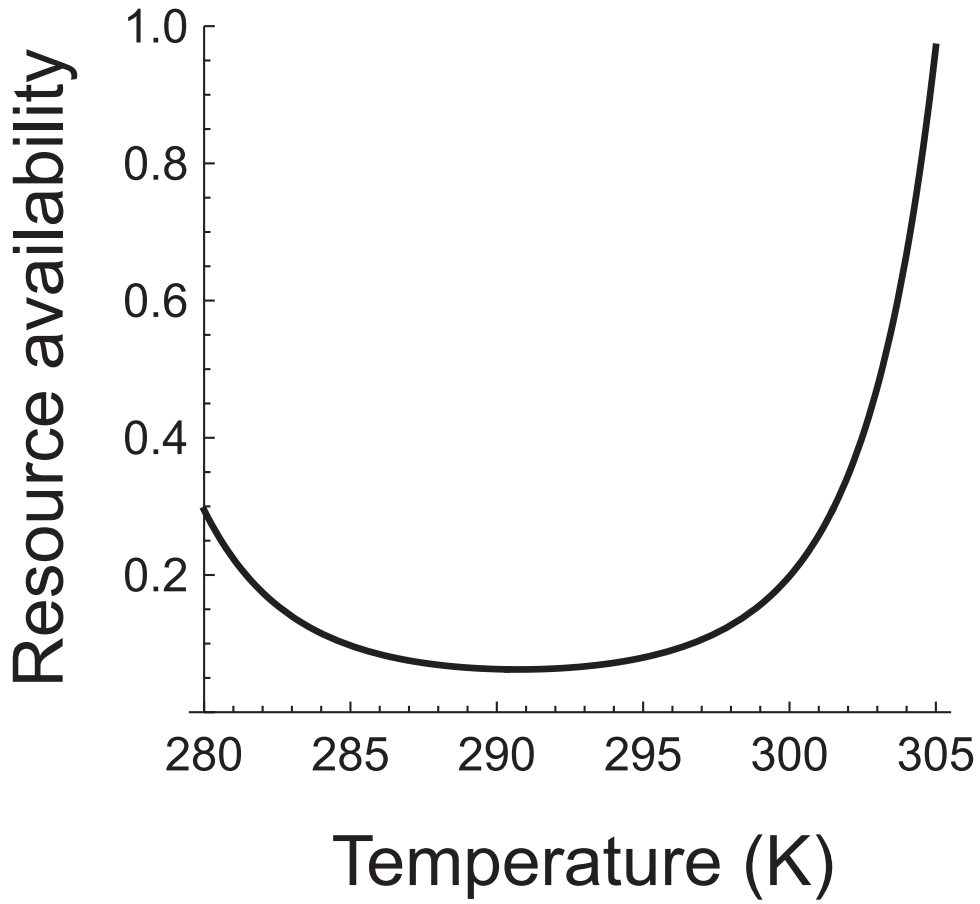
Invader's resource acquisition ability
(Invader's consumption rate)

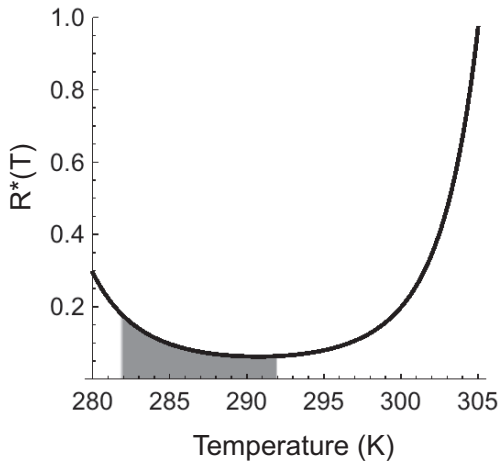
Resource availability set by resident

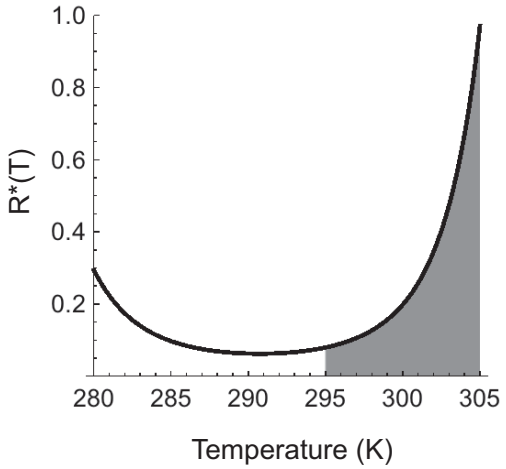
Resident species' consumption and mortality rates


Per capita mortality rate
0.4
0.3
0.2
0.1
280
285
290
295
300
305
310
Temperature (K)


Per capita consumption rate
1.0
0.8
0.6
0.4
0.2
270
280
290
300
310
Temperature (K)


Resource availability
1.0
0.8
0.6
0.4
0.2
280
285
290
295
300
305
Temperature (K)





Cold-adapted
Lower resource availability
(Lower R^*)

Warm-adapted
Higher resource availability
(Higher R^*)

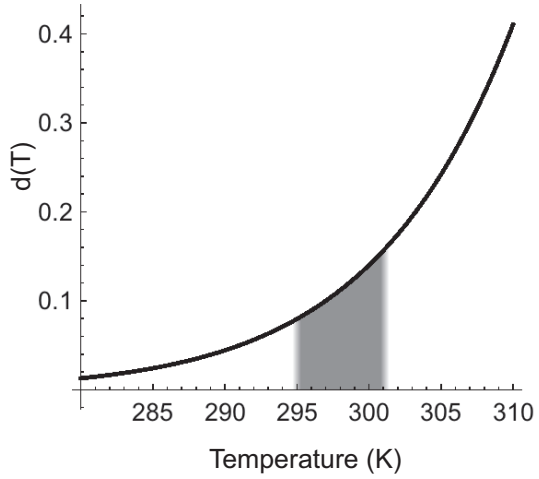
Cold-adapted species depress resources to lower levels than warm-adapted species

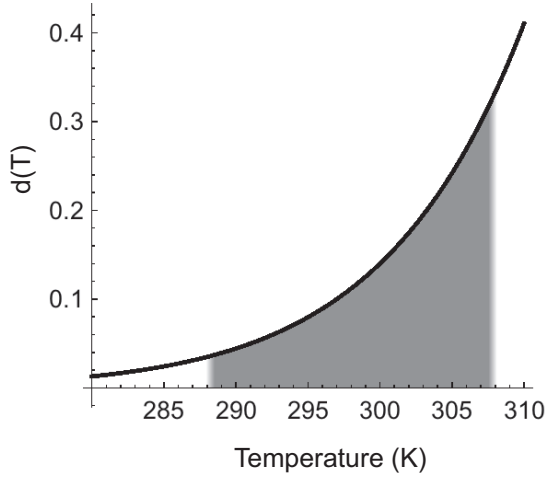
Differential adaptation to seasonal environments (thermal optima)

Cold-adapted species experience stronger self-limitation than their warm-adapted competitors

Cold-adapted species deplete resource to lower levels (have lower R^*) than do their warm-adapted competitors

Differential adaptation to seasonal environments (response breadth)

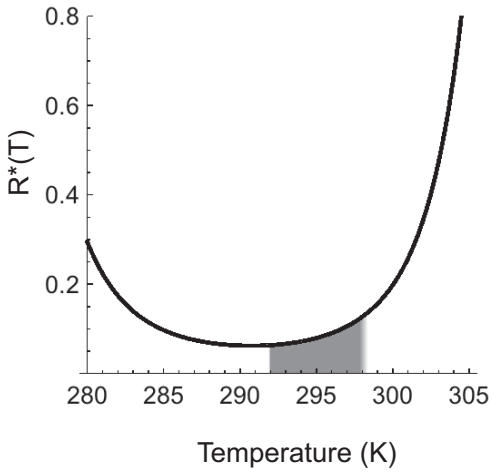


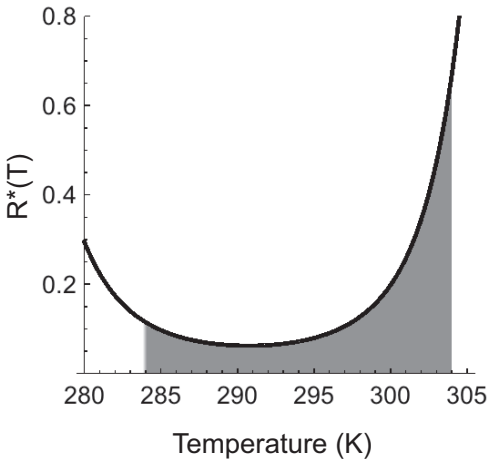


Thermal specialist
Lower average mortality
Stronger self-limitation

Thermal generalist
Higher average mortality
Weaker self-limitation

Thermal specialists experience stronger self-limitation than thermal generalists





Thermal specialist
Lower resource availability
(Lower R^*)

Thermal generalist
Higher resource availability
(Higher R^*)

Thermal specialists depress resources to lower levels than thermal generalists

Differential adaptation to seasonal environments (response breadth)

Thermal specialists limit themselves more than their generalist competitors

Thermal specialists deplete resource to lower levels (have lower R^*) than do their generalist competitors

Mechanistic basis of storage effect in thermally variable environments

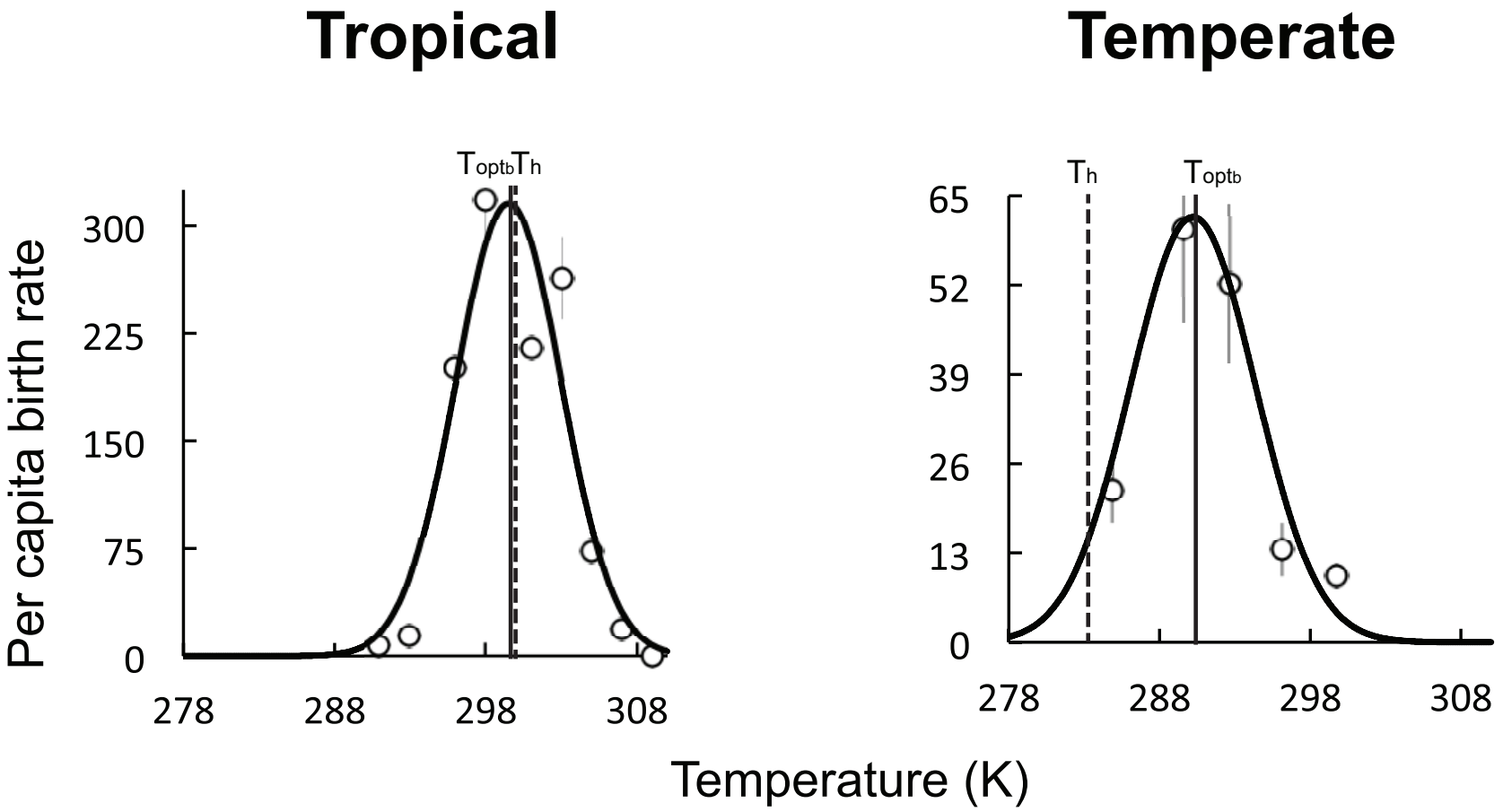
Species that exert **strong inter-specific competition** (e.g., cold-adapted species, thermal specialists) are **more self-limited** than those that exert only weak inter-specific competition (e.g., warm-adapted species and thermal generalists)

Developing testable predictions

Scaling temperature response parameters in terms of seasonal temperature regime

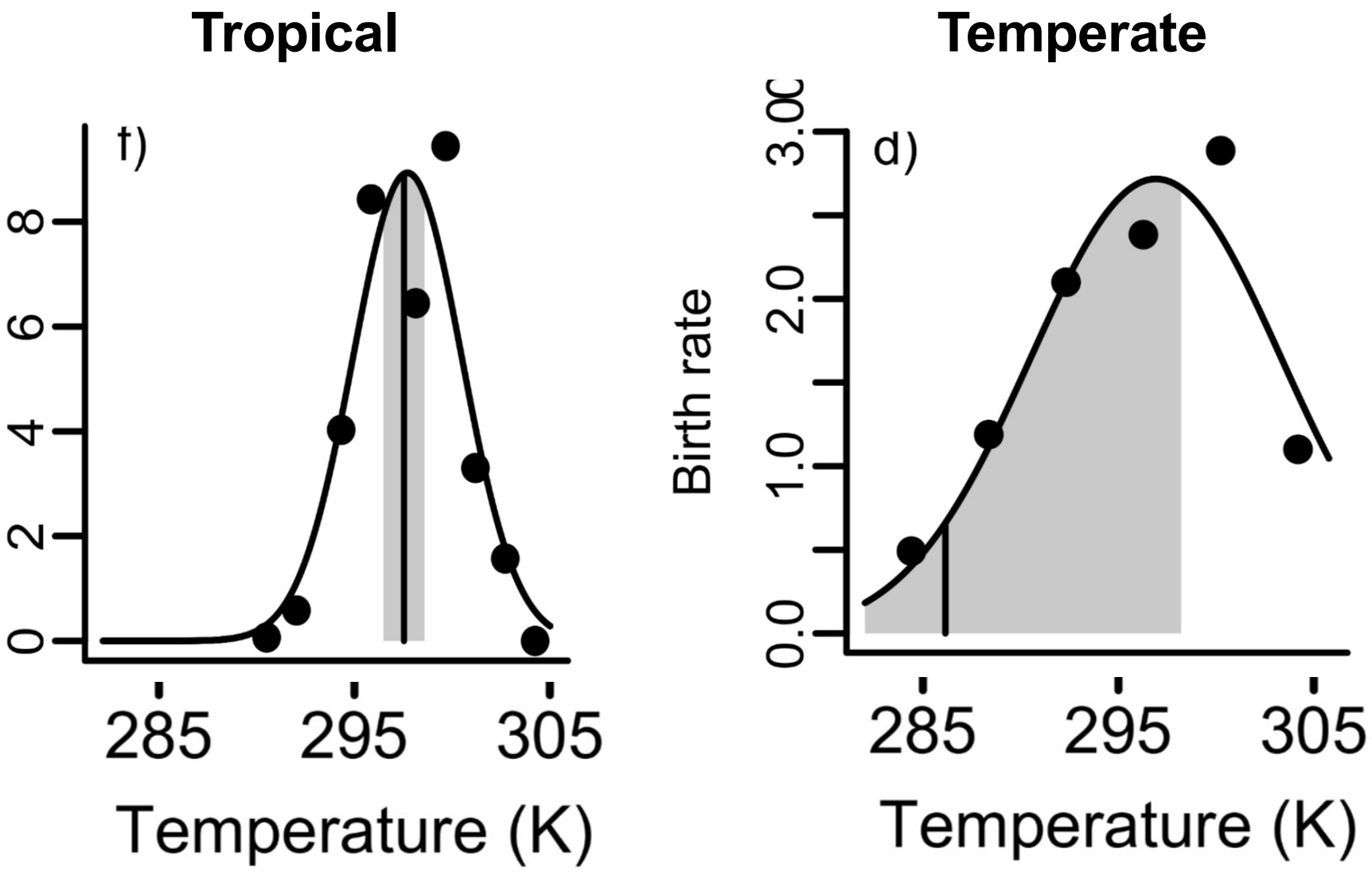
Empirical observations

1. Difference between thermal optimum and mean habitat temperature increases with increasing latitude


Tropical
Temperate
Per capita birth rate
Temperature (K)
T_{optb} T_h
T_h T_{optb}
0
75
150
225
300
0
13
26
39
52
65
278
288
298
308

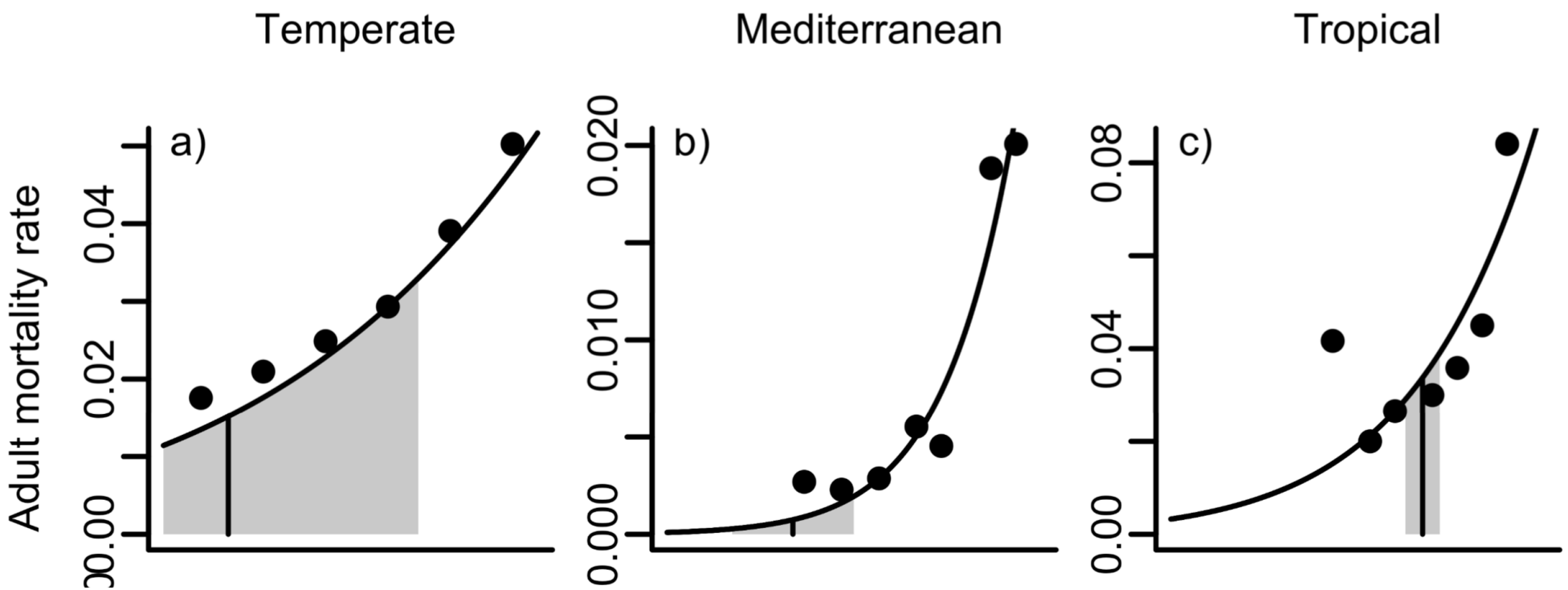
Empirical observations

2. Response breadth increases with increasing latitude (adaptation to larger seasonal fluctuations)


Tropical
Temperate
t)
d)
0
2
4
6
8
0.0
1.0
2.0
3.0
Birth rate
285
295
305
285
295
305
Temperature (K)
Temperature (K)

Empirical observations

3. Species differ in their temperature sensitivity of mortality


Temperate
Mediterranean
Tropical
Adult mortality rate
a)
b)
c)
0.00
0.02
0.04
0.000
0.010
0.020
0.00
0.04
0.08

Scaling of thermal optima

Let M_T denote the mean habitat temperature and A_T, the amplitude of seasonal fluctuations.

Consider Consumer 1 to be the resident species and Consumer 2 to be the invader.

Resident consumer's consumption rate: $T_{\mathrm{opt}_{\mathrm{a}_1}} = M_T + m$ where m is the deviation of the consumption optimum from mean habitat temperature.

Invader's consumption rate: $T_{\mathrm{opt}_{\mathrm{a}_2}} = T_{\mathrm{opt}_{\mathrm{a}_1}} + x$ where x is the deviation of invader's consumption optimum from that of resident.

Scaling of response breadth

Let s_{a_1} be the resident consumer's consumption response breadth.

Then $v = \frac{s_{a_2}}{s_{a_1}}$

where v is the ratio of invader's and resident's consumption response breadths

Scaling of temperature sensitivity of mortality

Let A_{d_1} be the resident consumer's Arrhenius constant for increase in mortality with temperature.

Then $p = \frac{A_{d_2}}{A_{d_1}}$

where p is the ratio of invader's and resident's temperature sensitivities of mortality.

By incorporating these scaling relationships into the mutual invisibility criteria

$$\left(\frac{\int_0^\tau d_1(T(t))\mathrm{d}t}{\int_0^\tau a_2(T(t))\frac{d_1(T(t))}{a_1(T(t))}\mathrm{d}t}\right)\left(\frac{\int_0^\tau d_2(T(t))\mathrm{d}t}{\int_0^\tau a_1(T(t))\frac{d_2(T(t))}{a_2(T(t))}\mathrm{d}t}\right) < 1 \tag{1}$$

and simplifying,

The necessary condition for mutual invasibility is given by:

$$\left(\frac{\int_0^\tau e^{-\frac{A_{d_1}}{M_T - A_T S(t)}}\,\mathrm{d}t}{\int_0^\tau e^{-AS(t)(S(t)+2n)-DS(t)-\frac{A_{d_1}}{M_T - A_T S(t)}}\,\mathrm{d}t}\right)\left(\frac{\int_0^\tau e^{-\frac{pA_{d_1}}{M_T - A_T S(t)}}\,\mathrm{d}t}{\int_0^\tau e^{AS(t)(S(t)+2n)+DS(t)-\frac{pA_{d_1}}{M_T - A_T S(t)}}\,\mathrm{d}t}\right) < 1$$

where $A = \frac{1-v^2}{2m^2v^2}, B_1 = \frac{A_{d_1}A_T}{M_T+nA_T}, B_2 = \frac{A_{d_1}A_T}{M_T+(n+x)A_T}, C = \frac{x}{m^2}, D = \frac{C}{v^2}$

Mechanistic description of mutual invasibility criteria consisting entirely of measurable parameters

Testable predictions with just five parameters

Abiotic

Seasonal temperature regime: M_T and A_T

Biotic

Differences between consumer species in:

Thermal optima (x)

Response breadth (v)

Temperature sensitivity of mortality (p)

Insights

Density-independent mortality, which drives intra-specific competition (self-limitation), is crucial to coexistence in thermally variable environments.

Trait-based model provides mechanism for species-specific responses to temperature variation (temperature sensitivity of mortality *p*).

Predictions

1. Mutual invasibility possible if cold-adapted species (lower thermal optimum) experiences greater temperature sensitivity of mortality (steeper mortality curve).

Cold-adapted species

Steeper mortality curve,
Lower attack rate at higher temperatures

Warm-adapted species

Shallower mortality curve
Higher attack rate at higher temperatures

Cold-adapted species

1. Steeper mortality curve means lower mortality at lower temperatures and stronger self-limitation during favorable (colder) periods of the year.

Cold-adapted species

2. Steeper mortality curve also means higher mortality at high temperatures.

This, combined with its lower attack rate at higher temperatures increases the cold-adapted species' R^*, leading to **weaker competition** on the warm-adapted species when the **thermal environment is favorable to the warm-adapted species**.

Cold-adapted species

Lower attack rate optimum and greater temperature sensitivity of mortality ==> cold-adapted species limits itself more than it does its warm-adapted competitor.

Warm-adapted species

1. Shallower mortality curve means lower mortality at higher temperatures and stronger self-limitation during favorable (warmer) periods of the year.

Warm-adapted species

Shallower mortality curve also means higher mortality at lower temperatures. This, combined with its lower attack rate at lower temperatures increases the warm-adapted species' R^*, leading to **weak competition on the cold-adapted species** when the thermal environment is favorable to the cold-adapted species.

Warm-adapted species

Higher attack rate optimum and lower temperature sensitivity of mortality ==> warm-adapted species limits itself more than it does its cold-adapted competitor.

Thermal adaptation leads to negative covariance between the abiotic environment and the strength of inter-specific competition

Criteria for coexistence in seasonal environments

Necessary and sufficient ==> species limit themselves more than they do others ==> **stable coexistence**

Necessary only ==> one species excludes the other ==> **competitive dominance**

Neither necessary nor sufficient ==> outcome depends on initial conditions ==> **priority effects**

Conditions for mutual invasibility

When **cold-adapted** species are **more** sensitive to temperature effects on density-independent mortality than warm-adapted species, *necessary condition for mutual invasibility criterion is always met*

Priority effects are not possible

Conditions for priority effects

When **cold-adapted** species are **less** sensitive to temperature effects on density-independent mortality than **warm-adapted** species, necessary condition for mutual invasibility is violated and **priority effects** arise.

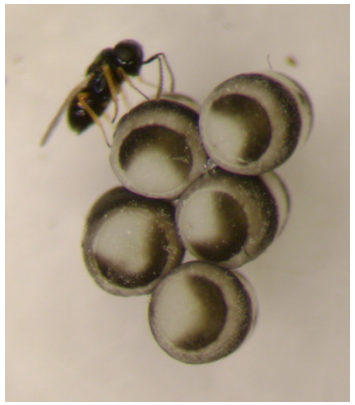
Trait-based invasibility criteria

Predict conditions for coexistence, competitive dominance, and priority effects in thermally varying environments

Testing predictions

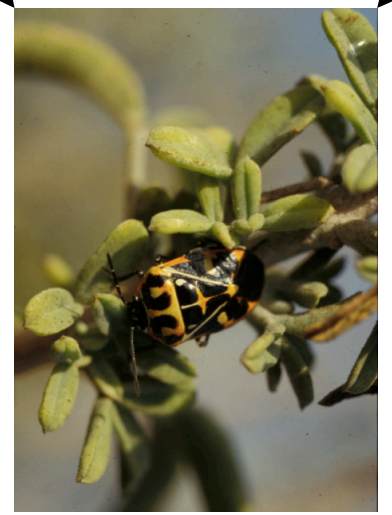
Data from host-parasitoid community

Exploitative competition



Trissolcus murgantiae

Ooencyrtus johnsonii

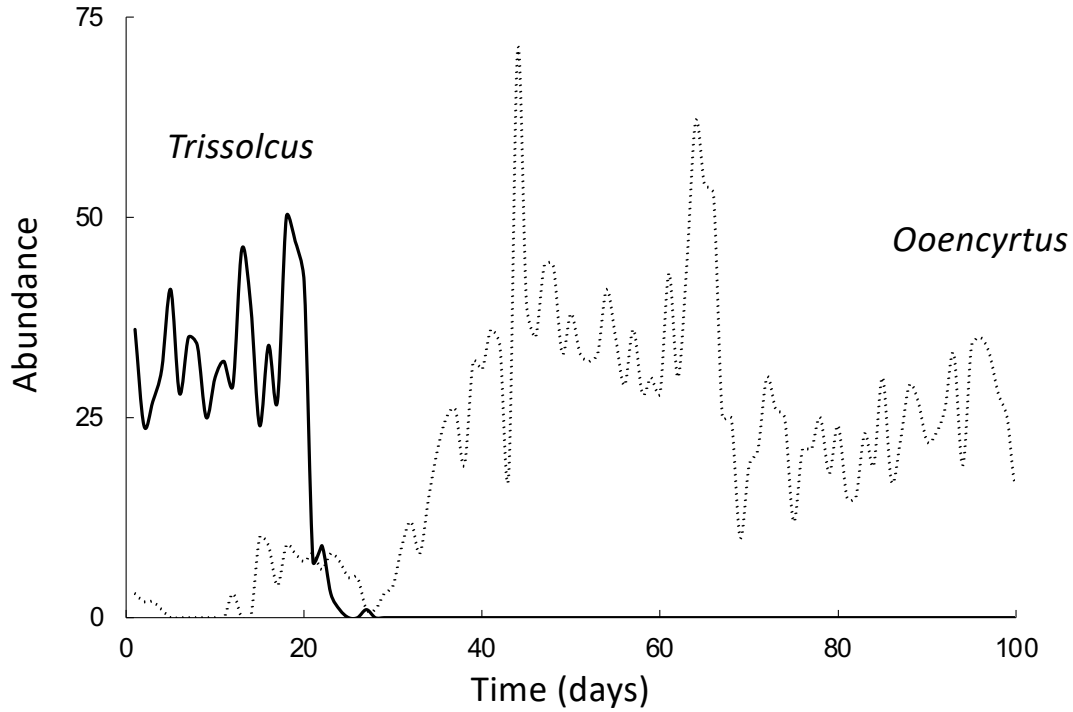


Host

Harlequin bug
(*Murgantia histrionica*)

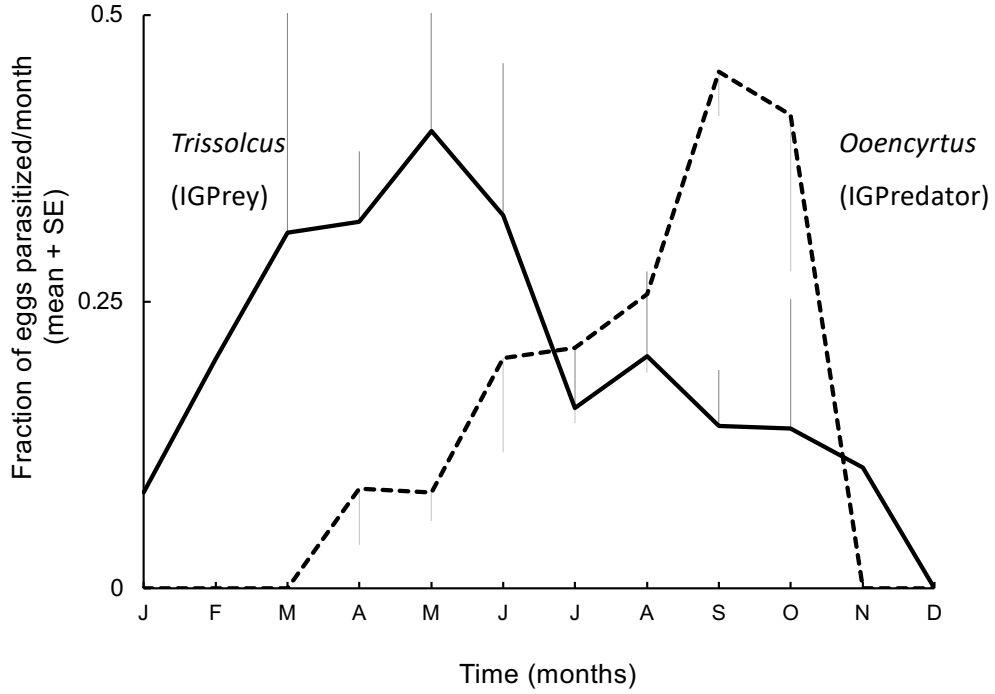
Coexistence of parasitoids on common host

Parasitoid coexistence patterns



Lab: ***Ooencyrtus*** **excludes** ***Trissolcus***

Parasitoid coexistence patterns



Field: **Coexistence,** temporal partitioning

Parasitoids have similar response breadths (v=0.98) but differ in attack rate optima (**x=1.04^{0}**) and temperature-sensitivity of mortality (**p=0.82**).

Species with the lower attack rate optimum (*Trissolcus*) exhibits greater temperature sensitivity of mortality.

Predictions

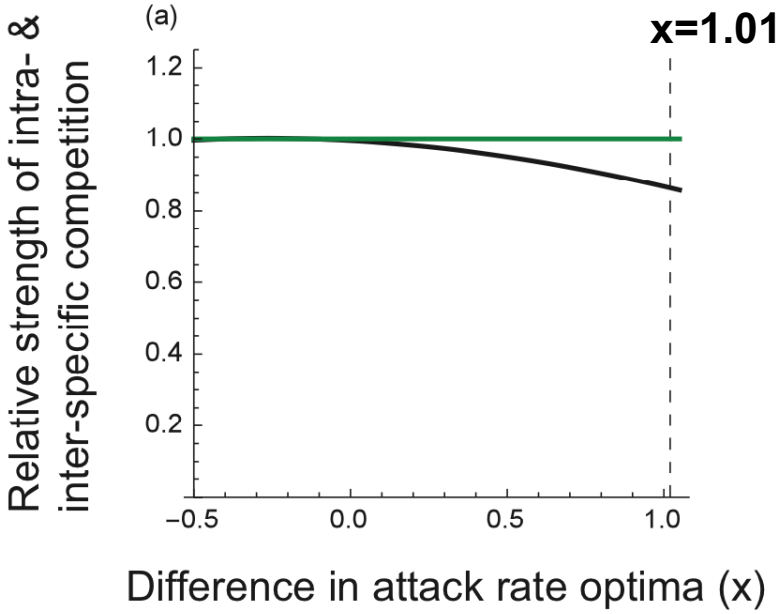
Necessary condition for mutual invasibility should be satisfied

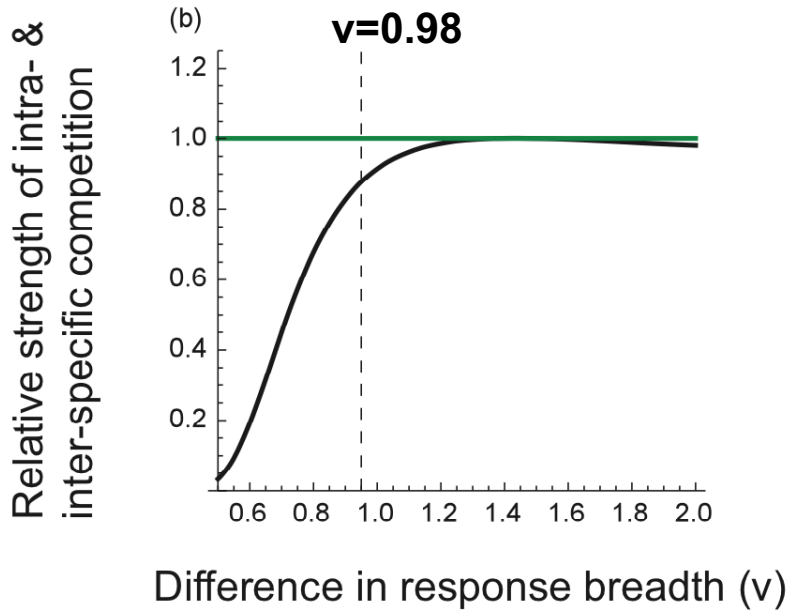
Priority effects should not be possible

Necessary condition for mutual invasibility

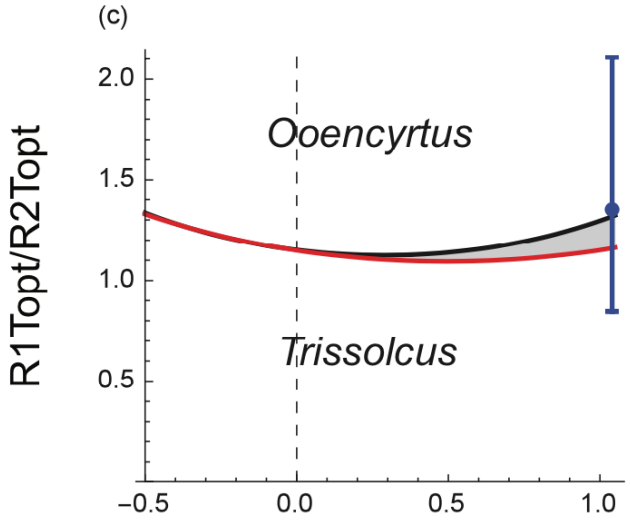
$$\left(\frac{\int_0^\tau d_1(T(t))\mathrm{d}t}{\int_0^\tau a_2(T(t))\frac{d_1(T(t))}{a_1(T(t))}\mathrm{d}t}\right)\left(\frac{\int_0^\tau d_2(T(t))\mathrm{d}t}{\int_0^\tau a_1(T(t))\frac{d_2(T(t))}{a_2(T(t))}\mathrm{d}t}\right) < 1 \qquad (1)$$

Necessary condition for mutual invasibility

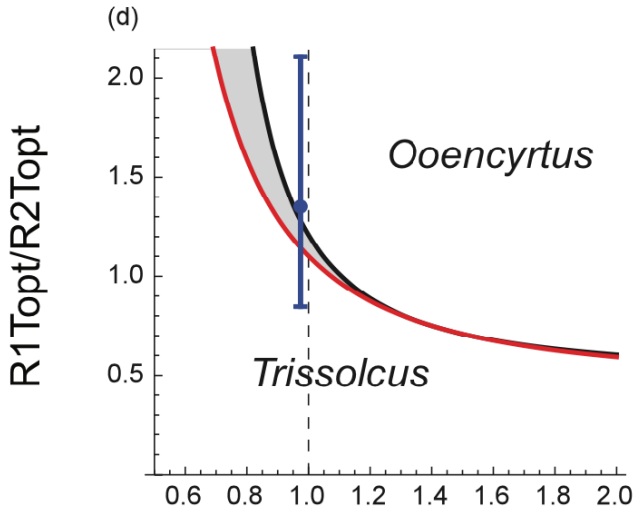




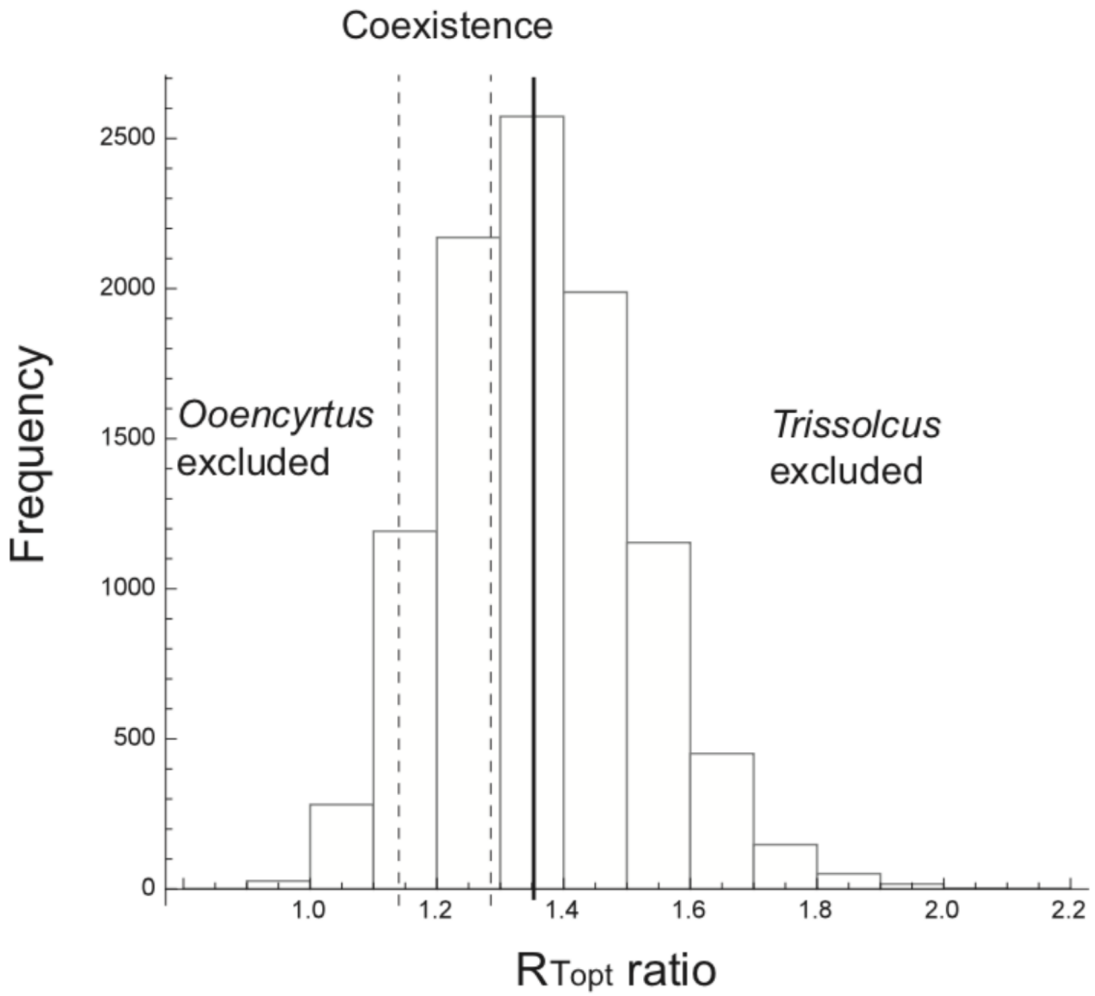
Sufficient condition for mutual invasibility



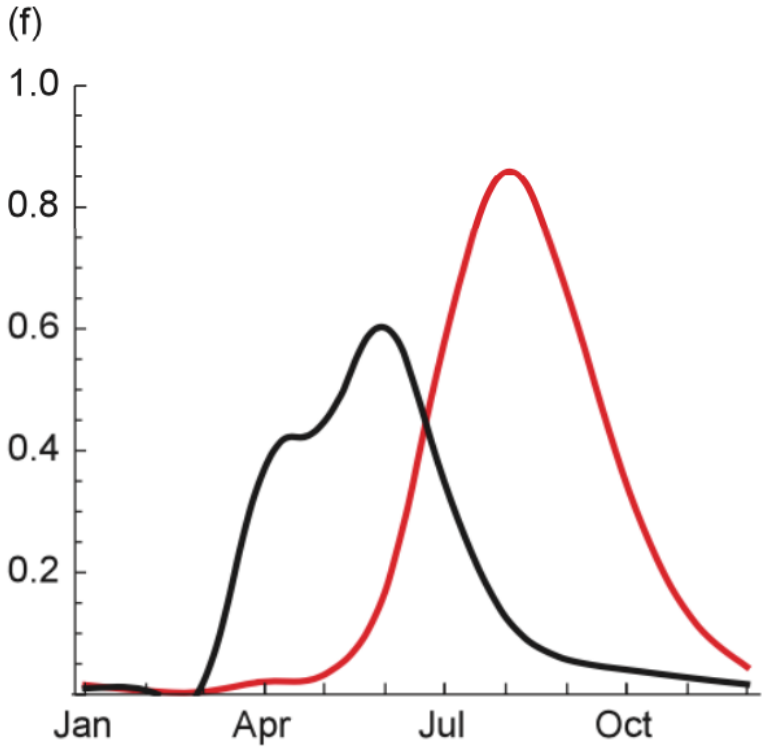
Difference in attack rate optima (x)



Difference in response breadth (v)

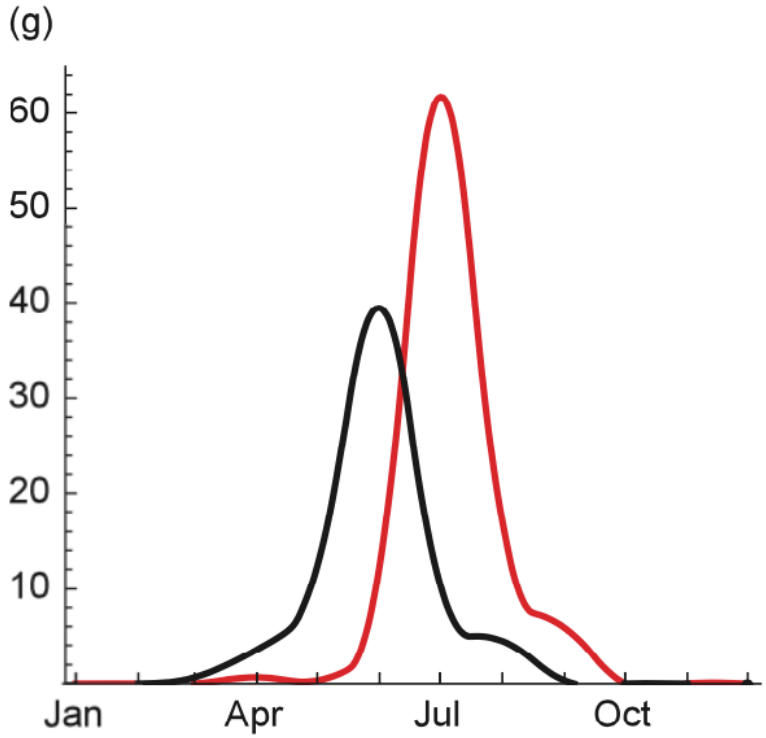

Coexistence
Frequency
2500
2000
1500
1000
500
0
Ooencyrtus
excluded
Trissolcus
excluded
1.0
1.2
1.4
1.6
1.8
2.0
2.2
RTopt ratio

Predicted by model



Time (months)

Observed in the field



Time (months)

Exploitative competition in seasonally varying environments

Approach: derive mutual invasibility criteria in terms of mechanistic descriptions of trait responses to temperature

Key insights

1. Exponential nature of the mortality response causes self-limitation strength to decrease with increasing temperature

==> cold-adapted species and thermal specialists experience stronger intra-specific competition than warm-adapted species and thermal generalists.

2. Exponential nature of the mortality response translates into lower R* and stronger inter-specific competition at temperatures below the attack rate optimum than above it.

Thermal adaptation is such that cold-adapted species and thermal specialists exert weaker competition warm-adapted species and thermal generalists when environment is favorable to warm-adapted species and thermal generalists and *vice versa*

Mechanistic basis on the storage effect in terms of temperature effects on life history and consumption traits

Species-specific responses arise from temperature effects on biochemical processes underlying species' traits

These trait effects translate into relative strengths of intra- vs. inter-specific competition at the population level.

Make testable predictions about population-level patterns of coexistence based solely on trait response data and completely independently on population-level information