Trait-based Eco-evolutionary Theory

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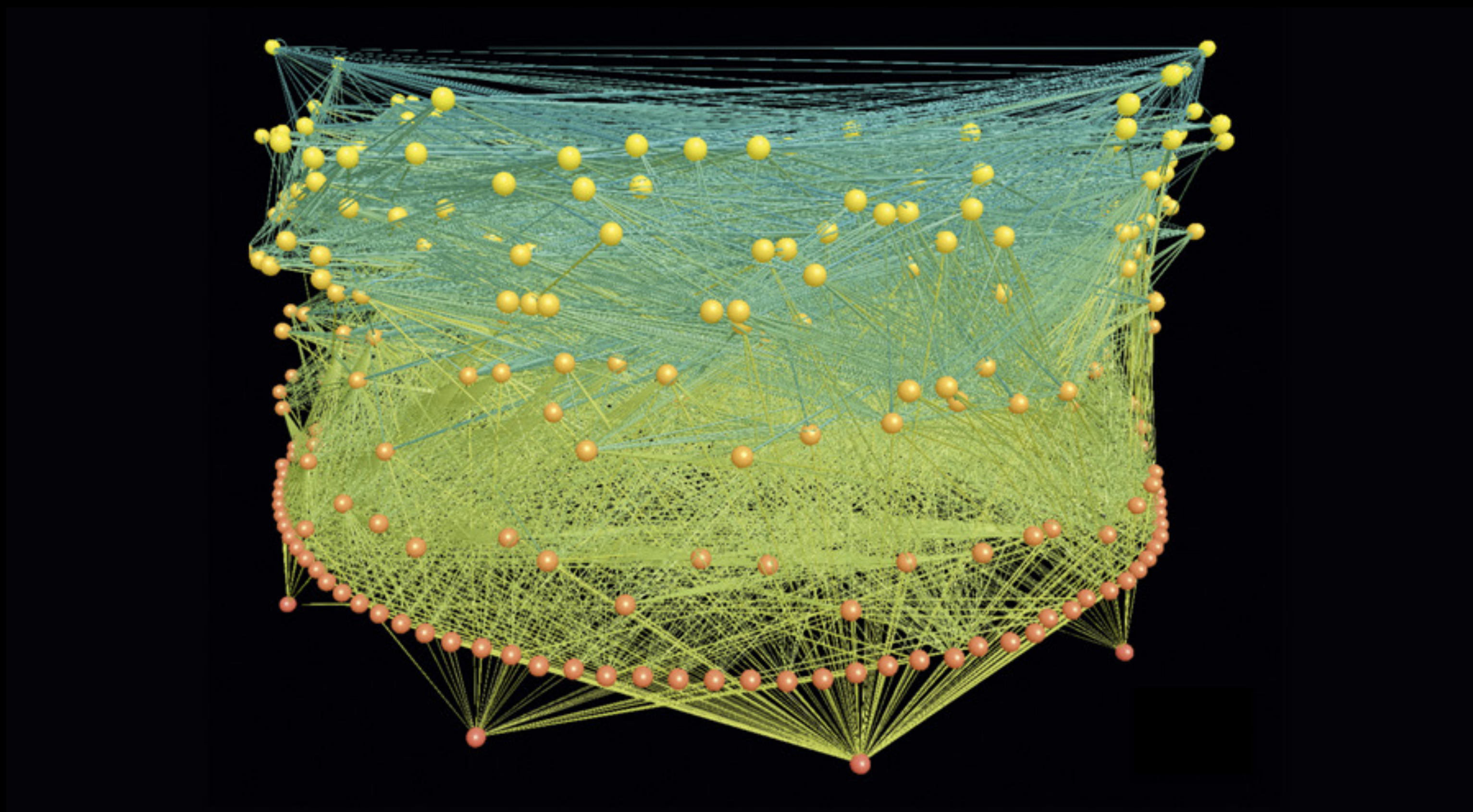
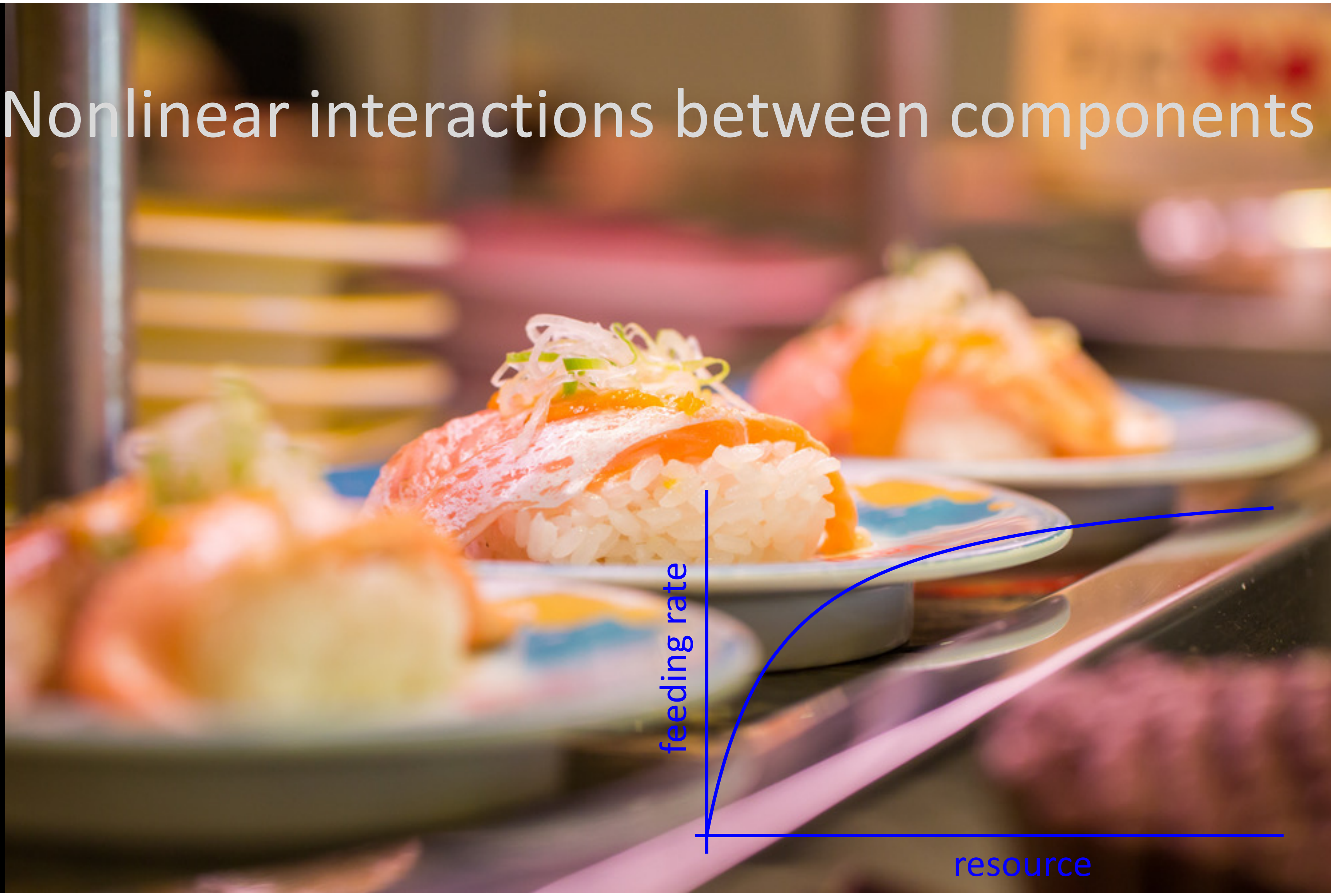
Many interacting components



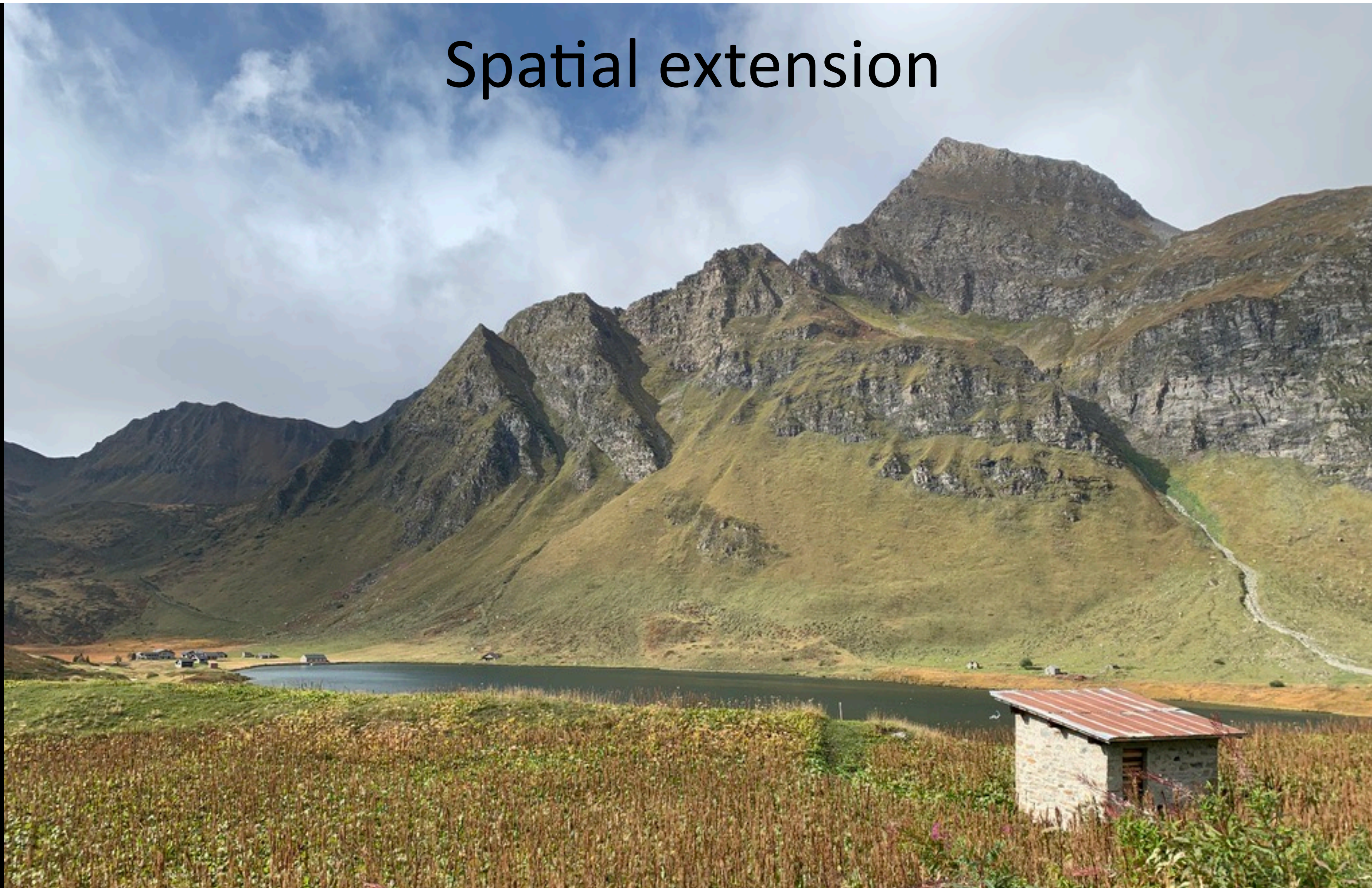
Weddell Sea food web from Jacob *et al.* 2011

Heterogeneity between & within components

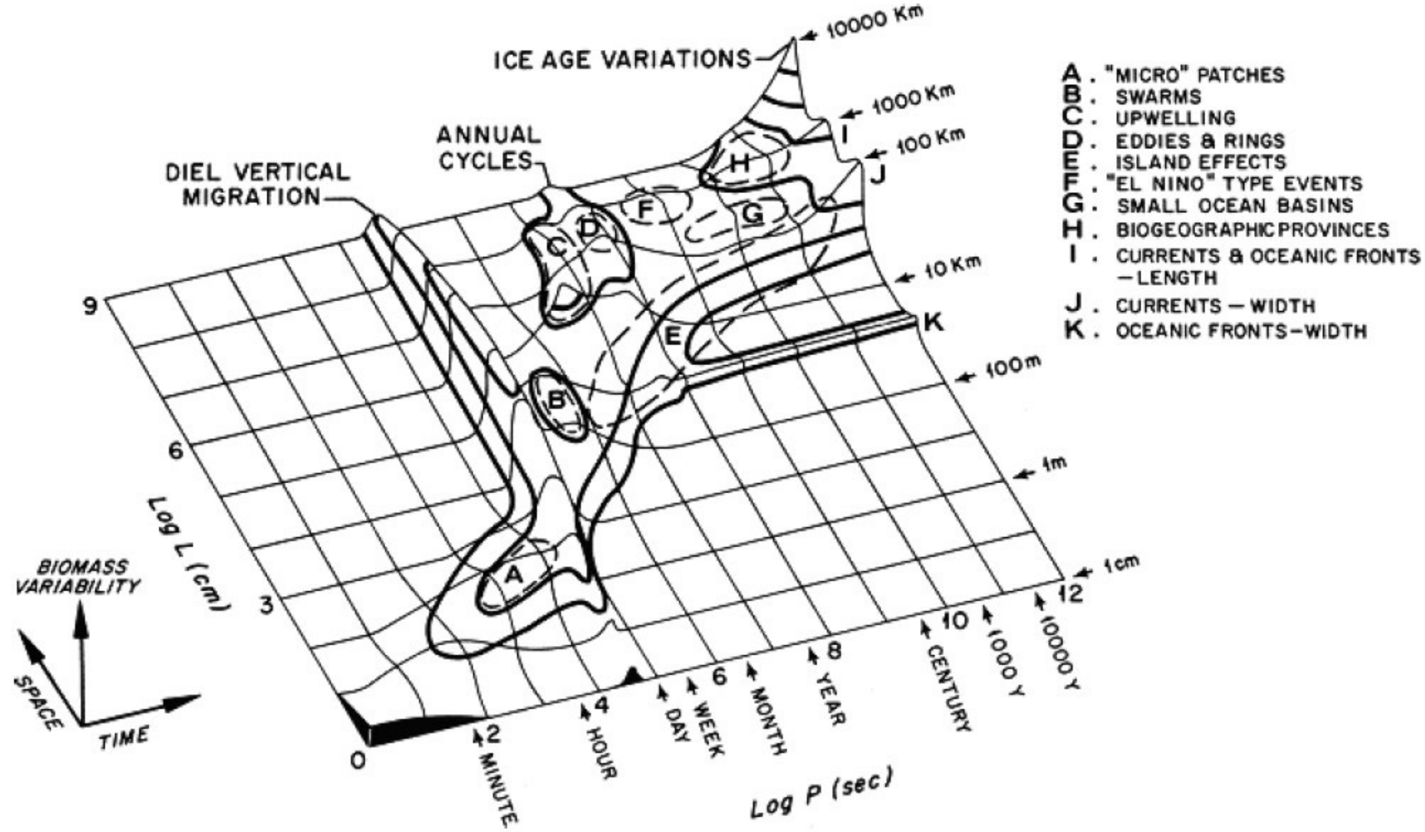

Nonlinear interactions between components
feeding rate
resource

Temporal variability

Spatial extension



Multiple scales



Stommel diagram from Haury *et al.* 1978

Communities as Complex Systems

Many interacting components
✅ Heterogeneity between & within components
✅ Nonlinear interactions
✅ Temporal variability
✅ Spatial extension
✅ Multiple scales

Communities as Complex Systems

- 🙀 Emergent properties
- 🙀 Indirect effects, network effects
- 🙀 Negative and positive feedback loops
- 🙀 Tipping points, hysteresis, alternative stable states
- 🙀 Self-organization

Predicting Ecosystem Responses to Environmental Change

Predicting Ecosystem Responses to Environmental Change

- Direct effects + indirect effects mediated by community structure
- Ecosystem function depends on environment *E*, population size *N*, traits, x — $F(E, N(E), x(E))$

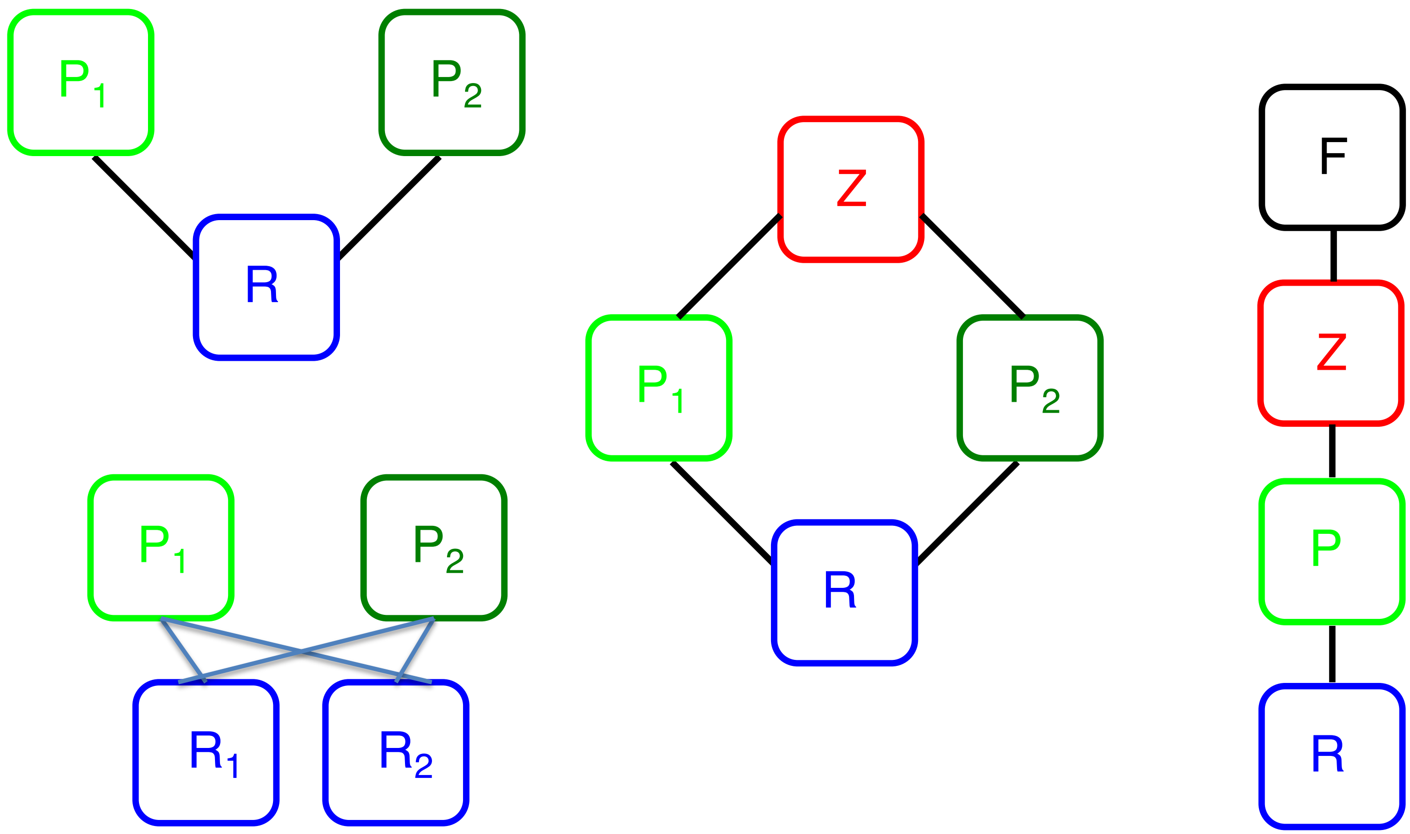
$$\frac{dF}{dE} = \frac{\partial F}{\partial E} + \frac{\partial F}{\partial N}\frac{dN}{dE} + \frac{\partial F}{\partial x}\frac{dx}{dE}$$

- Trait change through evolution or community reorganization could buffer or exacerbate response to change

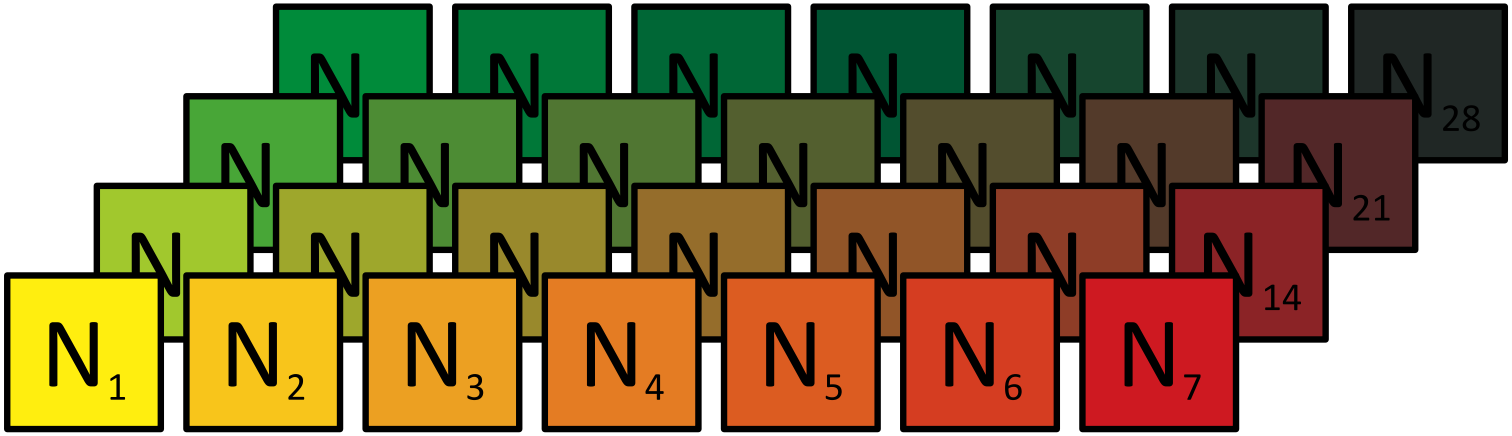
Outline

I. Ecological communities as complex systems
II. Introduction to trait-based eco-evolutionary theory (adaptive dynamics)
III. Evolutionary rescue (quantitative genetics)
IV. A general framework combining intra- and interspecific trait variation (multi-species moment methods)

Traditional Community Ecology Models

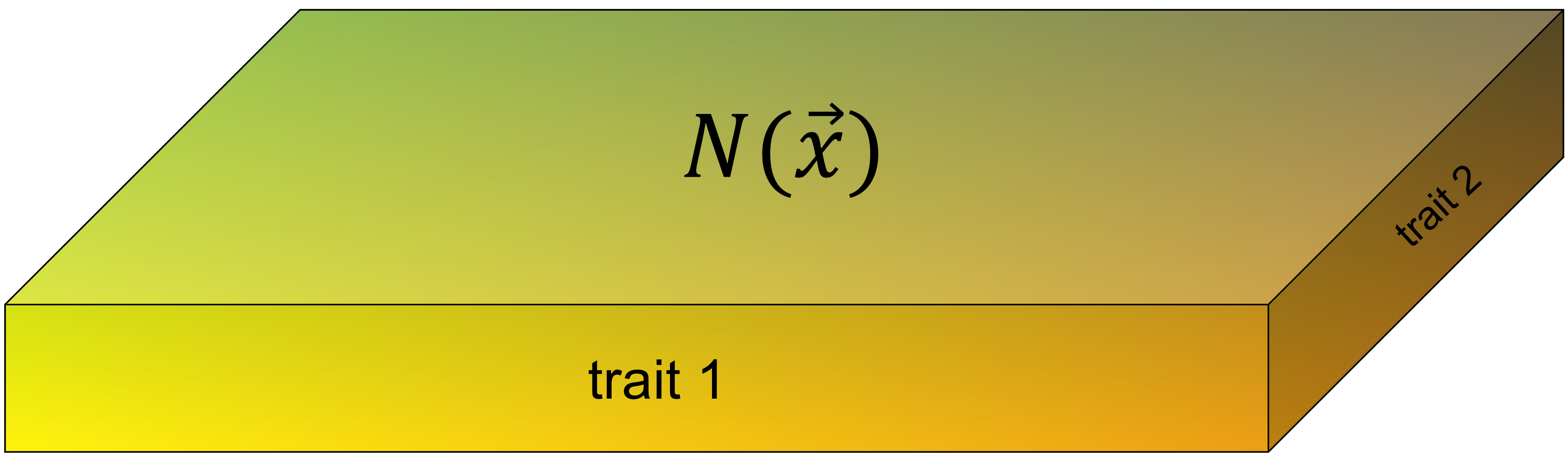


Problem: How to Incorporate Biodiversity?



- indirect effects & complex dynamics possible
- # of interaction coefficients scales with number of species $\mathcal{N}$ as $\mathcal{N}^2$

Trait-Based Eco-Evolutionary Theory



- parameterize species by their functional traits
- conceptual unification of ecology & evolution

Trait-Based Eco-Evolutionary Theory

When we turn to biological systems, composed of a number of "kindred-groups," we observe an analogous state of affairs. In general the individuals comprised within a kindred-group are not all precisely similar. Thus, expressing the matter analytically, out of a total N_1 of individuals of some group A_1, a certain fraction

$$N_1 C_1 (p, q, r, \quad . \quad . \quad . \quad) \, dp \, dq \, dr \, . \quad . \quad .$$

will have the values of certain characteristic features P, Q, R, . . . comprised between the limits

$$\begin{array}{l} p \text{ and } (p + dp) \\ q \text{ and } (q + dq) \\ r \text{ and } (r + dr) \\ . \quad . \quad . \quad . \quad . \quad . \quad . \end{array}$$

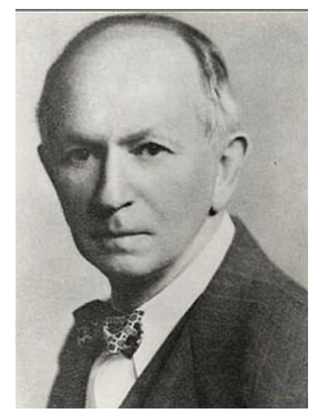
A similar statement holds for each of the other groups A_2, A_3, . . .

As time goes on both the values of N_1, N_2, . . . will in general change, and also the form of the frequency functions C_1, C_2, . . . In other words, the matter of the system undergoes a change in distribution: (1) among the several kindred-groups; (2) among the several types of individuals of which each group is composed. The former change may be spoken of as "Inter-Group Evolution," the latter as "Intra-Group Evolution."[5]

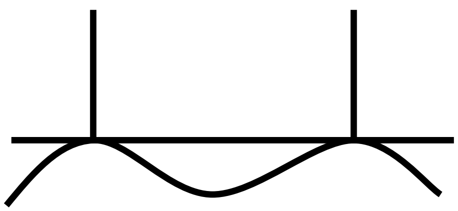
It is intra-group evolution, the change in time of the character of a species, with the possibility of the origin of a new species as its outcome, which has hitherto mainly engaged the attention of the biologist.

We, on the contrary, will here turn our attention chiefly to certain aspects of inter-group evolution.

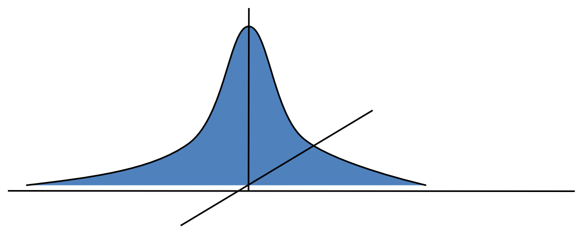
(Lotka 1912 *J Wash Acad Sci*)



Trait-Based Eco-Evolutionary Theory



ESS Maximum Approach
(Brown, Vincent)



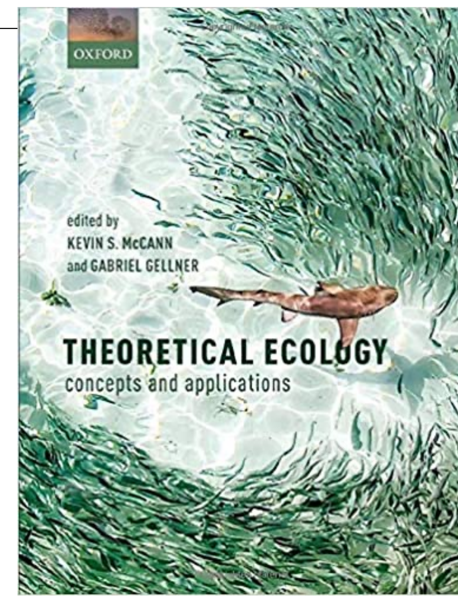
Quantitative Genetics
(Lande, Abrams)

Reviewed in:

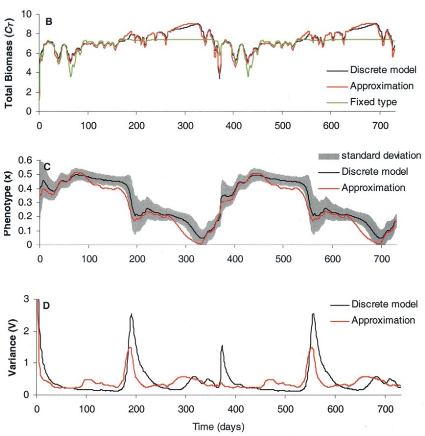
CHAPTER 11

Trait-based ecological and eco-evolutionary theory

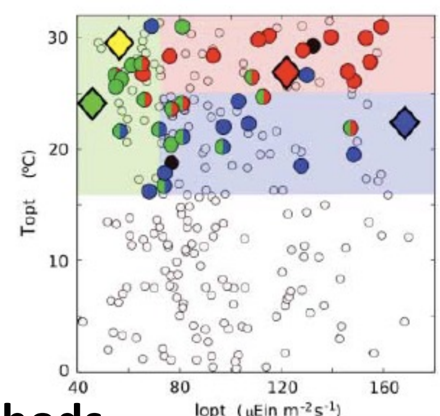
Christopher A. Klausmeier, Colin T. Kremer, and Thomas Koffel



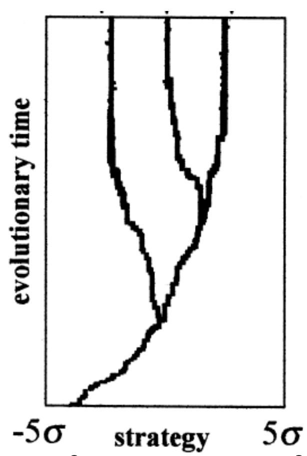
(in McCann & Gellner, *eds.*, 2020)



Ecological Moment Methods
(Wirtz, Norberg,
Webb, Savage, Bruggeman)

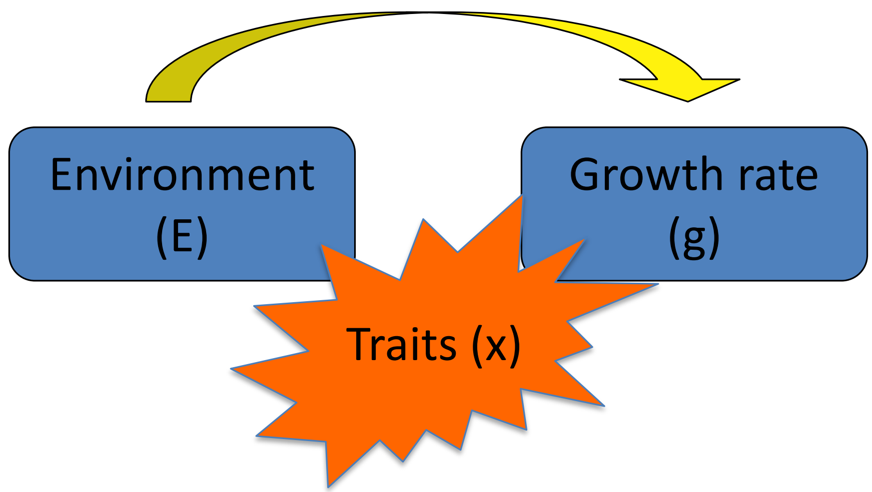


Monte Carlo
(Follows et al.)



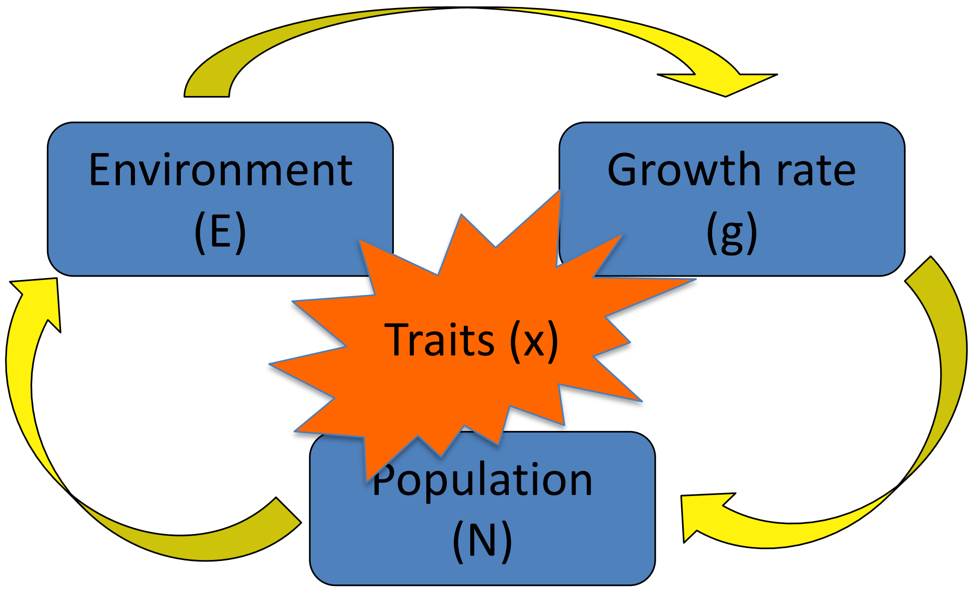
Adaptive Dynamics
(Geritz, Metz, Dieckmann, Law)

Optimization



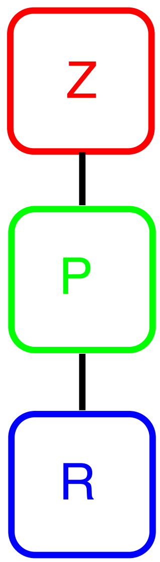
$$\frac{dN_i}{dt} = g(x_i; E)N_i$$

Game Theoretical Approach



$$\frac{dN_i}{dt} = g\left(x_i; E(\vec{x}, \vec{N}\right)N_i$$

1) Start with a mechanistic model of growth



zooplankton

$$\frac{dZ}{dt} = \left[ecP - m_Z\right]Z$$

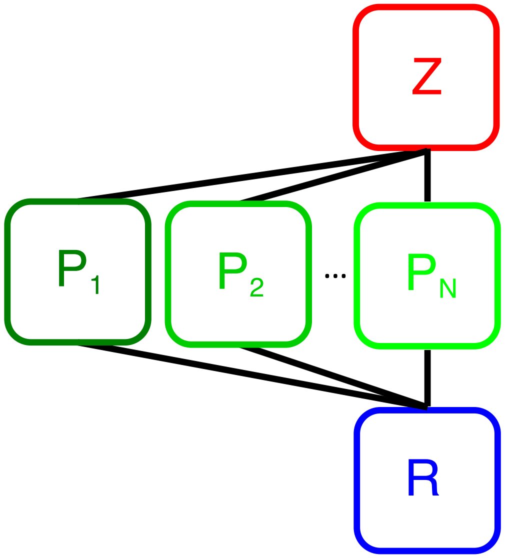
phytoplankton

$$\frac{dP}{dt} = \left[\mu \frac{R}{R+K} - m - cZ\right]P$$

nutrient

$$\frac{dR}{dt} = a(R_{in} - R) - \mu \frac{R}{R+K} QP$$

2) Generalize to $\mathcal{N}$ strategies

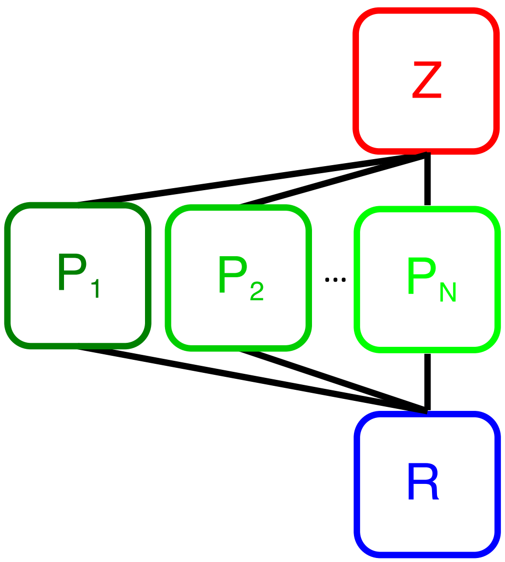


$$\frac{dZ}{dt} = \left[\sum_{j=1}^{N} e_j c_j P_j - m_Z\right] Z$$

$$\frac{dP_i}{dt} = \left[\mu_i \frac{R}{R+K_i} - m_i - c_i Z\right] P_i$$

$$\frac{dR}{dt} = a(R_{in} - R) - \sum_{j=1}^{N} \mu_j \frac{R}{R+K_j} Q_j P_j$$

3) Identify fitness



$$\frac{dZ}{dt} = \left[\sum_{j=1}^{N} e_j c_j P_j - m_Z\right] Z$$

$$\frac{dP_i}{dt} = \left[\mu_i \frac{R}{R+K_i} - m_i - c_i Z\right] P_i = g\left(x_i; E(\vec{x}, \vec{P})\right) P_i$$

$$\frac{dR}{dt} = a(R_{in} - R) - \sum_{j=1}^{N} \mu_j \frac{R}{R+K_j} Q_j P_j$$

How should we define fitness for general ecological scenarios? (Metz et al. 1992 *TREE*)

	Constant environment	Periodic environment	Aperiodic environment
Unstructured population	$\frac{dN}{dt} = gN$ fitness = g	$\frac{dN}{dt} = g(t)N$ fitness = $\frac{1}{\tau}\int_0^\tau g(t)dt$	$\frac{dN}{dt} = g(t)N$ fitness = $\lim_{\tau\to\infty} \frac{1}{\tau}\int_0^\tau g(t)dt$
Extensively structured population	$\frac{d\vec{N}}{dt} = G\vec{N}$ fitness = $\max\left[\mathrm{Re}[\lambda(G)]\right]$ (dominant eigenvalue) (Caswell 2001)	$\frac{d\vec{N}}{dt} = G(t)\vec{N}$ fitness = … (dominant Floquet exponent) (Klausmeier 2008)	$\frac{d\vec{N}}{dt} = G(t)\vec{N}$ fitness = … (dominant Lyapunov exponent) (Metz et al. 1992)

Separation of Time Scales in Adaptive Dynamics

evolution, dx/dt ecology, dN/dt

$$\frac{dN_i}{dt} = g(x_i)N_i = 0$$

Either: $N_i = 0$ or $g(x_i) = 0$

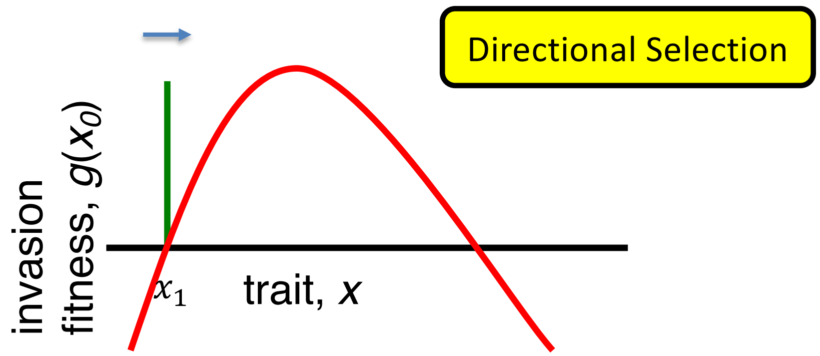
(Geritz *et al*. 1998, *Evol Ecol*)

Evolutionary Equilibria & Their Stability

<u>Eco Eq:</u>

$g(x_1) = 0$

$$\left.\frac{\partial g}{\partial x_0}\right|_{x_1} > 0$$



(Geritz *et al*. 1998, *Evol Ecol*)

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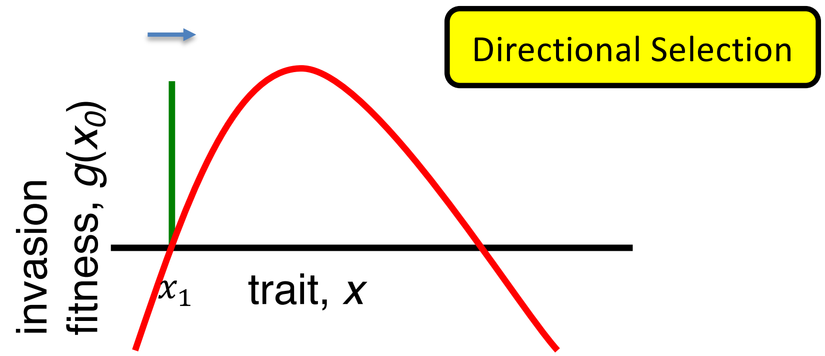
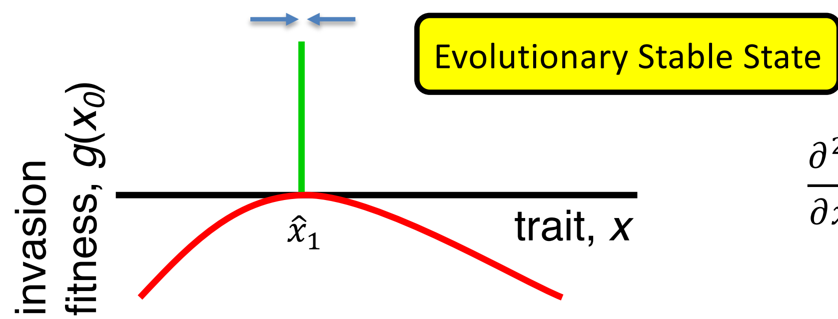


<u>Eco Eq:</u>

$g(\hat{x}_1) = 0$

<u>Evo Eq:</u>

$$\left.\frac{\partial g}{\partial x_0}\right|_{\hat{x}_1} = 0$$



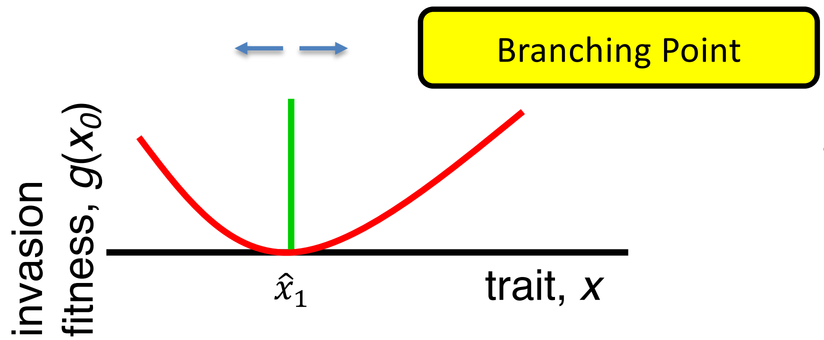
$$\left.\frac{\partial^2 g}{\partial x_0^2}\right|_{\hat{x}_1} < 0$$

(Geritz *et al*. 1998, *Evol Ecol*)

Evolutionary Equilibria & Their Stability

Eco Eq:
$g(\hat{x}_1) = 0$

Evo Eq:
$$\left.\frac{\partial g}{\partial x_0}\right|_{\hat{x}_1} = 0$$



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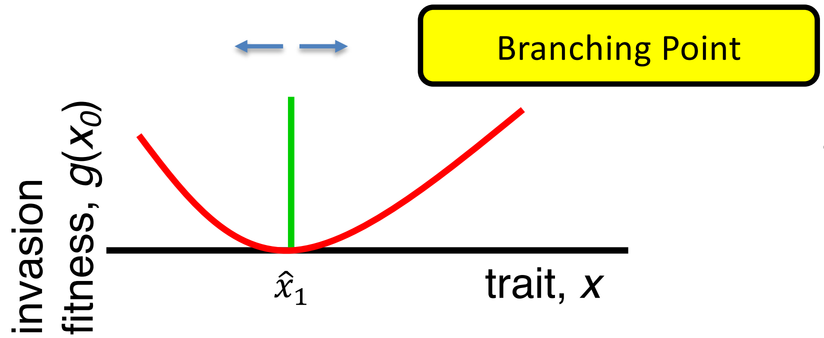
Evolutionary Equilibria & Their Stability

Eco Eq:
$g(\hat{x}_1) = 0$

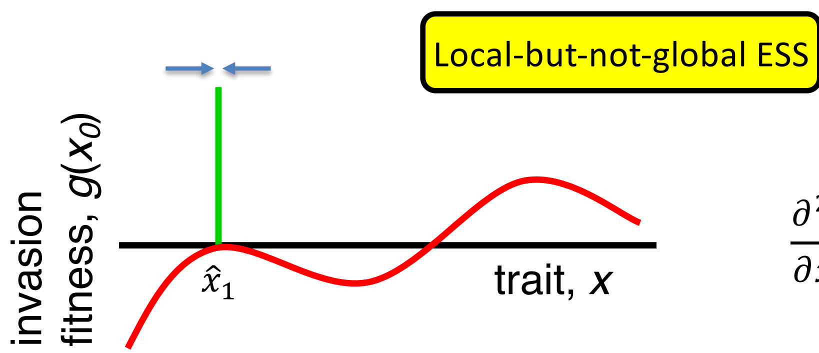
Evo Eq:
$\left.\frac{\partial g}{\partial x_0}\right|_{\hat{x}_1} = 0$



$\left.\frac{\partial^2 g}{\partial x_0^2}\right|_{\hat{x}_1} > 0$

Eco Eq:
$g(\hat{x}_1) = 0$

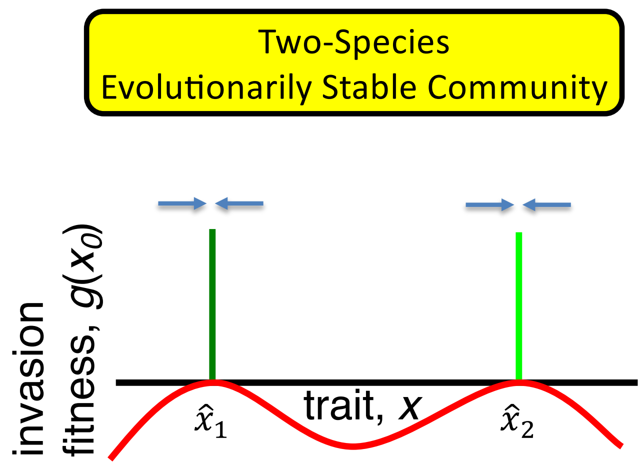
Evo Eq:
$\left.\frac{\partial g}{\partial x_0}\right|_{\hat{x}_1} = 0$



$\left.\frac{\partial^2 g}{\partial x_0^2}\right|_{\hat{x}_1} < 0, \exists x \text{ s.t. } g(x) > 0$

(Geritz *et al*. 1998, *Evol Ecol*)

Evolutionary Equilibria & Their Stability



Eco Eq:

$g(\hat{x}_1) = 0,$
$g(\hat{x}_2) = 0$

Evo Eq:

$$\left.\frac{\partial g}{\partial x_0}\right|_{\hat{x}_1} = 0, \left.\frac{\partial g}{\partial x_0}\right|_{\hat{x}_2} = 0$$

$$\left.\frac{\partial^2 g}{\partial x_0^2}\right|_{\hat{x}_1} < 0,$$

$$\left.\frac{\partial^2 g}{\partial x_0^2}\right|_{\hat{x}_2} < 0$$

$$g(x) \leq 0 \; \forall x$$

(Geritz *et al*. 1998, *Evol Ecol*)

Evolutionary Equilibria & Their Stability

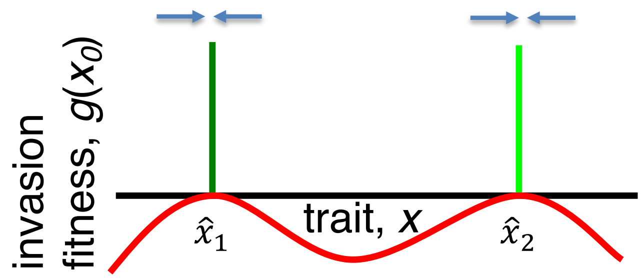
Two-Species
Evolutionarily Stable Community

<u>Eco Eq:</u>

$$g(\hat{x}_1) = 0, \quad g(\hat{x}_2) = 0$$

<u>Evo Eq:</u>

$$\left.\frac{\partial g}{\partial x_0}\right|_{\hat{x}_1} = 0, \left.\frac{\partial g}{\partial x_0}\right|_{\hat{x}_2} = 0$$



$$\left.\frac{\partial^2 g}{\partial x_0^2}\right|_{\hat{x}_1} < 0, \quad \left.\frac{\partial^2 g}{\partial x_0^2}\right|_{\hat{x}_2} < 0$$

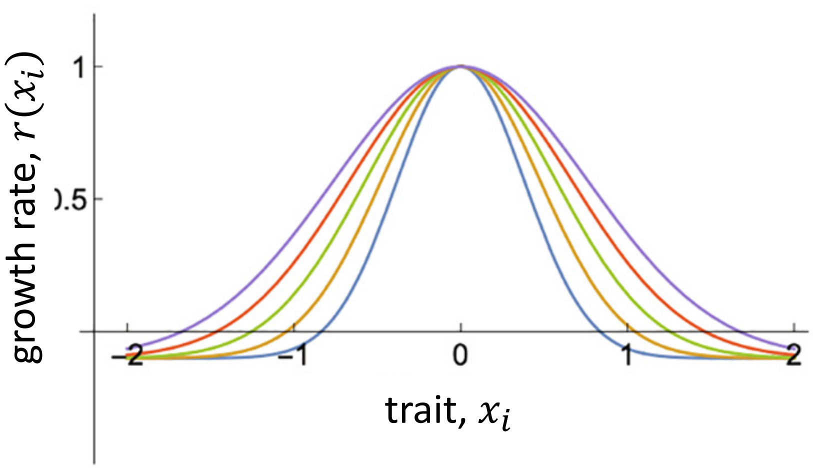
$$g(x) \leq 0 \ \forall x$$

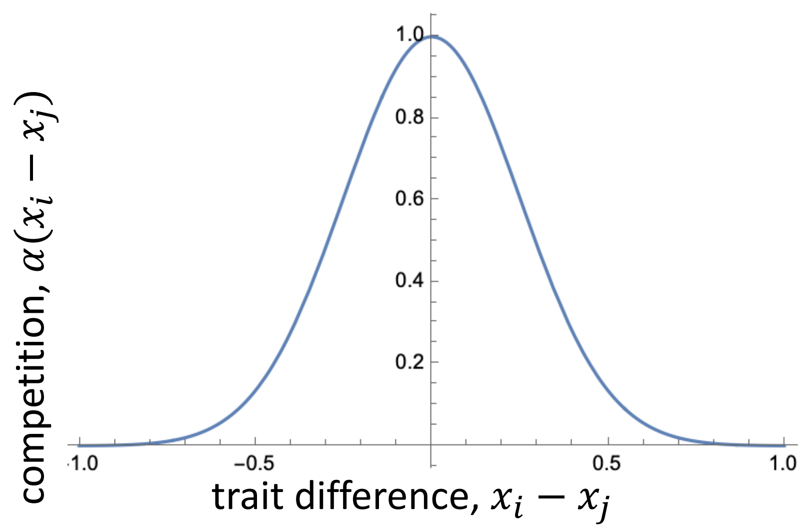
☞ An ESC is an endpoint of evolution AND community assembly (Edwards *et al*. 2018 *Ecol Let*)

(Geritz *et al*. 1998, *Evol Ecol*)

Example: Lotka-Volterra Competition

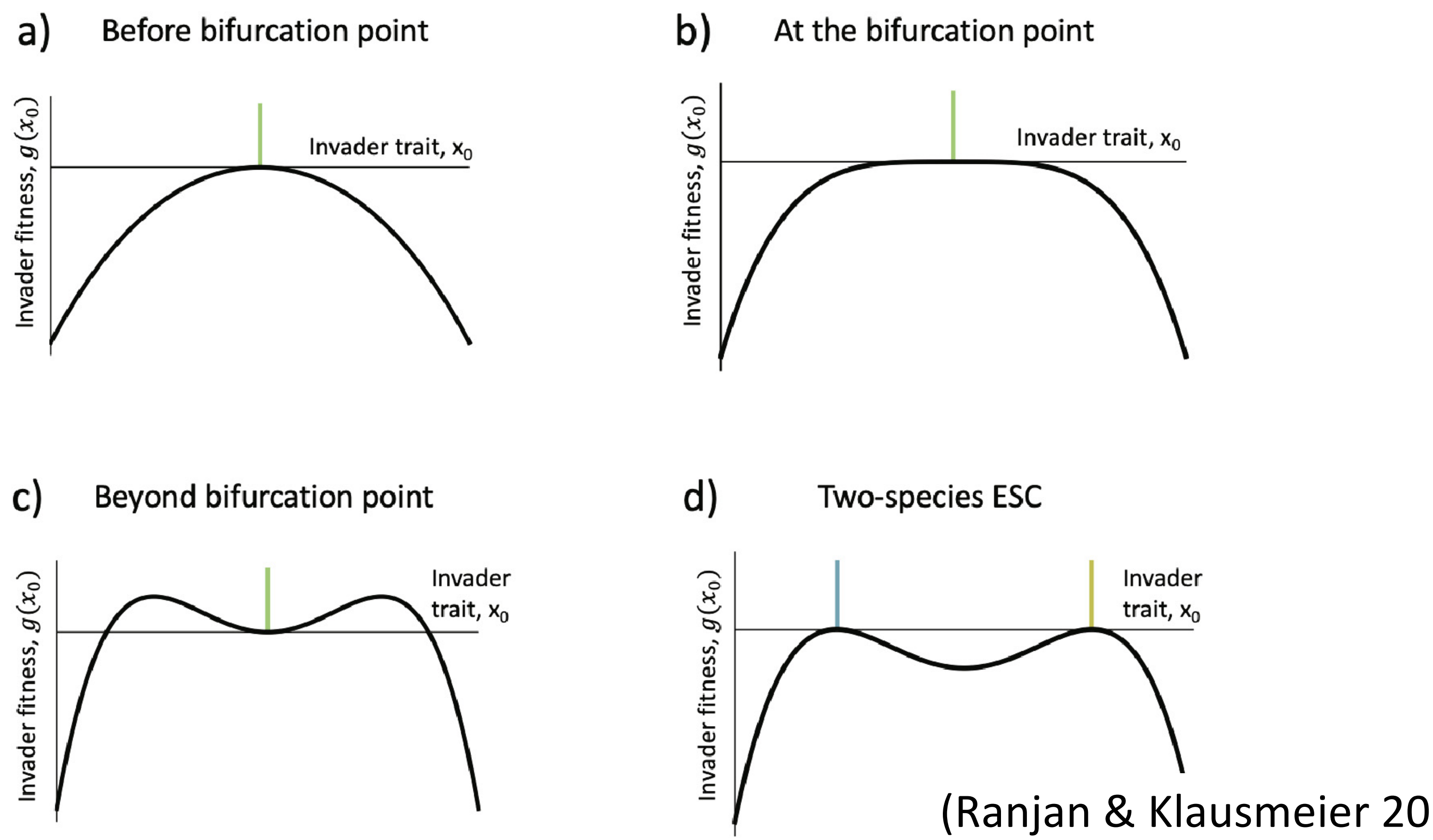
$$\frac{dN_i}{dt} = g(x_i)N_i = \left(r(x_i) - \sum_{j=1}^{\mathcal{N}} \alpha(x_i, x_j)N_j \right) N_i$$





(Ranjan & Klausmeier 2022 *JTB*)

Expanding the resource distribution



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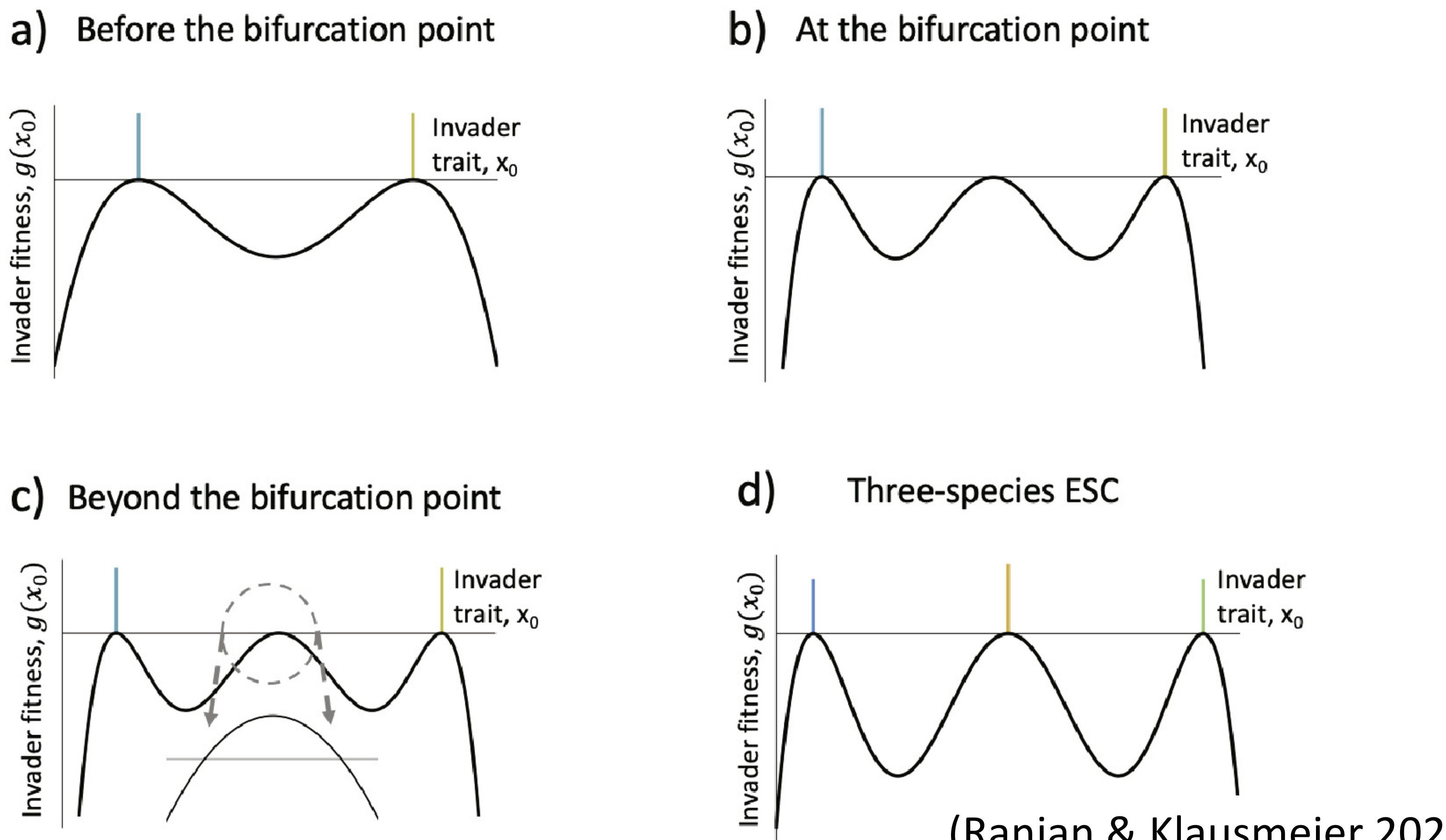
Expanding the resource distribution



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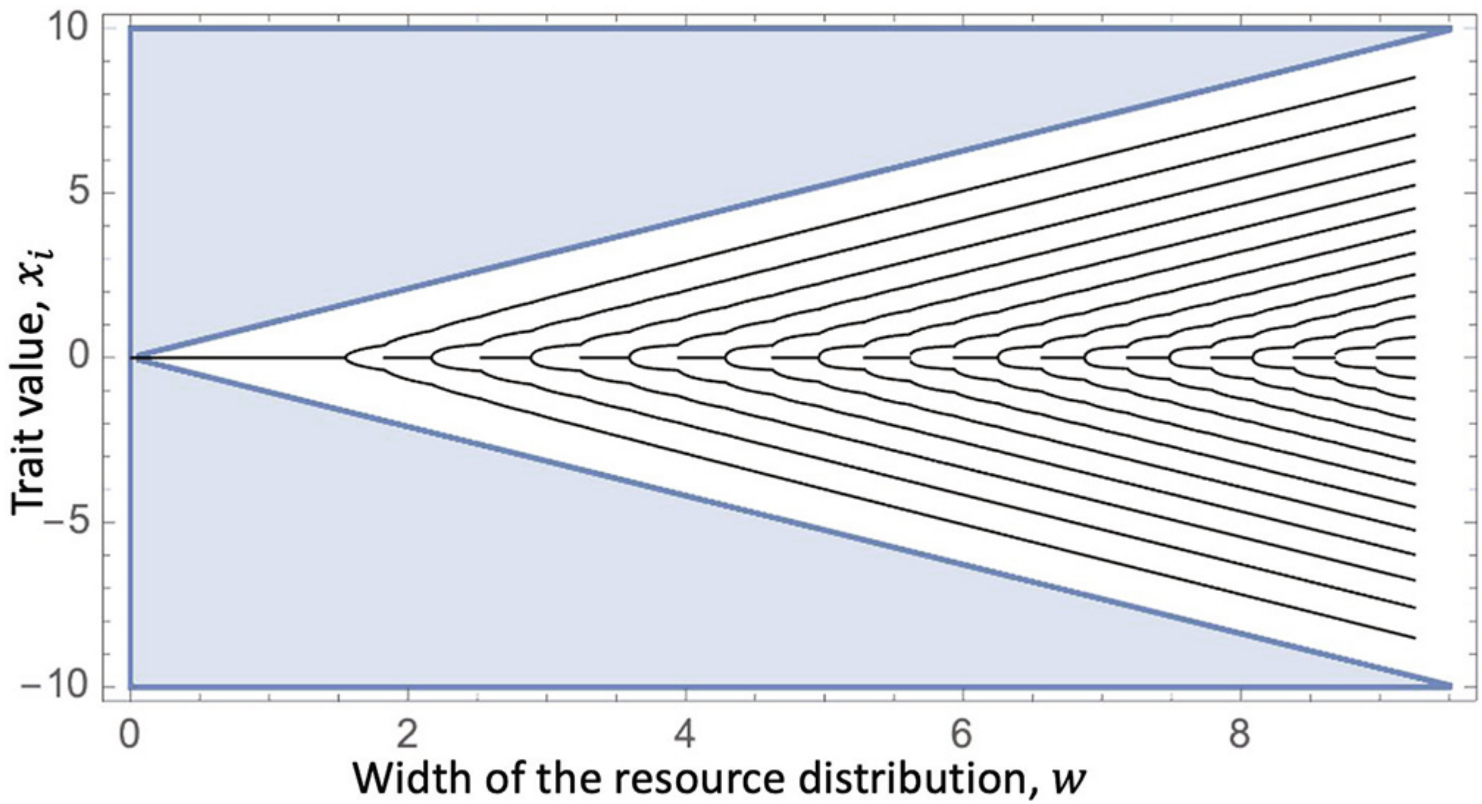
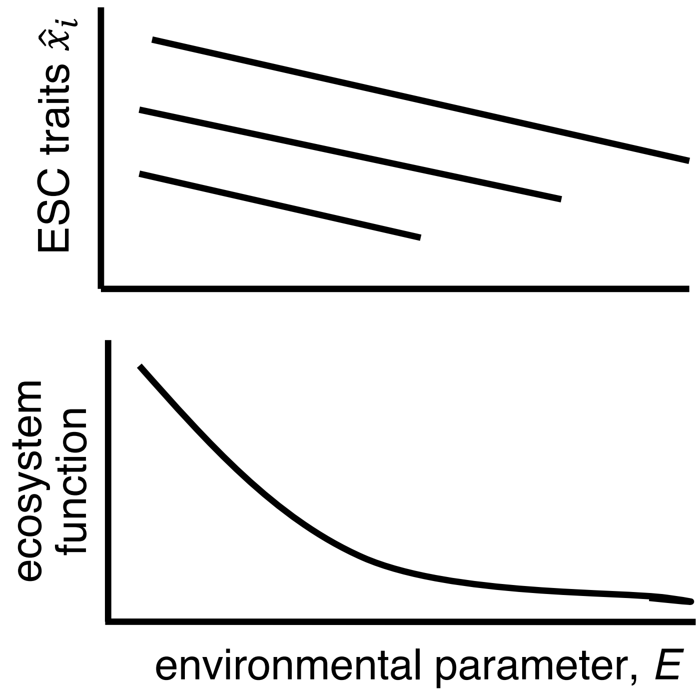
Example: Lotka-Volterra Competition



(Ranjan & Klausmeier 2022 *JTB*)

Eco-evolutionary Bifurcation Diagrams

- How do community structure (diversity, species traits) and ecosystem functions depend on abiotic environmental parameters?
- How will ecosystems reorganize in the face of human impacts?



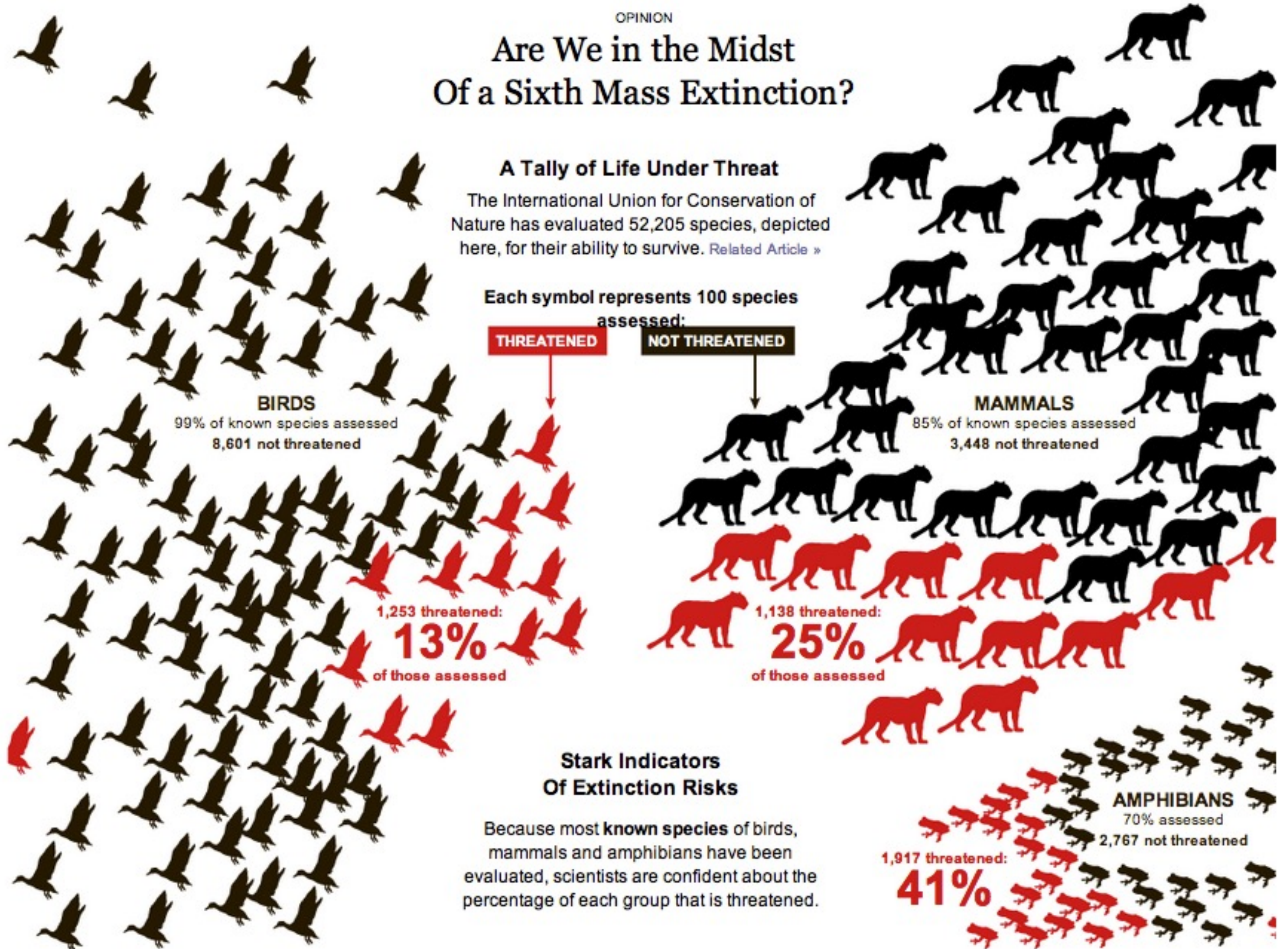
Separation of Time Scales in Adaptive Dynamics

environmental change,
dE/dt

evolution, dx/dt

ecology, dN/dt

Predicting Population Responses to Environmental Change



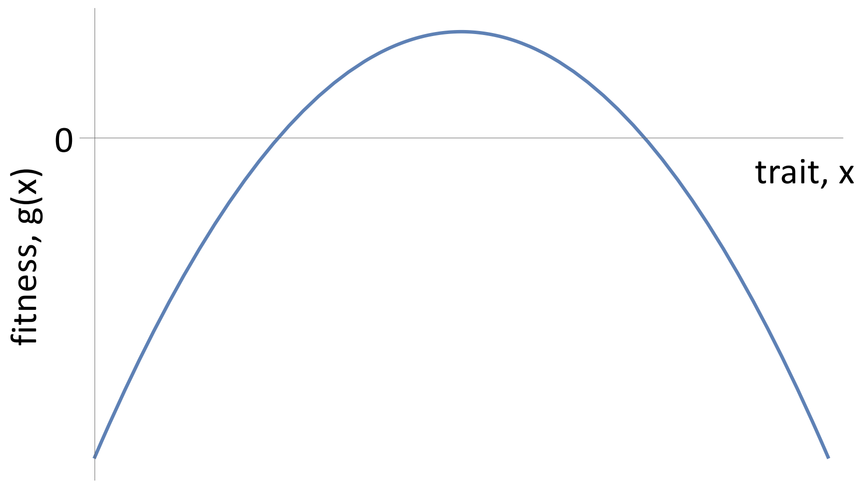
Bill Marsh, New York Times

III. Evolutionary Rescue

evolutionary rescue — the recovery and persistence of a population through natural selection acting on heritable variation

Charles Darwin GIF by Diego Sanches

Evolution in a constant environment



Quantitative Genetics:

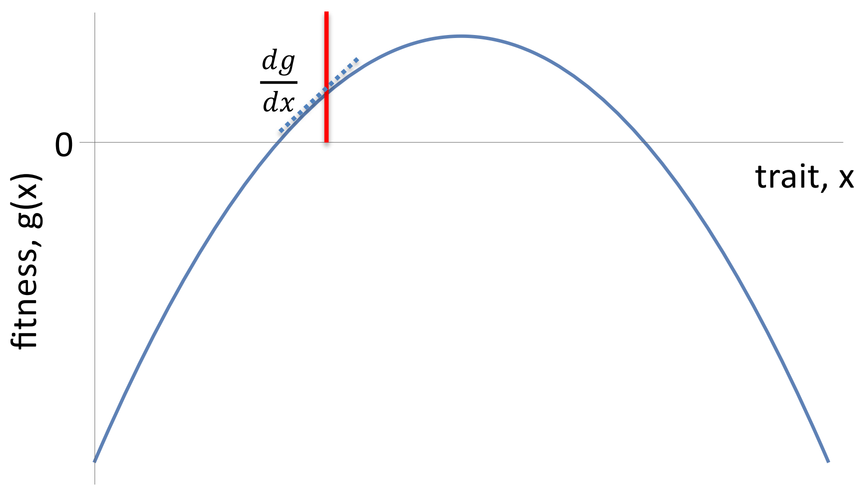
$$\frac{dx}{dt} = V\frac{dg}{dx}$$

Population Dynamics:

$$\frac{dN}{dt} = g(x)N$$

Lynch M, Lande R (1993) Evolution and extinction in response to environmental change. In: Kareiva P, Kingsolver J, Huey R (eds) Biotic Interactions and Global Change. Sinauer, pp 234–250

Evolution in a constant environment



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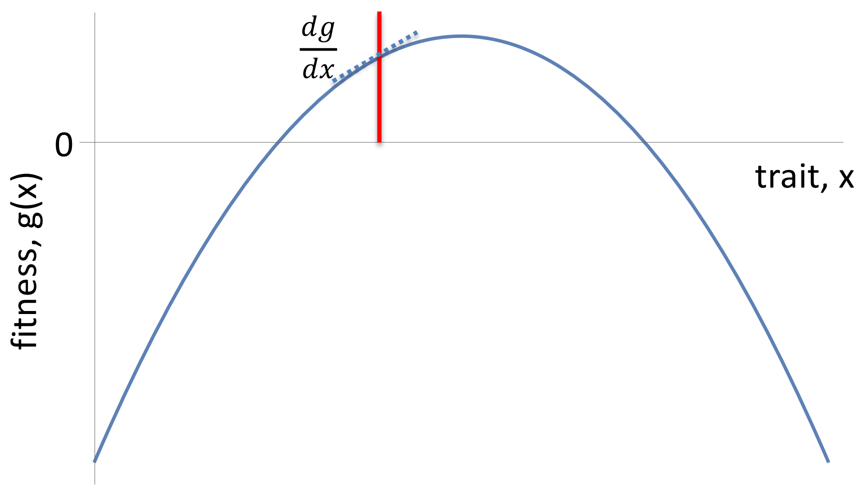

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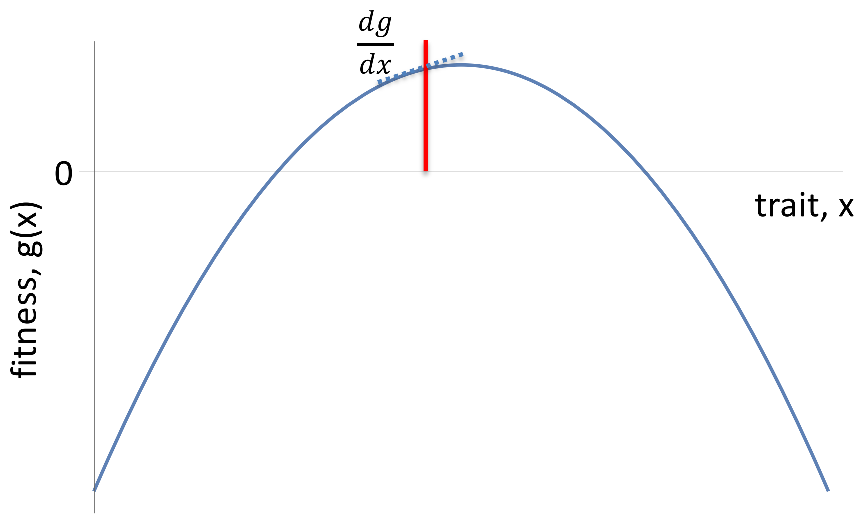

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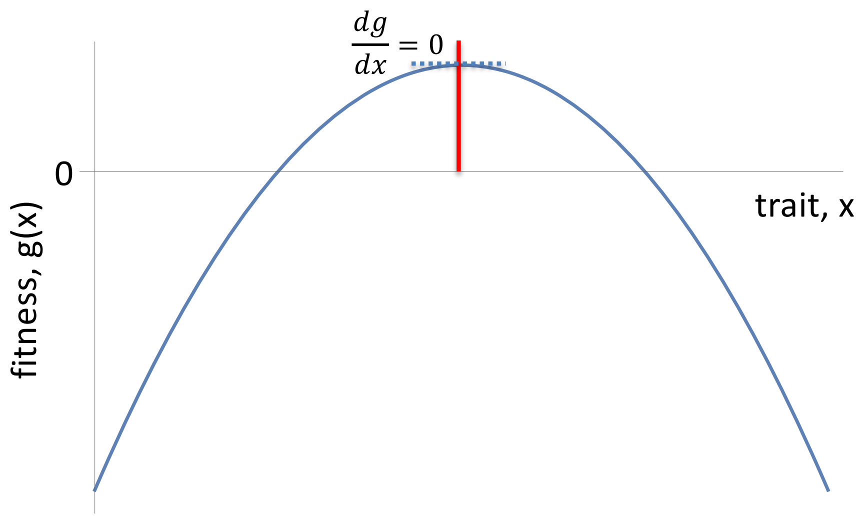
Evolution in a constant environment



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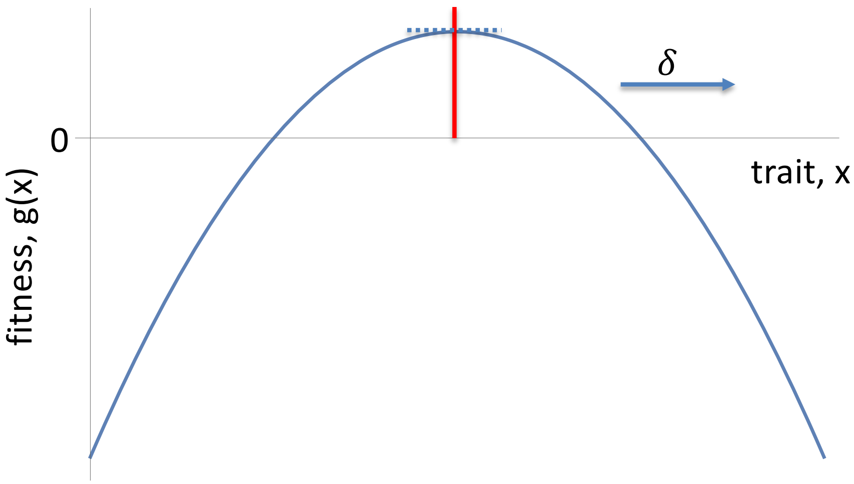
Evolution in a changing environment



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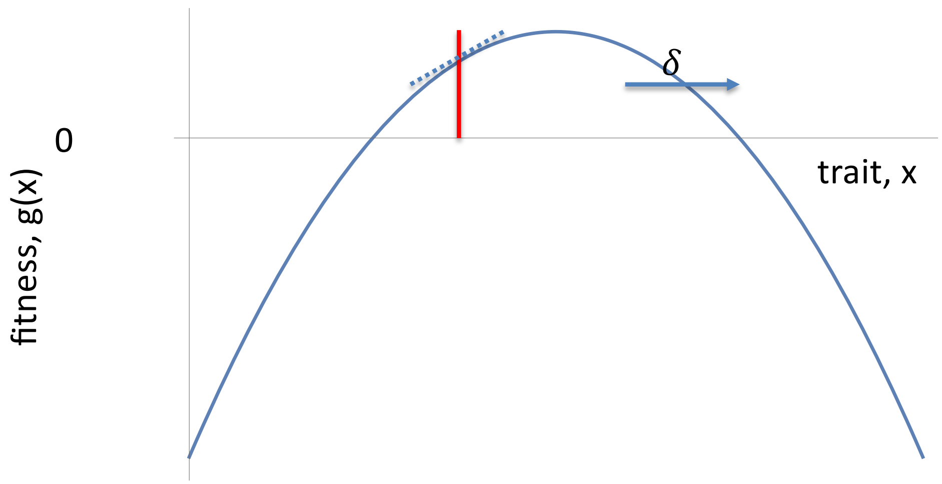
Lynch M, Lande R (1993) Evolution and extinction in response to environmental change. In: Kareiva P, Kingsolver J, Huey R (eds) Biotic Interactions and Global Change. Sinauer, pp 234–250

Evolution in a changing environment



Quantitative Genetics:

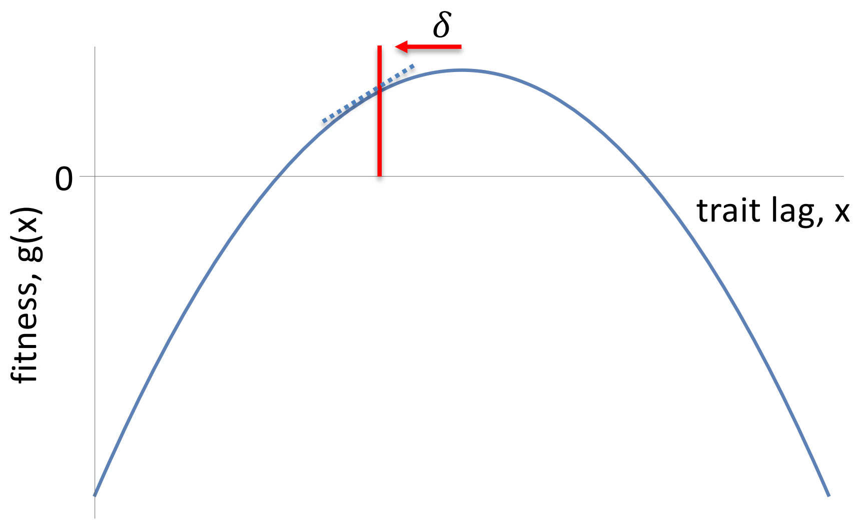
$$\frac{dx}{dt} = V\frac{dg}{dx}$$

Population Dynamics:

$$\frac{dN}{dt} = g(x)N$$

Lynch M, Lande R (1993) Evolution and extinction in response to environmental change. In: Kareiva P, Kingsolver J, Huey R (eds) Biotic Interactions and Global Change. Sinauer, pp 234–250

Clever trick: moving frame of reference



Quantitative Genetics:

$$\frac{dx}{dt} = V\frac{dg}{dx} - \delta$$

Population Dynamics:

$$\frac{dN}{dt} = g(x)N$$

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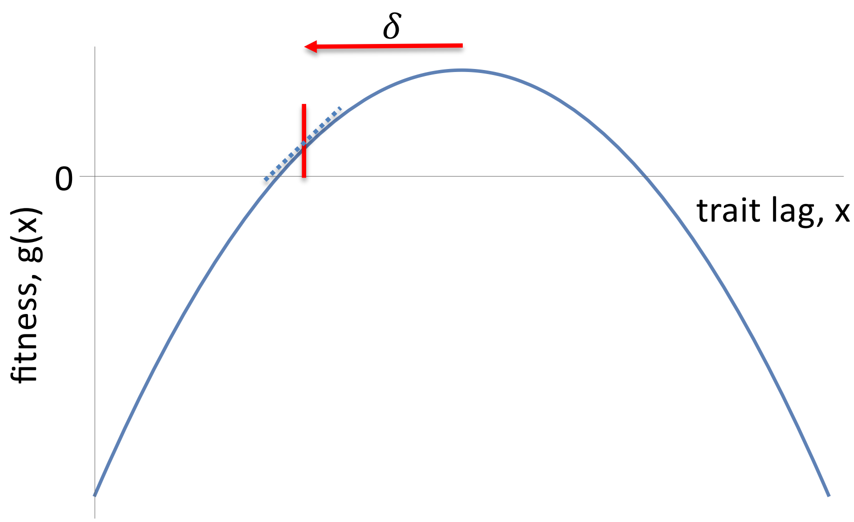

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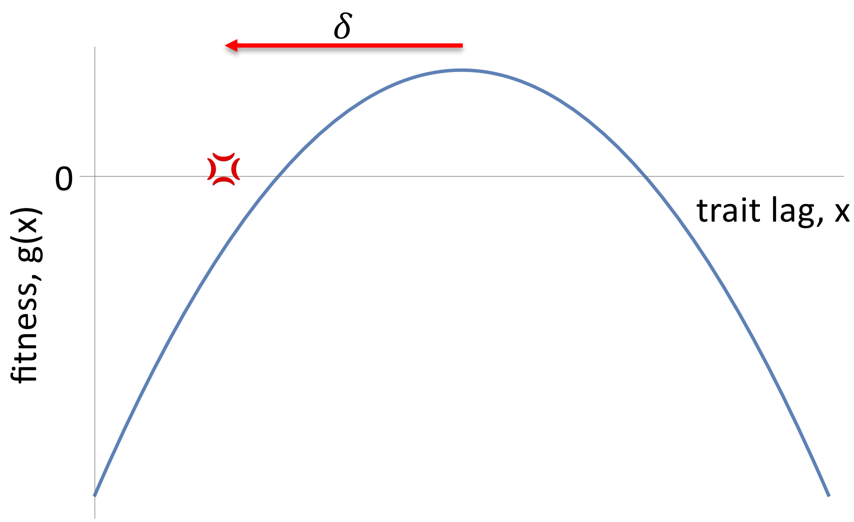

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Lynch & Lande (1993) Conclusions

1) Environmental change causes trait to lag optimum
2) Equilibrium lag increases linearly with rate of environmental change δ
3) Increased genetic variance *V* helps species keep up
4) There is a critical rate of environmental change δ_c where $g(\hat{x}) = 0$ that leads to extinction

Lynch M, Lande R (1993) Evolution and extinction in response to environmental change. In: Kareiva P, Kingsolver J, Huey R (eds) Biotic Interactions and Global Change. Sinauer, pp 234–250

PHILOSOPHICAL TRANSACTIONS B

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Research

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One contribution of 17 to a theme issue 'Integrative research perspectives on marine conservation'.

Subject Areas:
ecology, evolution

Keywords:
climate change, eco-evolutionary dynamics, environmental change, evolutionary rescue, moving optimum, quantitative genetics

Ecological limits to evolutionary rescue

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Environments change, for both natural and anthropogenic reasons, which can threaten species persistence. Evolutionary adaptation is a potentially powerful mechanism to allow species to persist in these changing environments. To determine the conditions under which adaptation will prevent extinction (evolutionary rescue), classic quantitative genetics models have assumed a constantly changing environment. They predict that species traits will track a moving environmental optimum with a lag that approaches a constant. If fitness is negative at this lag, the species will go extinct. There have been many elaborations of these models incorporating increased genetic realism. Here, we review and explore the consequences of four ecological complications: non-quadratic fitness functions, interacting density- and trait-dependence, species interactions and fundamental limits to adaptation. We show that non-quadratic fitness functions can result in evolutionary tipping points and existential crises, as can the interaction between density- and trait-dependent mortality. We then review the literature on how interspecific interactions affect adaptation and persistence. Finally, we suggest an alternative theoretical framework that considers bounded environmental change and fundamental limits to adaptation. A research programme that combines theory and experiments and integrates across organizational scales will be needed to predict whether adaptation will prevent species extinction in changing environments.

This article is part of the theme issue 'Integrative research perspectives on marine conservation'.

Ecological Complications

1) Non-quadratic fitness functions
2) Population regulation
3) Community context
4) Fundamental niche limits

Ecological Complications

1) Non-quadratic fitness functions
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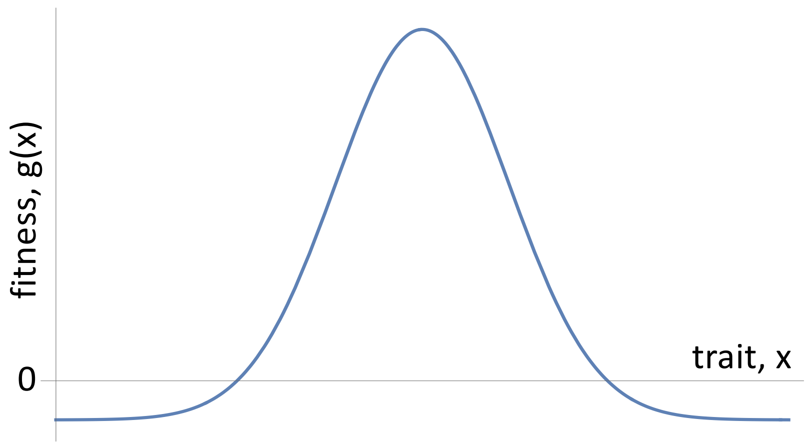
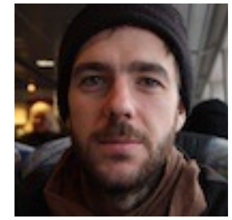
Gaussian Fitness Function





Matt Osmond
(Toronto)

Quantitative Genetics:

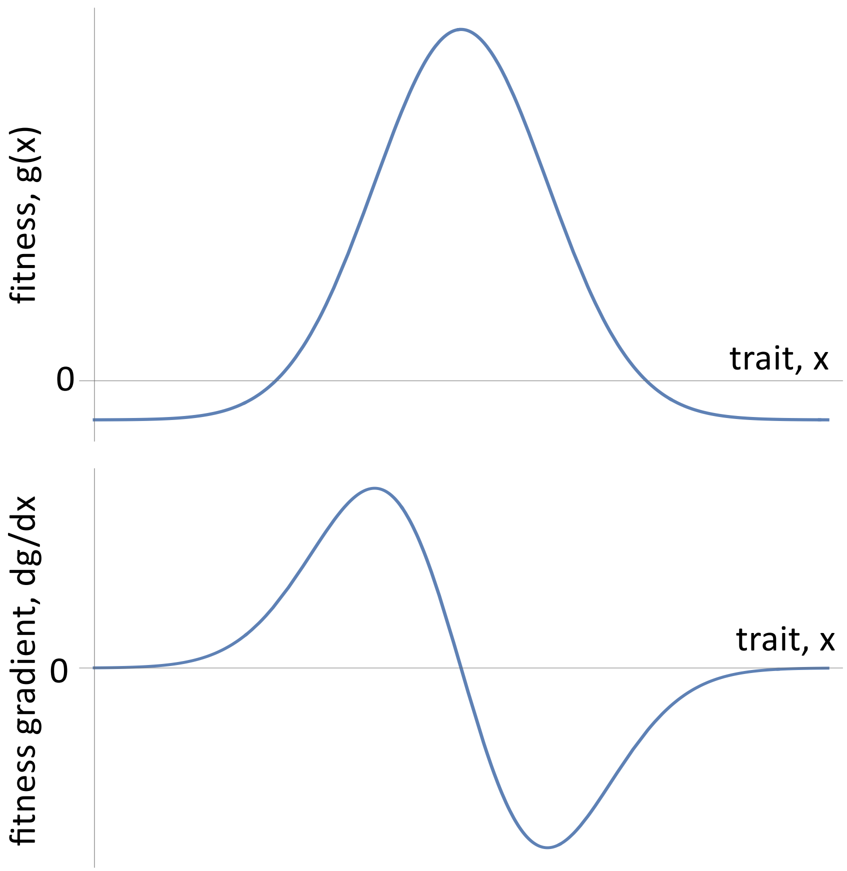
$$\frac{dx}{dt} = V\frac{dg}{dx} - \delta$$

Population Dynamics:

$$\frac{dN}{dt} = g(x)N$$

Osmond MM, Klausmeier CA (2017) An evolutionary tipping point in a changing environment. Evolution 71:2930–2941

Gaussian Fitness Function



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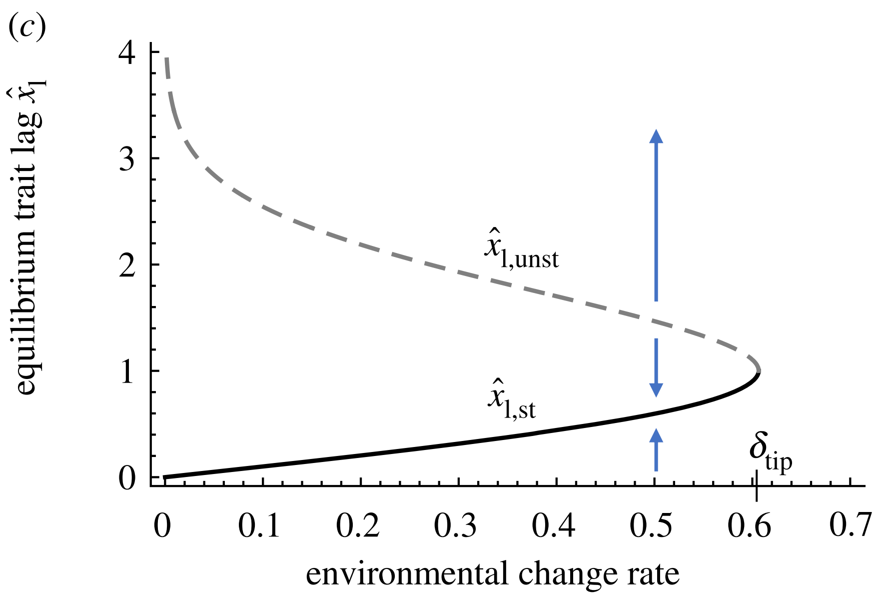
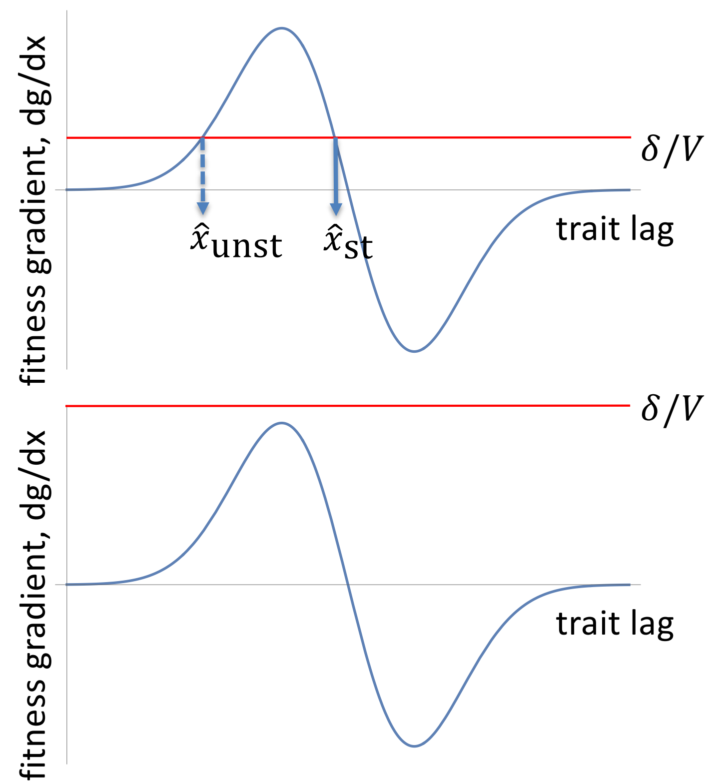
Existential Crises & Evolutionary Tipping Points





Osmond MM, Klausmeier CA (2017) An evolutionary tipping point in a changing environment. Evolution 71:2930–2941

Ecological Complications

1) Non-quadratic fitness functions
2) Population regulation
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4) Fundamental niche limits

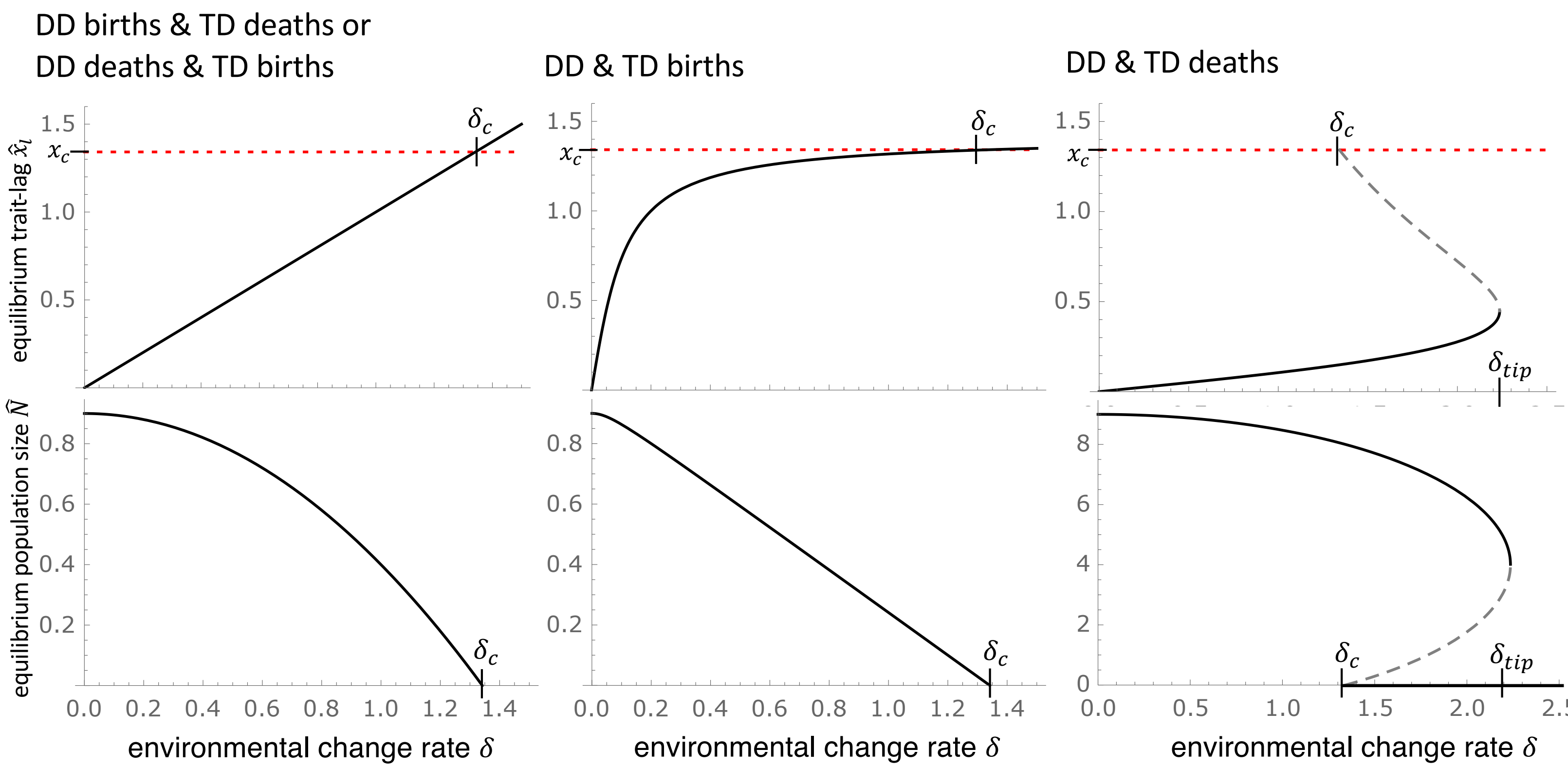
Population Regulation

Density-dependence (DD) & trait-dependence (TD) of growth can each affect births & deaths

Trait-Dependence	Density-Dependence	Growth Rate, $g(x, E, N)$
Births	Deaths	$\left(b_{\max} - \frac{(x-E)^2}{2\sigma_r^2}\right) - d(1+N)$
Deaths	Births	$b(1-N) - \left(d_{\min} + \frac{(x-E)^2}{2\sigma_r^2}\right)$
Births	Births	$\left(b_{\max} - \frac{(x-E)^2}{2\sigma_r^2}\right)(1-N) - d$
Deaths	Deaths	$b - \left(d_{\min} + \frac{(x-E)^2}{2\sigma_r^2}\right)(1+N)$

Klausmeier CA, Osmond MM, Kremer CT, Litchman E (2020) Ecological limits to evolutionary rescue. Phil Trans R Soc B 375:20190453

Equilibrium trait-lag & abundance



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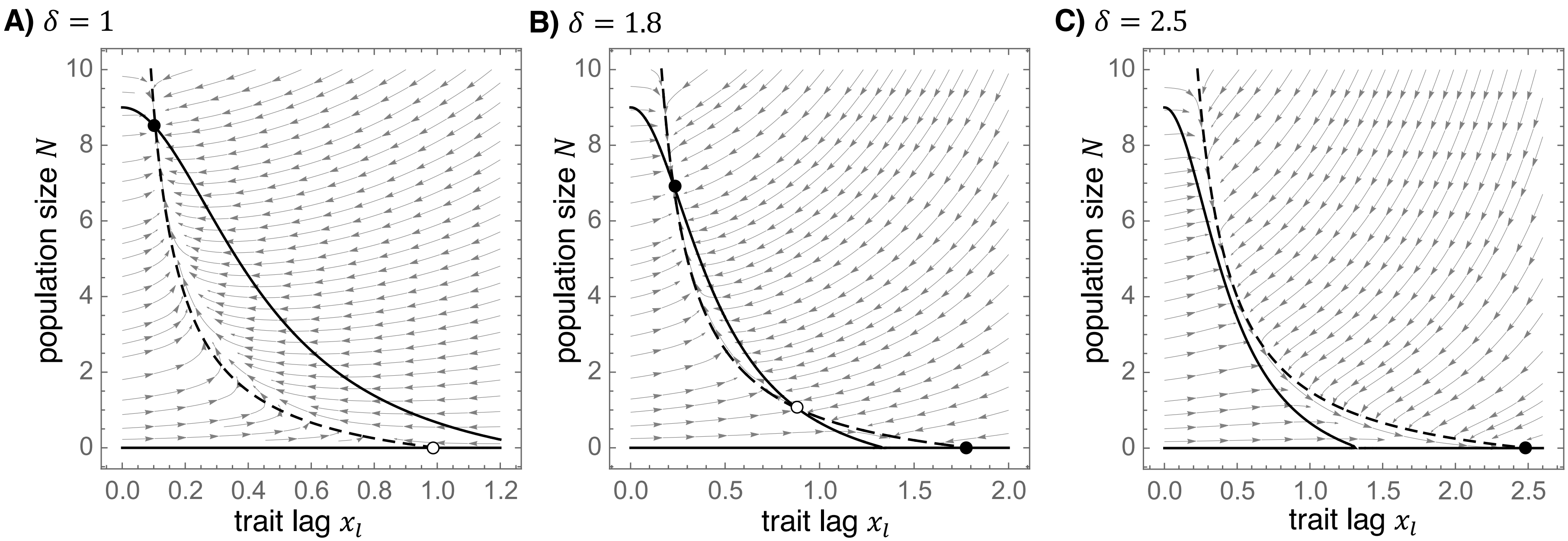
Eco-evo phase planes (DD & TD deaths)



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Ecological Complications

1) Non-quadratic fitness functions
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Predator-prey

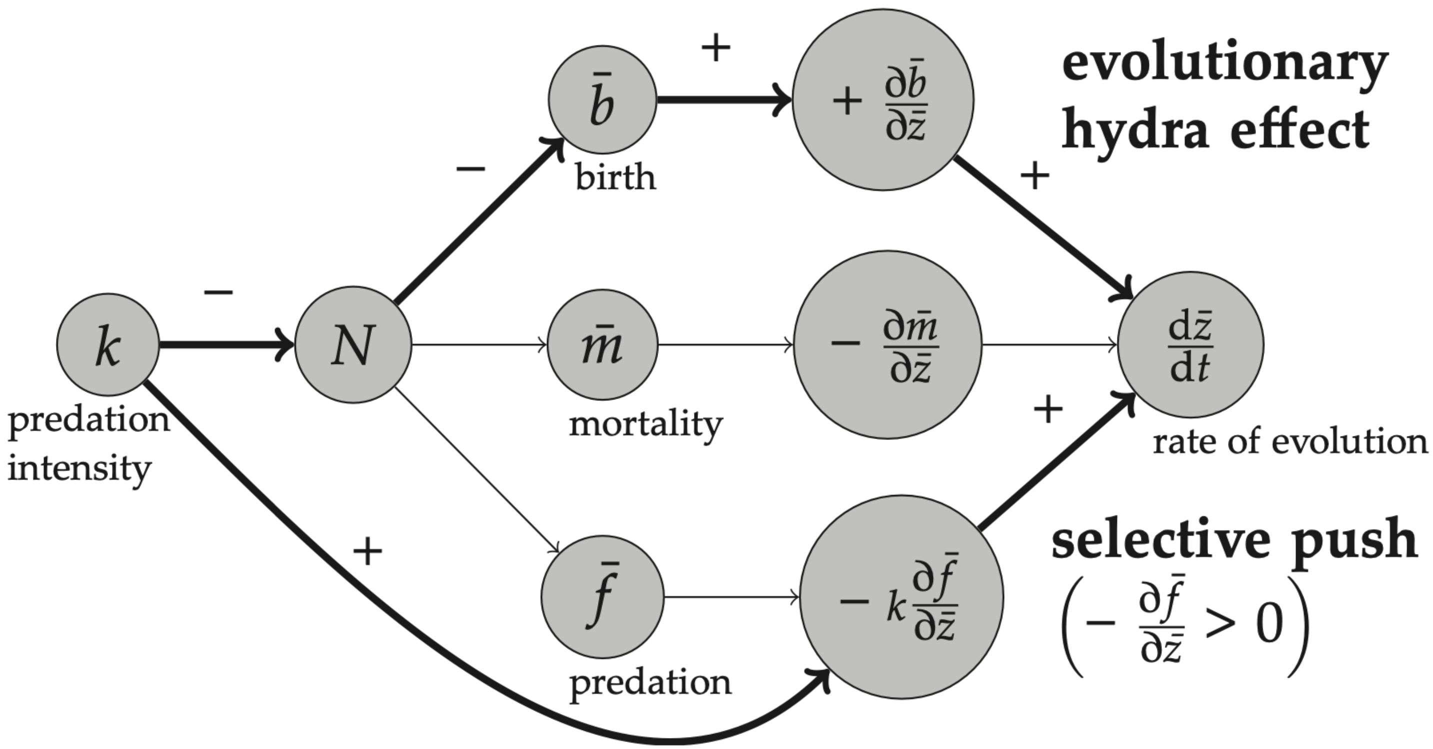
- Death due to predation from a generalist predator (*k* is strength of predation)

$$\frac{dN}{dt} = \left[\bar{b}(\bar{z}, N) - \bar{m}(\bar{z}, N) - k\bar{f}(\bar{z}, N)\right]N$$

- Does predator help prey *adapt* and *persist* in changing environments?

Osmond MM, Otto SP, Klausmeier CA (2017) When predators help prey adapt and persist in a changing environment. American Naturalist 190: 83–98.

Two ways predators help prey adapt



Osmond MM, Otto SP, Klausmeier CA (2017) When predators help prey adapt and persist in a changing environment. American Naturalist 190: 83–98.

Two ways predators help prey persist

Predators help prey persist if…

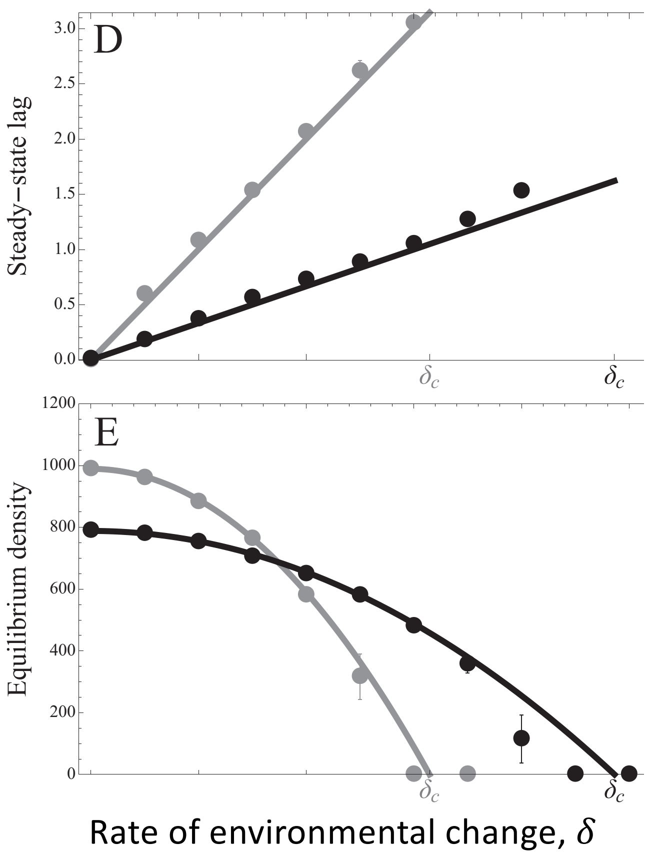
$$\frac{d\delta_c}{dk} = V_A\left(\frac{\partial^2 g}{\partial \bar{z}\,\partial k} + \frac{\partial \bar{z}_c}{\partial k}\cdot\frac{\partial^2 g}{\partial \bar{z}^2}\right) > 0$$

$$\left(\begin{bmatrix}\text{selective}\\ \text{push}\end{bmatrix} + \begin{bmatrix}\text{evolutionary}\\ \text{hydra}\\ \text{effect}\end{bmatrix}\cdot\begin{bmatrix}\text{fitness}\\ \text{function}\\ \text{curvature}\end{bmatrix}\right) > 0$$

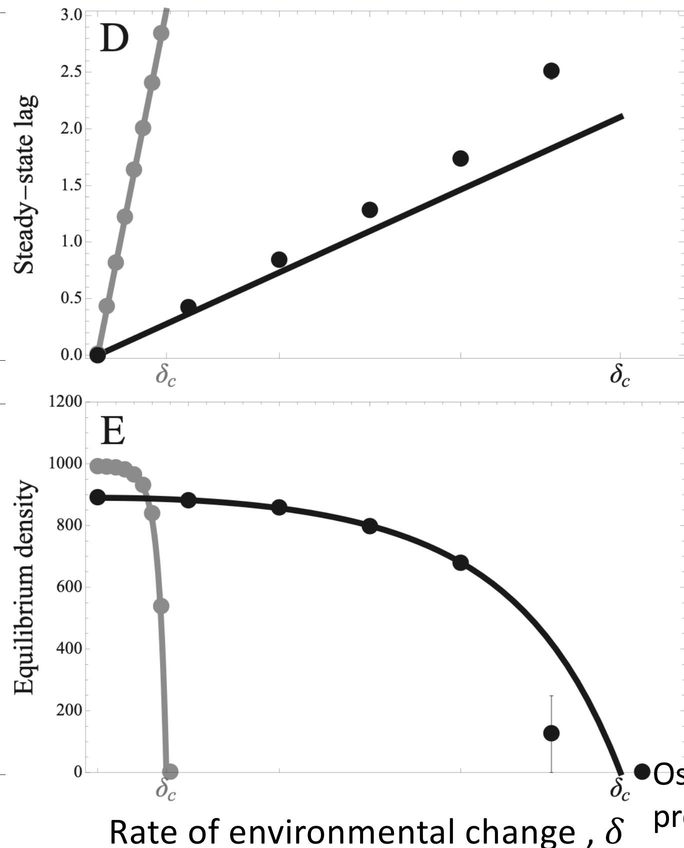
Osmond MM, Otto SP, Klausmeier CA (2017) When predators help prey adapt and persist in a changing environment. American Naturalist 190: 83–98.

Two ways predators help prey persist

Selective push



Evol. hydra effect * positive curvature



With predation

Without predation

Osmond MM, Otto SP, Klausmeier CA (2017) When predators help prey adapt and persist in a changing environment. American Naturalist 190: 83–98.

Ecological Complications

1) Non-quadratic fitness functions
2) Population regulation
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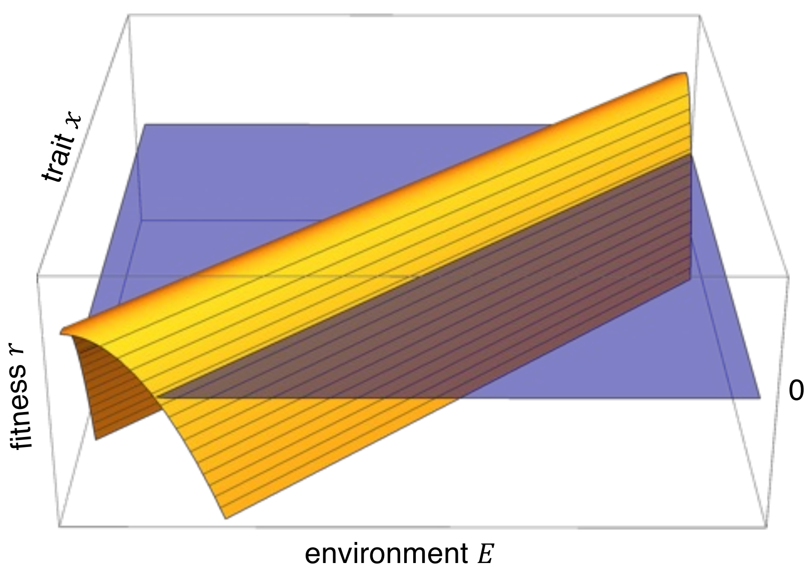
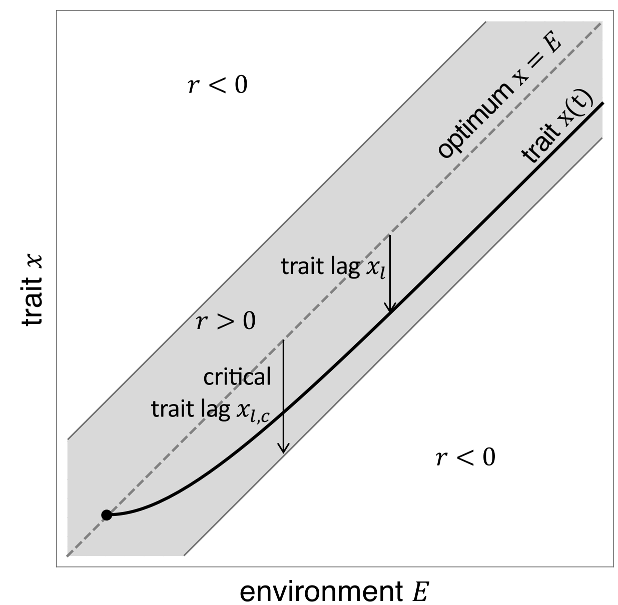
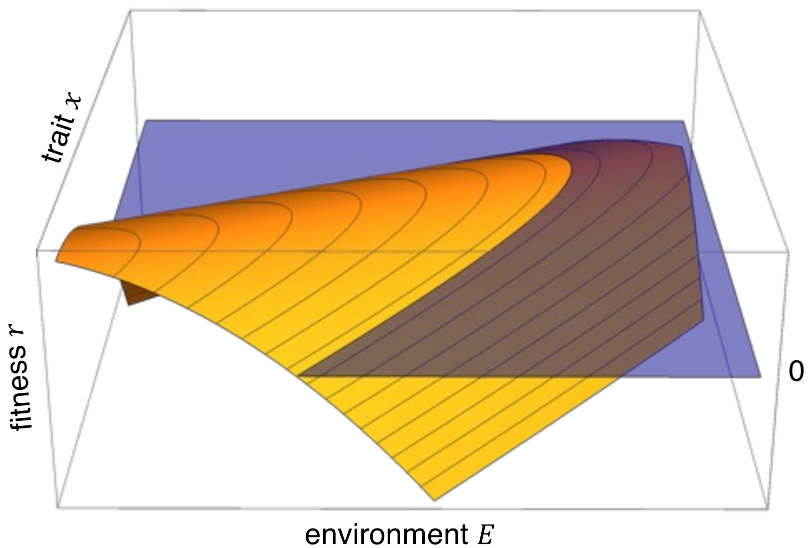
Continuous environmental change

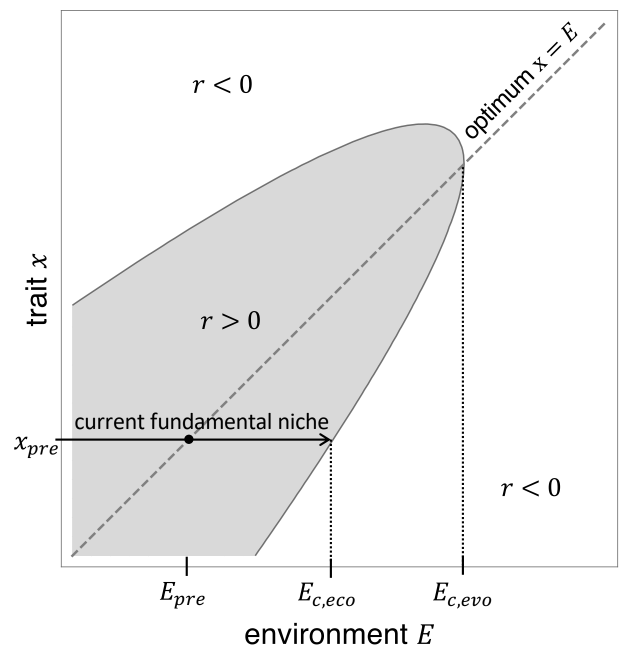




Klausmeier CA, Osmond MM, Kremer CT, Litchman E (2020) Ecological limits to evolutionary rescue. Phil Trans R Soc B 375:20190453

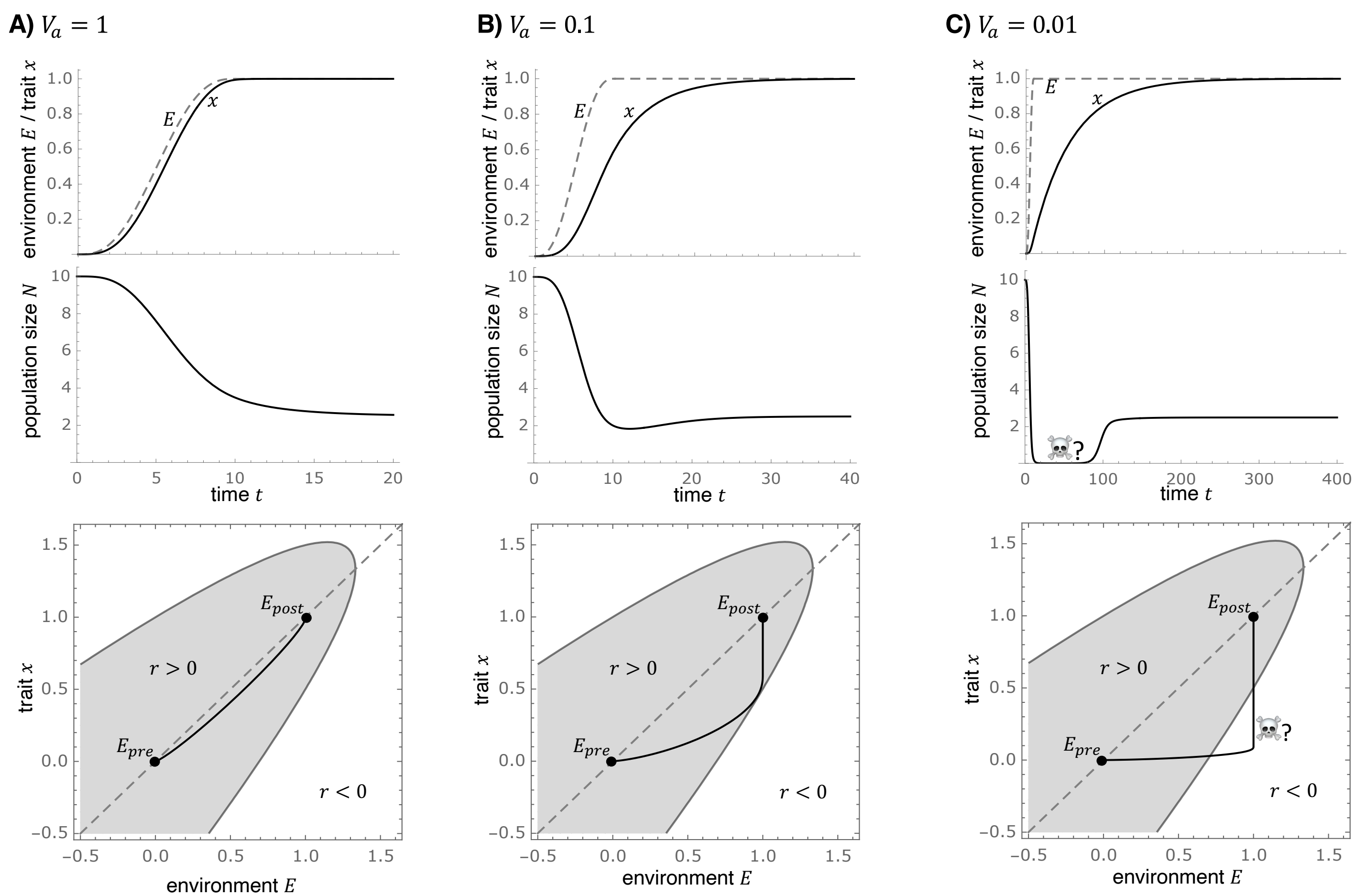
Fundamental niche limits





Klausmeier CA, Osmond MM, Kremer CT, Litchman E (2020) Ecological limits to evolutionary rescue. Phil Trans R Soc B 375:20190453

Speed of adaptation still matters



III. Conclusions

- Non-quadratic fitness functions and the interplay between density-dependence & trait-dependence can lead to *evolutionary tipping points* and *existential crises*
- Community context matters: predators can help prey adapt & persist, trailing-edge competitors at heightened risk
- Fundamental niche limits might constrain evolutionary rescue more than rate-dependent processes

Norberg J, Urban MC, Vellend M, Klausmeier CA, Loeuille N (2012) Eco-evolutionary responses of biodiversity to climate change. Nature Climate Change 2: 747–751

Osmond MM, Klausmeier CA (2017) An evolutionary tipping point in a changing environment. Evolution 71: 2930–2941

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Klausmeier CA, Osmond MM, Kremer CT, Litchman E (2020) Ecological limits to evolutionary rescue. Phil Trans R Soc B 375: 20190453

IV. A general framework combining intra- and interspecific trait variation

- Many trait-based theoretical frameworks ignore intraspecific trait variation (adaptive dynamics, ESS maximum approach) or treat it as fixed
- Quantitative genetics can model intraspecific trait variation but typically focuses on a single species

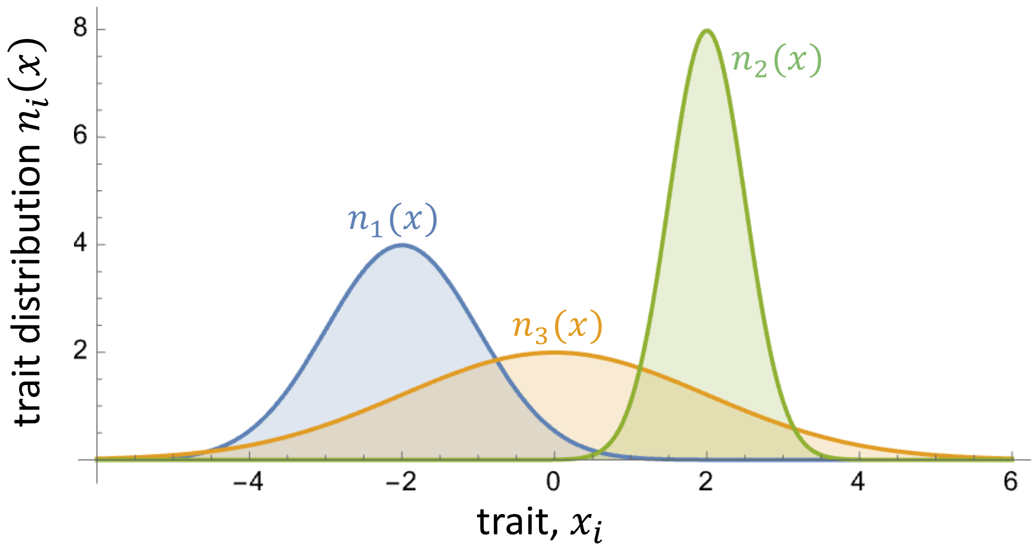
IV. A general framework combining intra- and interspecific trait variation

1. Multi-species moment methods
   A. Moment dynamical equations
   B. Invasion criteria / branching conditions
   C. Example: Lotka-Volterra competition
2. Extension to class-structured populations
   A. Moment dynamical equations
   B. Example: two-patch model

(Wickman, Koffel & Klausmeier *Am Nat* 2023)

1. Multi-species Moment Methods

- Consider $\mathcal{N}$ species ($\mathcal{N}$ to be determined) with normally distributed traits
- Each species has a trait distribution $n_i(x)$ characterized by its first three moments
  - – 0th – total abundance, N_i
  - – 1st – mean trait, x_i
  - – 2nd – trait variance, V_i



1. Multi-species Moment Methods

- Individual-level fitness function

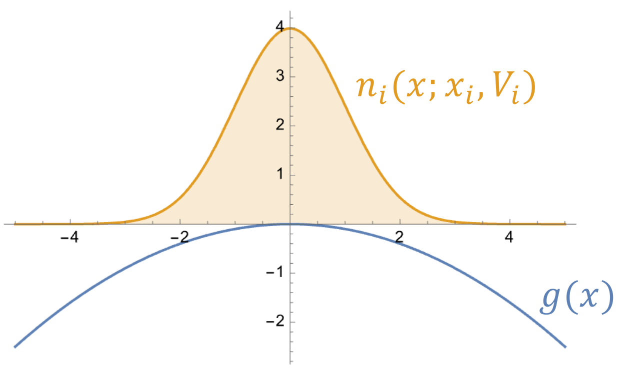
$$g(x; n(\cdot)) = \frac{dn}{ndt}$$

(*N.B.* includes species interactions!)

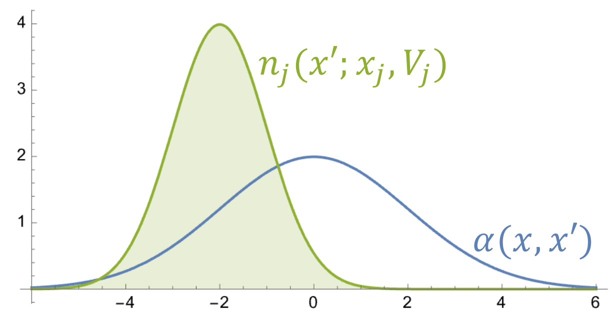
1. Multi-species Moment Methods

- Fitness and interactions need to be averaged over trait distributions to derive population-level fitness (Gaussian integral)

$$\hat{g}(x_i, V_i)N_i = \int g(x)n_i(x; x_i, V_i)dx$$



$$g(x) = 1 - x^2$$
$$\hat{g}(x_i, V_i) = 1 - x_i^2 - V_i$$



$$\alpha(x, x')n_j(x') = \exp(\frac{-(x - x')^2}{2\sigma})n_j(x')$$

$$\hat{\alpha}(x, x_j, V_j) = \exp\left(\frac{-(x-x_j)^2}{2(\sigma+\sqrt{V_j})}\right)\frac{\sigma}{\sqrt{\sigma^2+V_j}}N_j$$

1. Multi-species Moment Methods

Total abundance:

$$\frac{dN_i}{dt} = \hat{g}(x_i, V_i)N_i$$

Trait mean:

$$\frac{dx_i}{dt} = V_i \frac{\partial \hat{g}}{\partial x}(x_i, V_i)$$

Trait variance:

$$\frac{dV_i}{dt} = V_i^2 \frac{\partial^2 \hat{g}}{\partial x^2}(x_i, V_i) + \hat{b}(x_i, V_i)M$$

($\hat{b}$ is birth rate, M is mutation variance)

Example: Lotka-Volterra Competition

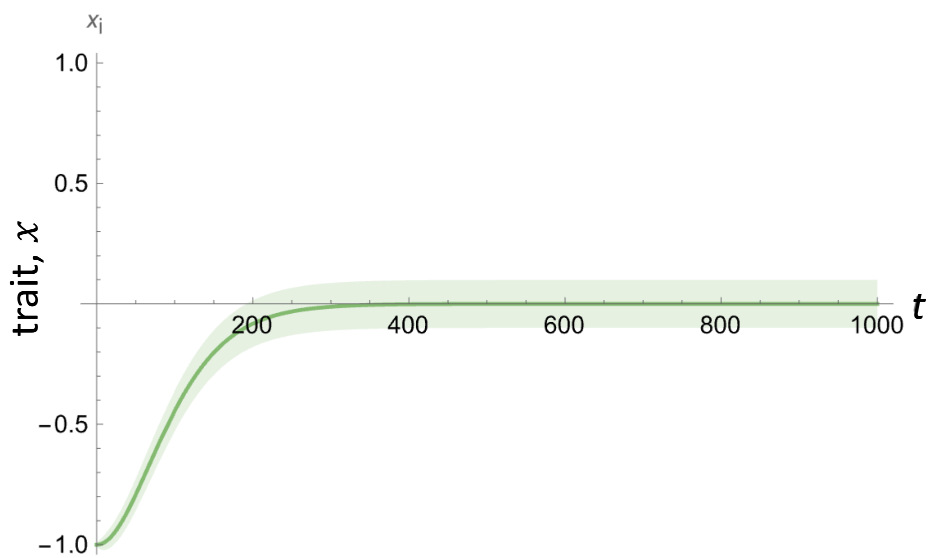
$$\frac{dN_i}{dt} = \left(1 - x_i^2 - V_i - \sum_{j=1}^{\mathcal{N}} \frac{\sigma}{\sqrt{\sigma^2 + V_i + V_j}} \exp(-\left(x_i - x_j\right)^2 / \left(2\left(\sigma^2 + V_i + V_j\right)\right) N_j\right) N_i \right)$$

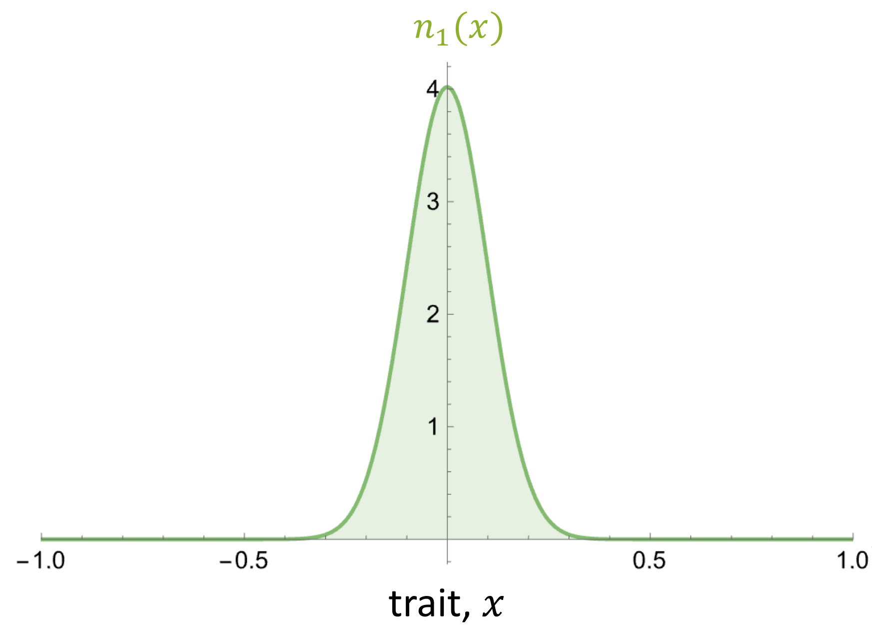
$$\frac{dx_i}{dt} = V_i \left(-2x_i + \sum_{j=1}^{\mathcal{N}} \frac{\sigma(x_i - x_j)}{\left(\sigma^2 + V_i + V_j\right)^{3/2}} \exp(-\left(x_i - x_j\right)^2 / \left(2\left(\sigma^2 + V_i + V_j\right)\right)\right) N_j \right)$$

$$\frac{dV_i}{dt} = V_i^2 \left(-2 + \sum_{j=1}^{\mathcal{N}} \frac{\sigma \left(\sigma^2 + V_i + V_j - \left(x_i - x_j\right)^2\right)}{\left(\sigma^2 + V_i + V_j\right)^{5/2}} \exp(-\left(x_i - x_j\right)^2 / \left(2\left(\sigma^2 + V_i + V_j\right)\right)\right) N_j \right) + M$$

Example: Lotka-Volterra Competition

$(\mathcal{N} = 1, \sigma = 1, M = 10^{-4})$



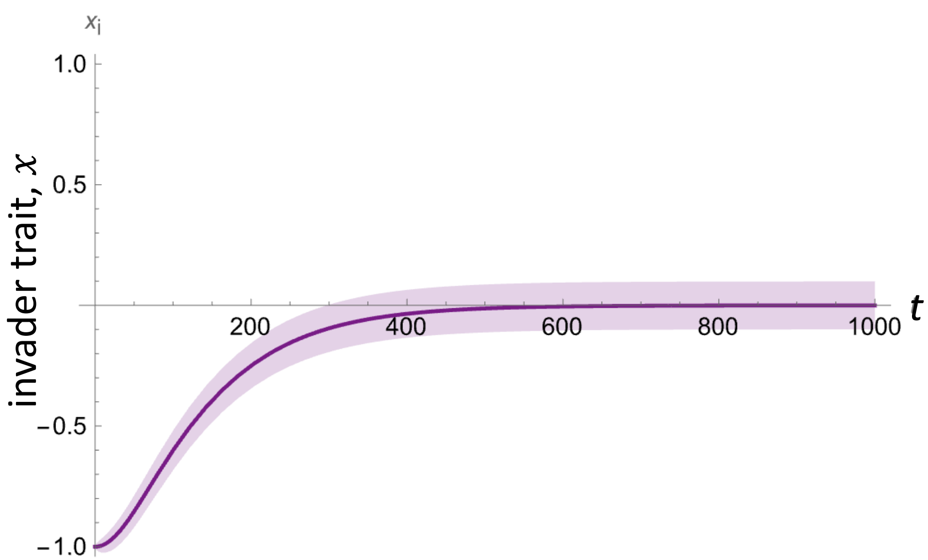


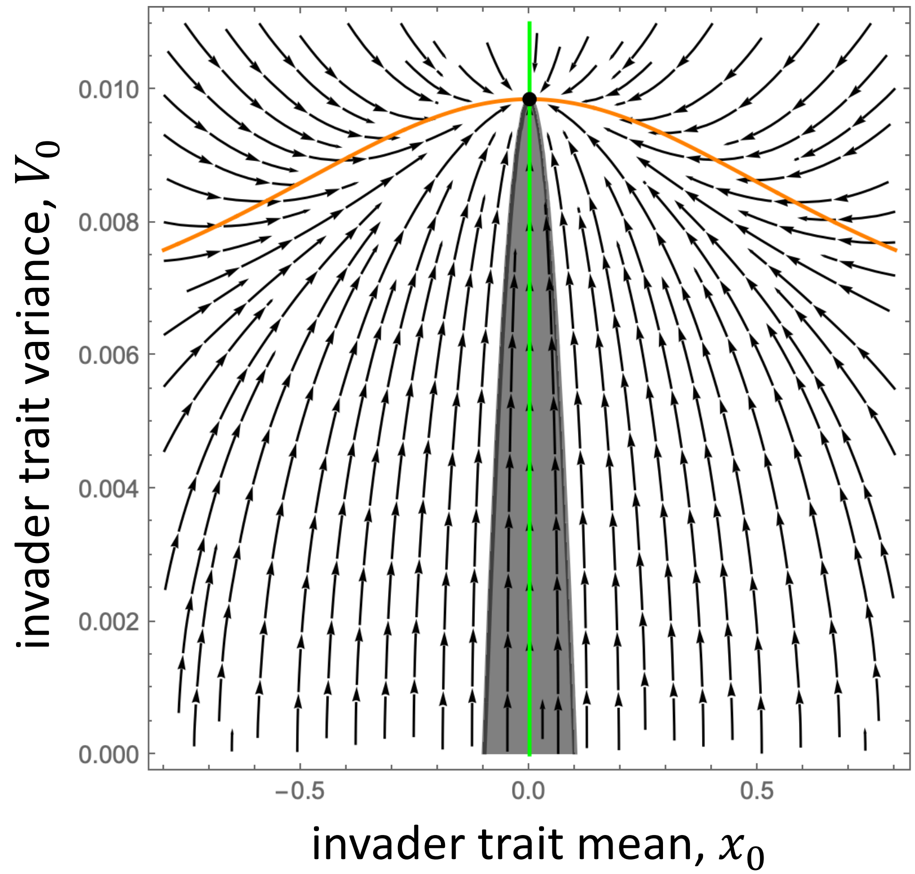
1.B. Invasion Criteria in Moment-Structured Populations

- To determine the evolutionarily stable community, we need invasion criteria
- 💡Idea: introduce rare invader ($N_0 \approx 0$), evolve its trait mean, x_0, and trait variance, V_0, in the environment set by resident(s) until it reaches a stable equilibrium (x_0^*, V_0^*), then calculate its population growth rate, $\hat{g}(x_0^*, V_0^*)$
- Can be visualize with phase-plane

Example: Lotka-Volterra Competition

$(\mathcal{N} = 1, \sigma = 1, M = 10^{-4})$



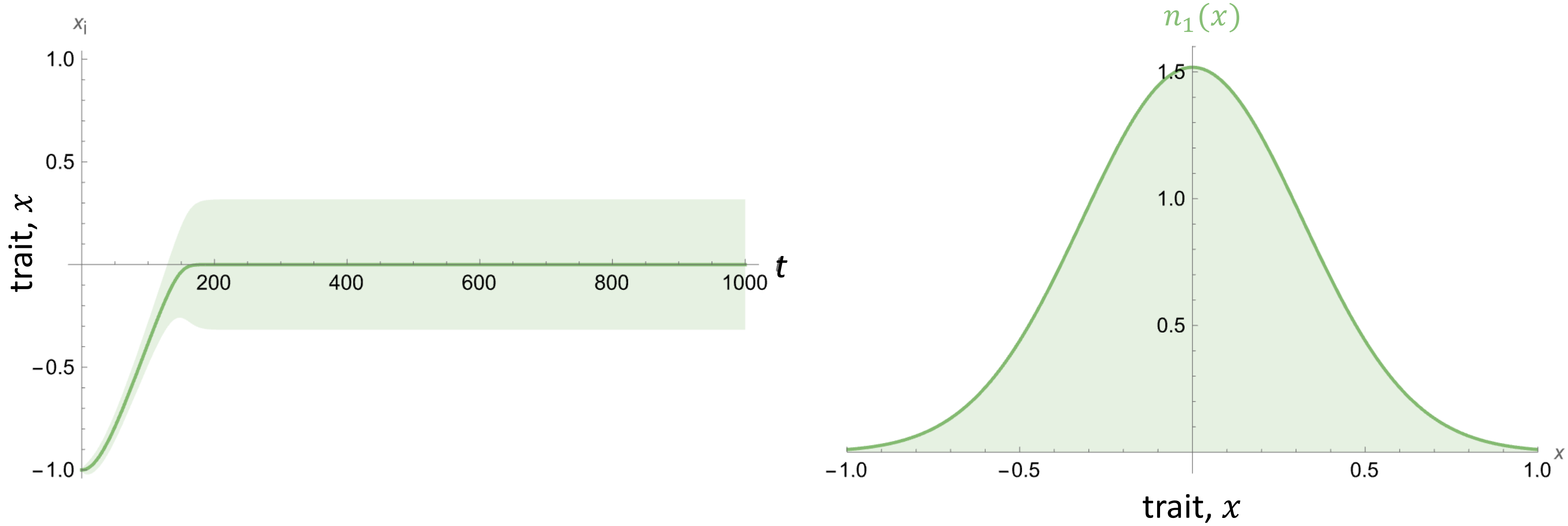


Convergence to resident, then neutral invasion rate ($\hat{g}(x_0^*, V_0^*) = 0$) ⇒ <u>failed invasion</u>

⇒ one-species evolutionarily stable community

Example: Lotka-Volterra Competition

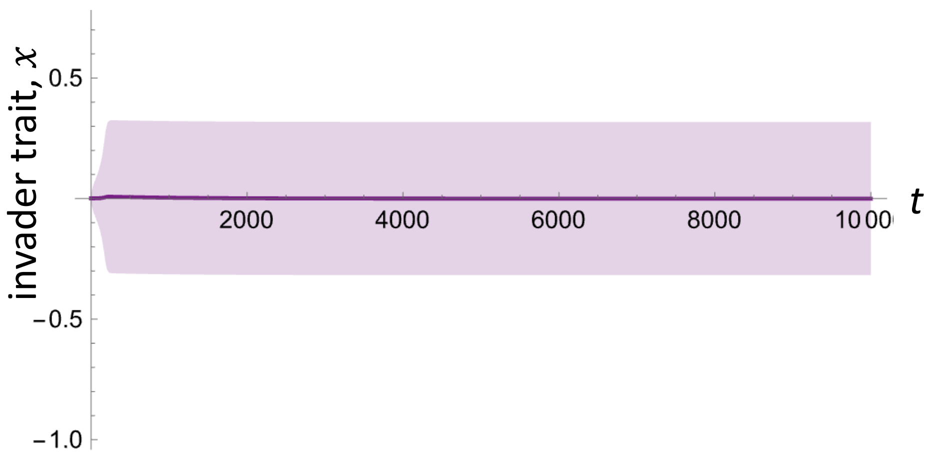
$(\mathcal{N} = 1, \sigma = 0.5, M = 10^{-4})$

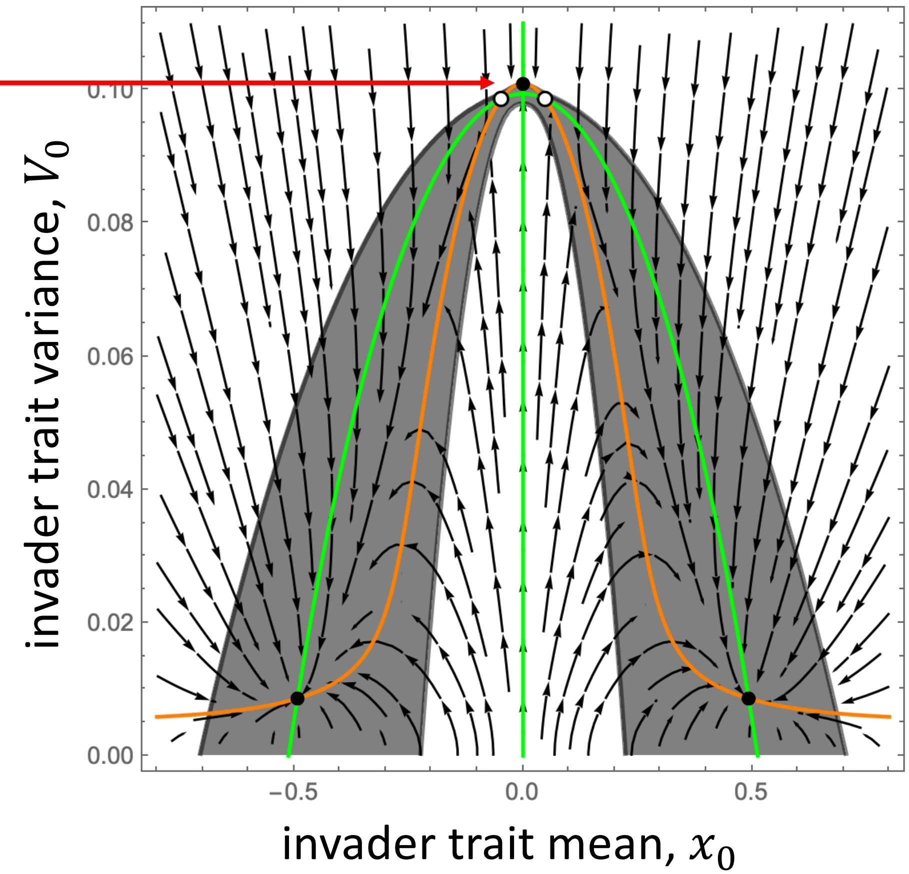


Example: Lotka-Volterra Competition

$(\mathcal{N} = 1, \sigma = 0.5, M = 10^{-4})$

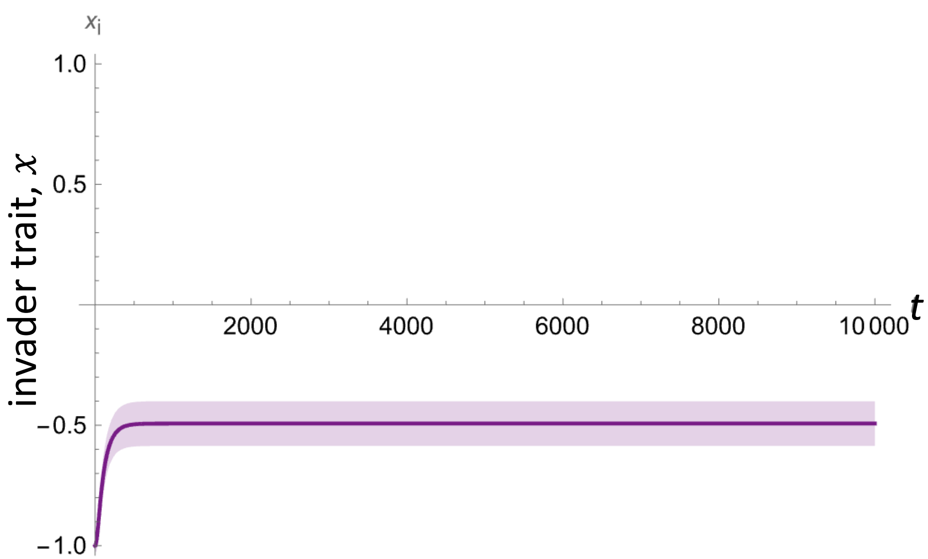
Convergence to resident, then neutral invasion rate ($\hat{g}(x_0^*, V_0^*)$=0) ⇒ <u>failed invasion</u>





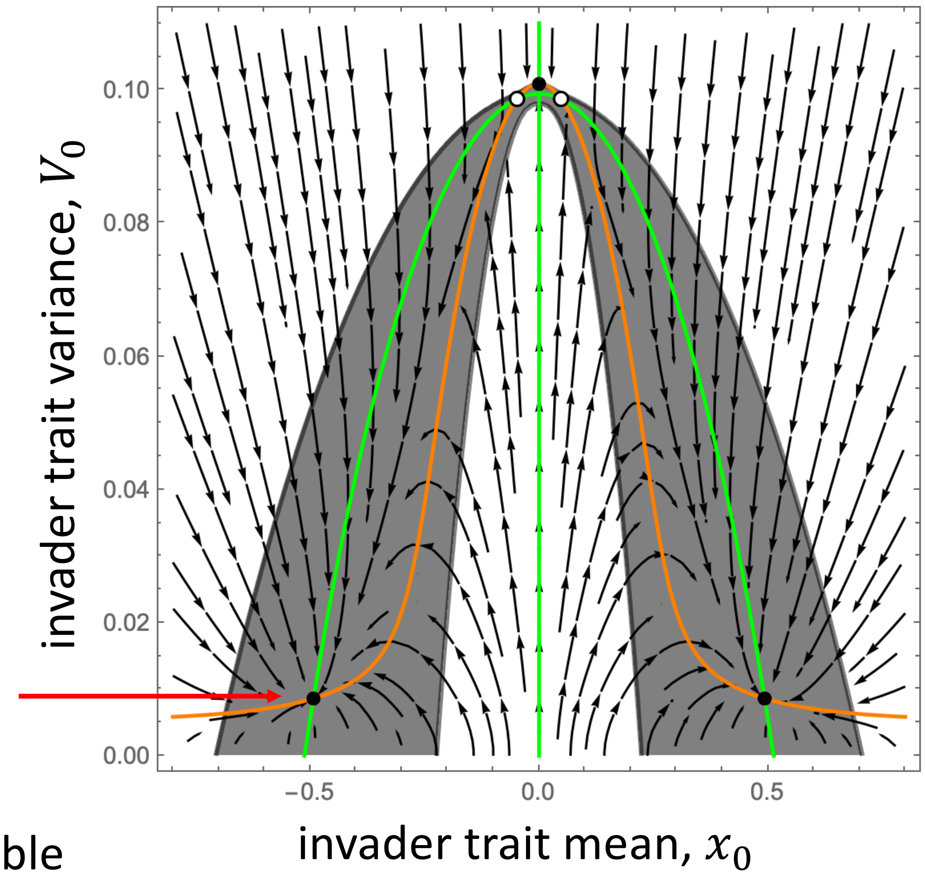
Example: Lotka-Volterra Competition

$(\mathcal{N} = 1, \sigma = 0.5, M = 10^{-4})$



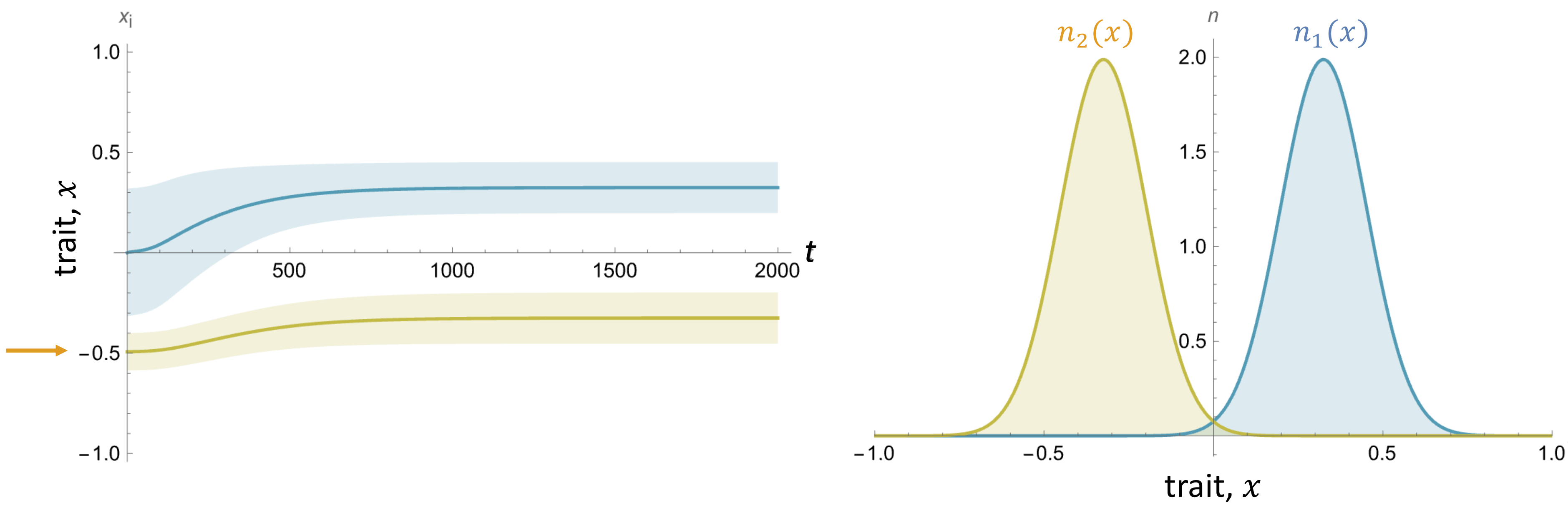
Distinct equilibrium moments, then positive invasion rate ($\hat{g}(x_0^*, V_0^*) = 0.0295$)
⇒ <u>successful invasion</u>

⇒ locally evolutionarily stable, but globally invasible



Example: Lotka-Volterra Competition

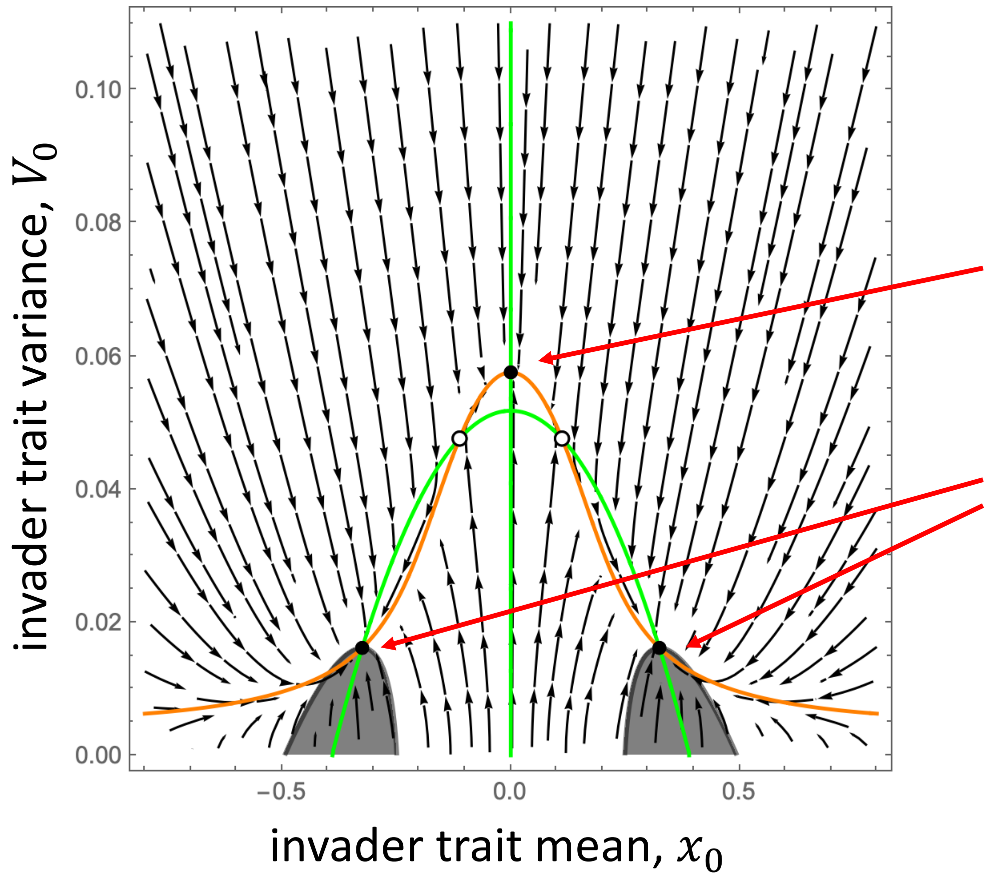
$(\mathcal{N} = 2, \sigma = 0.5, M = 10^{-4})$



After invasion, two species coexist

Example: Lotka-Volterra Competition

$(\mathcal{N} = 2, \sigma = 0.5, M = 10^{-4})$



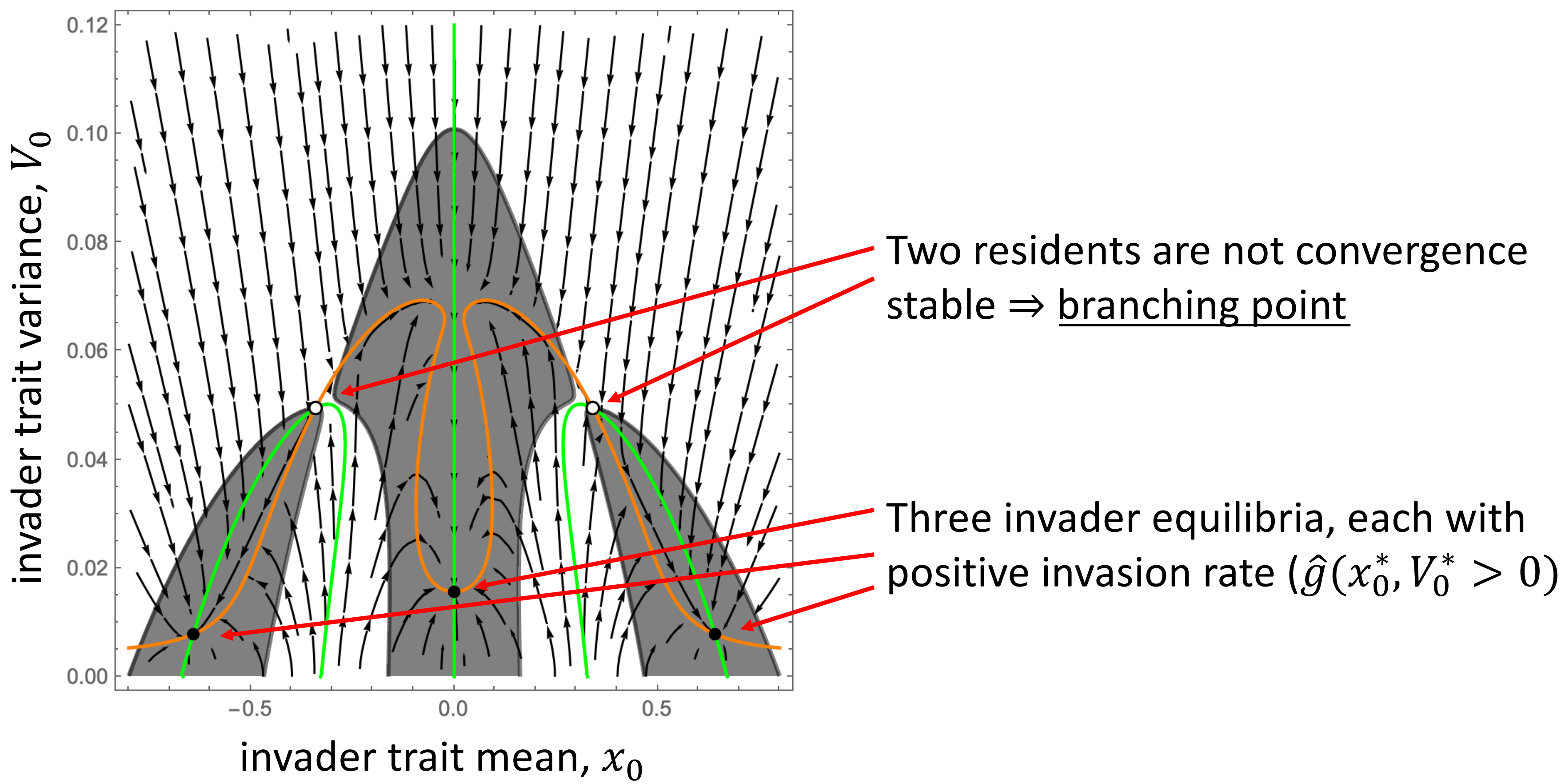
Convergence to another equilibrium, then negative invasion rate $(\hat{g}(x_0^*, V_0^*) < 0) \Rightarrow$ failed invasion

Convergence to resident, then neutral invasion rate $(\hat{g}(x_0^*, V_0^* = 0) \Rightarrow$ failed invasion

$\Rightarrow$ two-species evolutionarily stable community

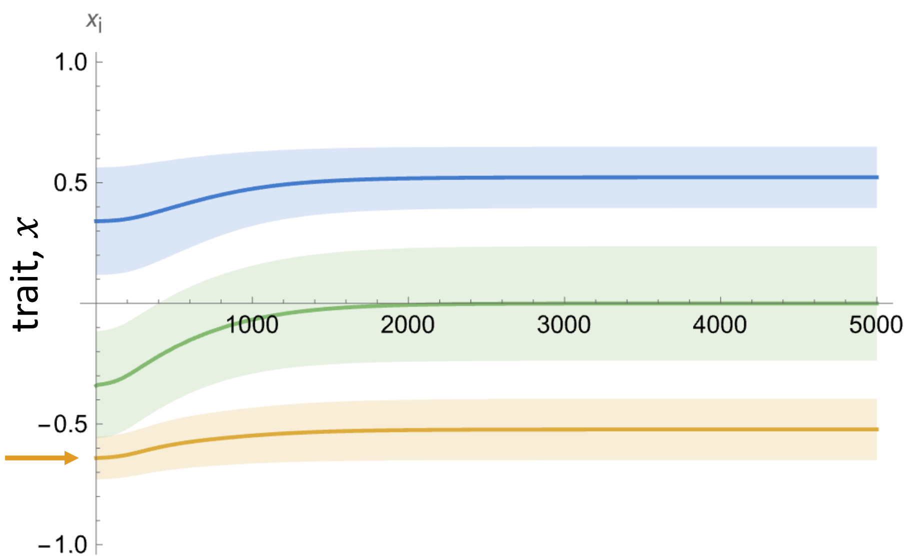
Example: Lotka-Volterra Competition

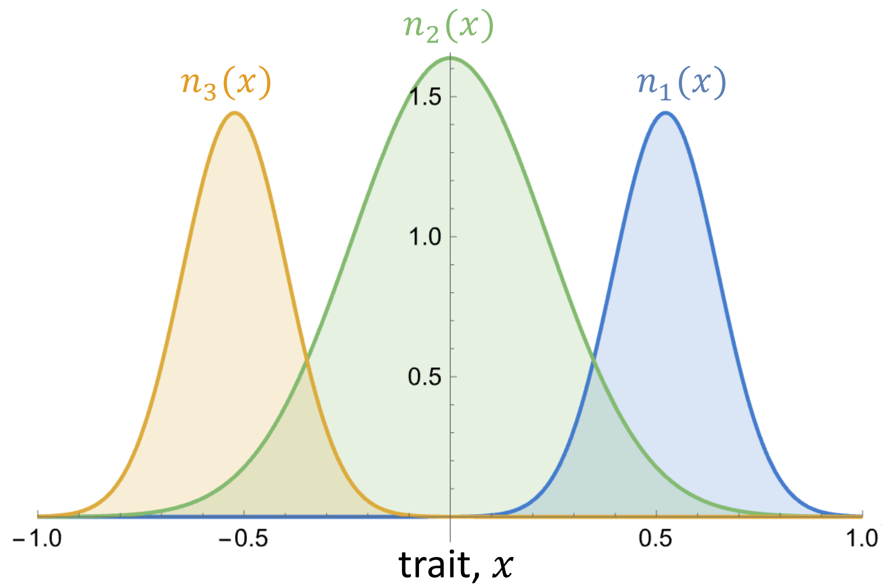
$(\mathcal{N} = 2, \sigma = 0.3, M = 10^{-4})$



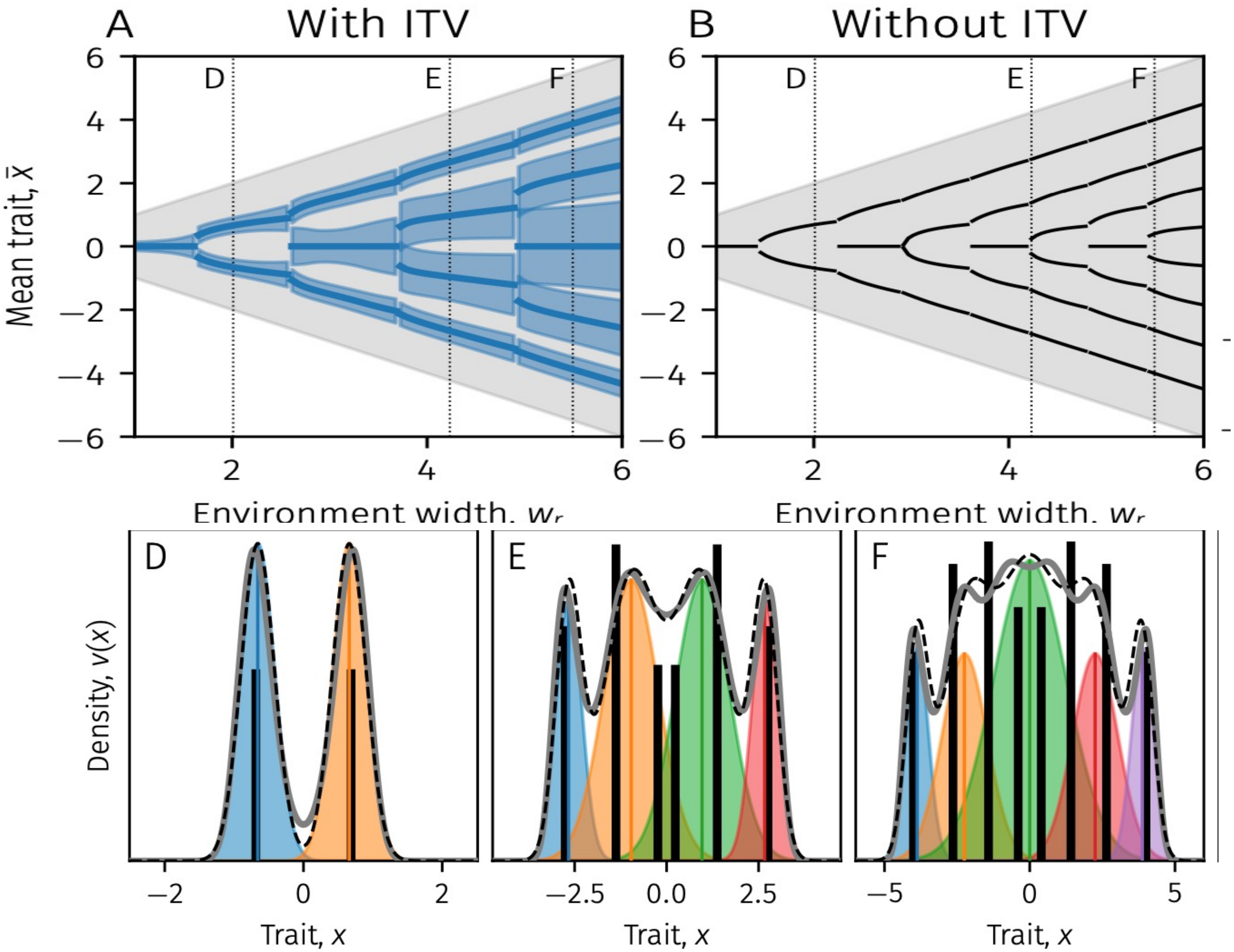
Example: Lotka-Volterra Competition

$(\mathcal{N} = 3, \sigma = 0.3, M = 10^{-4})$



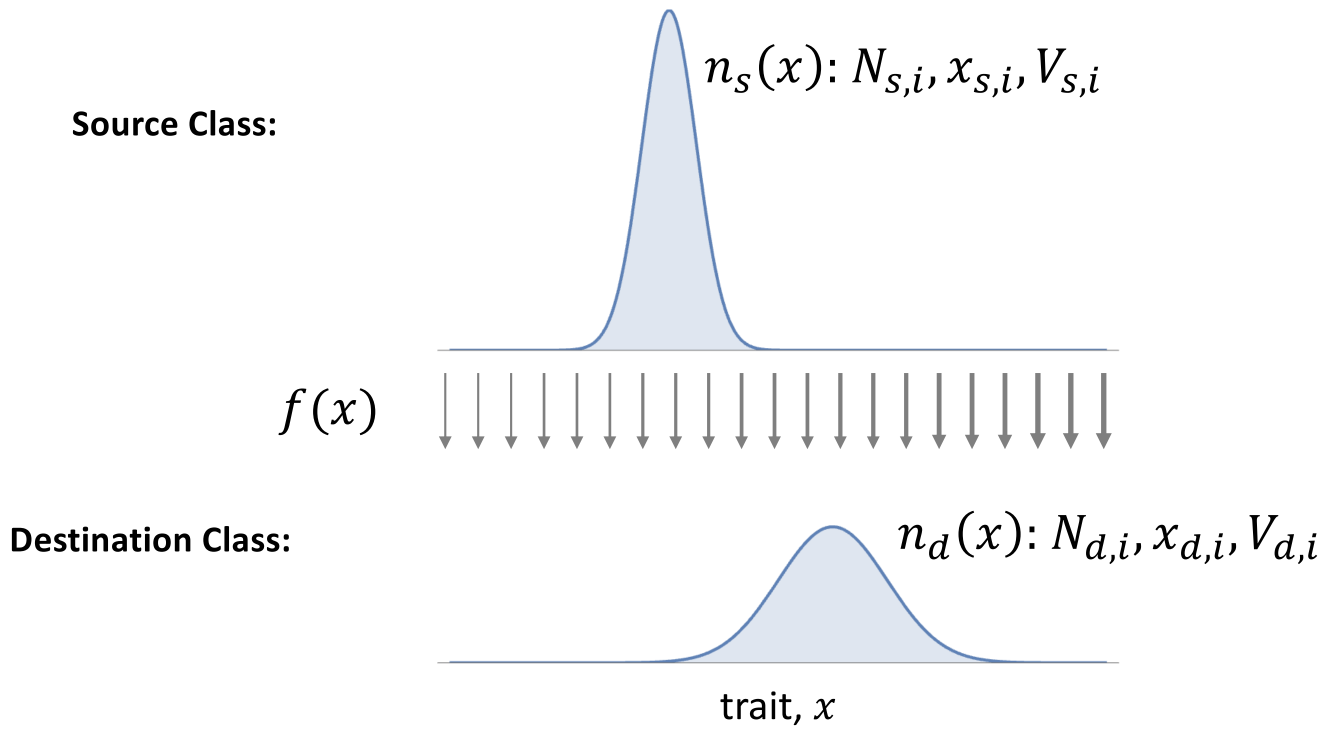


After invasion, three species coexist.



A
With ITV
B
Without ITV
D
E
F
Mean trait, $\bar{x}$
Environment width, w_r
Density, $v(x)$
Trait, x

2. Extension to Class-Structured Populations



$$\frac{dn_{d,i}(x)}{dt} += f(x)n_{s,i}(x)$$

2. Extension to Class-Structured Populations

Total abundance:

$$\frac{dN_{d,i}}{dt} += \hat{f}(x_{s,i}, V_{s,i})N_{s,i}$$

$$\begin{bmatrix}\text{change in}\\ \text{destination}\\ \text{abundance}\end{bmatrix} += \begin{bmatrix}\text{population}-\text{level}\\ \text{rate}\end{bmatrix}\begin{bmatrix}\text{source}\\ \text{abundance}\end{bmatrix}$$

2. Extension to Class-Structured Populations

Trait mean:

$$\frac{dx_{d,i}}{dt} \mathrel{+}= \frac{N_{s,i}}{N_{d,i}}\left(V_{s,i}\,\frac{\partial \hat{f}}{\partial x}\left(x_{s,i}, V_{s,i}\right) + \hat{f}(x_{s,i}, V_{s,i})(x_{s,i} - x_{d,i})\right)$$

$$\begin{bmatrix}\text{change in}\\ \text{destination}\\ \text{trait}-\text{mean}\end{bmatrix} \mathrel{+}= \begin{bmatrix}\text{relative}\\ \text{abundance}\end{bmatrix} \times \left(\begin{bmatrix}\text{directional}\\ \text{selection}\end{bmatrix} + \begin{bmatrix}\text{trait}-\text{mean}\\ \text{flow}\end{bmatrix}\right)$$

2. Extension to Class-Structured Populations

Trait variance:

$$\frac{dV_{d,i}}{dt} \mathrel{+}= \frac{N_{s,i}}{N_{d,i}}\left(\begin{array}{c} V_{s,i}^2 \frac{\partial^2 \hat{f}}{\partial x^2}(x_{s,i}, V_{s,i}) + \hat{f}(x_{s,i}, V_{s,i})(V_{s,i} - V_{d,i}) + \hat{f}(x_{s,i}, V_{s,i})(x_{s,i} - x_{d,i})^2 \\ +2V_{s,i} \frac{\partial \hat{f}}{\partial x}(x_{s,i}, V_{s,i})(x_{s,i} - x_{d,i}) + \hat{f}(x_{s,i}, V_{s,i})M \end{array}\right)$$

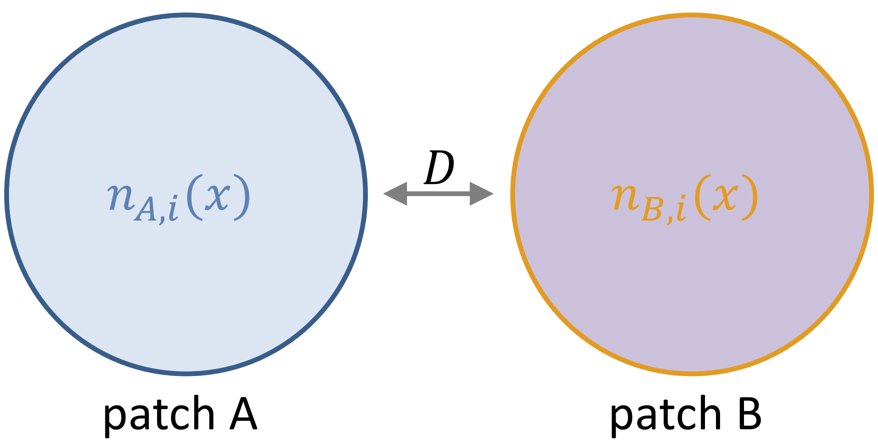
$$\begin{bmatrix} \text{change in} \\ \text{destination} \\ \text{trait−variance} \end{bmatrix} \mathrel{+}= \begin{bmatrix} \text{relative} \\ \text{abundance} \end{bmatrix} \times$$

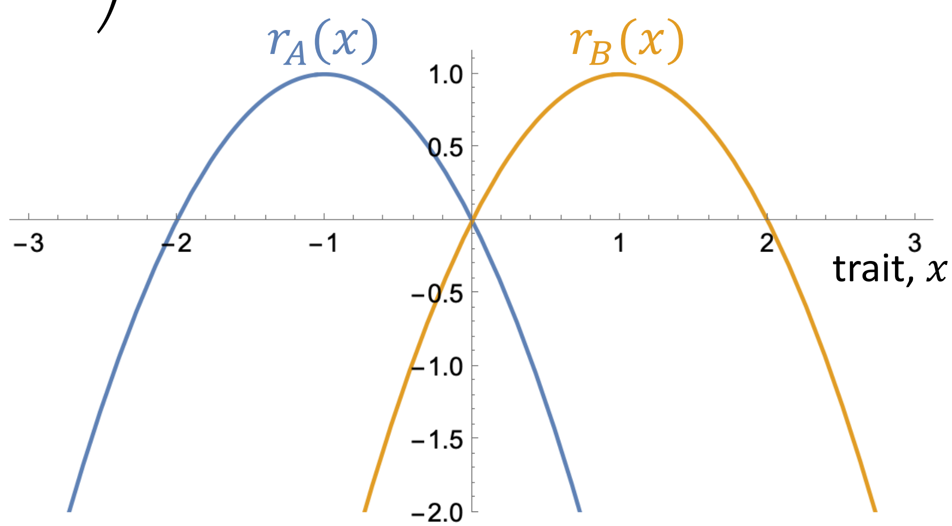
$$\left(\begin{bmatrix} \text{quadratic} \\ \text{selection} \end{bmatrix} + \begin{bmatrix} \text{trait−variance} \\ \text{flow} \end{bmatrix} + \begin{bmatrix} \text{between−to−} \\ \text{within−class} \\ \text{variance flow} \end{bmatrix} + \begin{bmatrix} \text{directional−selection} \times \\ \text{trait−mean interaction} \end{bmatrix} + [\text{mutation}]\right)$$

Example: Two-Patch Model

$$\frac{dn_{A,i}(x)}{dt} = \left(r_A(x) - \sum_{j=1}^{\mathcal{N}} n_{A,j} \right) n_{A,i} + D\left(n_{B,i} - n_{A,i}\right)$$

$$\frac{dn_{B,i}(x)}{dt} = \left(r_B(x) - \sum_{j=1}^{\mathcal{N}} n_{B,j} \right) n_{B,i} + D\left(n_{A,i} - n_{B,i}\right)$$





Example: Two-Patch Model

Total Abundance:

$$\frac{dN_{A,i}}{dt} = \left(1 - \left(x_{A,i} - x_A^*\right)^2 - V_{A,i} - \sum_{j=1}^{\mathcal{N}} N_{A,j}\right) N_{A,i} + D\left(N_{B,i} - N_{A,i}\right)$$

$$\frac{dN_{B,i}}{dt} = \left(1 - \left(x_{B,i} - x_B^*\right)^2 - V_{B,i} - \sum_{j=1}^{\mathcal{N}} N_{B,j}\right) N_{B,i} + D\left(N_{A,i} - N_{B,i}\right)$$

Trait Mean:

$$\frac{dx_{A,i}}{dt} = -2V_{A,i}\left(x_{A,i} - x_A^*\right) + D\,\frac{N_{B,i}}{N_{A,i}}\left(x_{B,i} - x_{A,i}\right)$$

$$\frac{dx_{B,i}}{dt} = -2V_{B,i}\left(x_{B,i} - x_B^*\right) + D\,\frac{N_{A,i}}{N_{B,i}}\left(x_{A,i} - x_{B,i}\right)$$

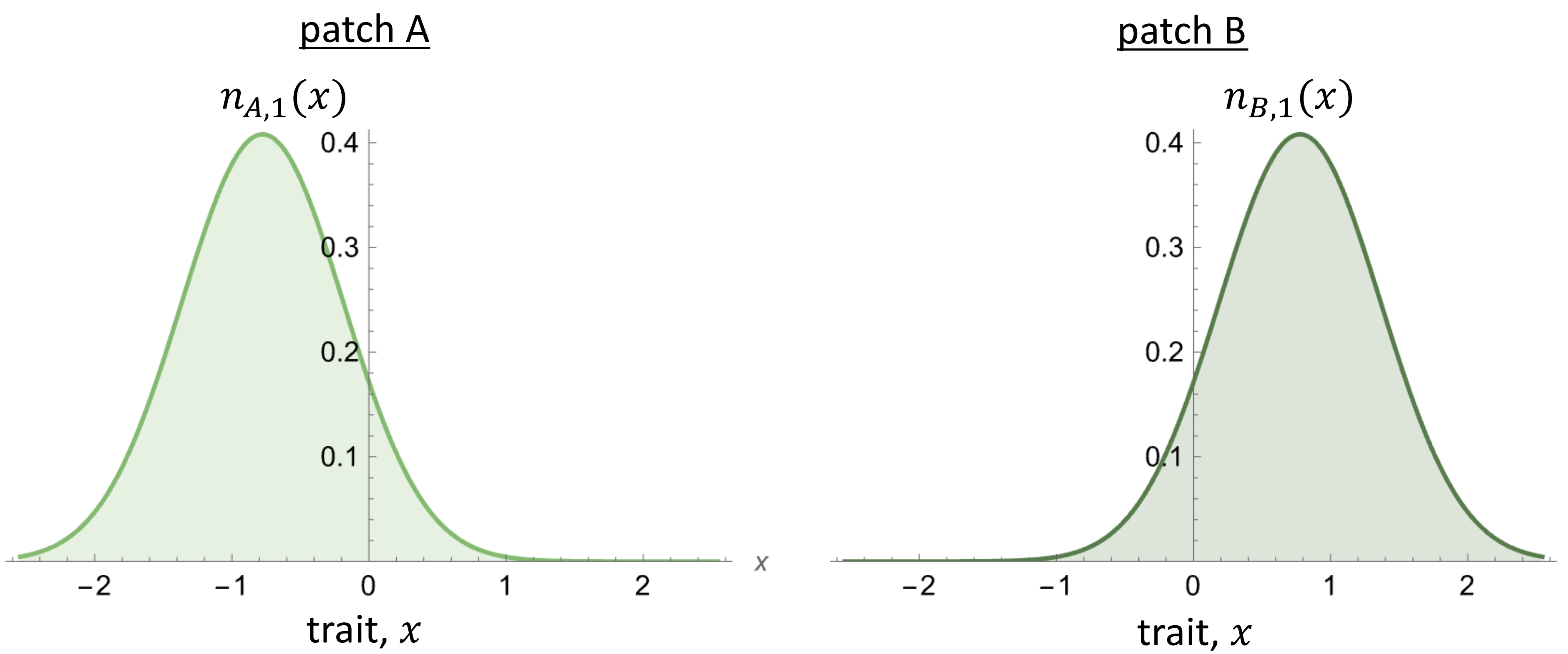
Trait Variance:

$$\frac{dV_{A,i}}{dt} = M - 2V_{A,i}^2 + D\,\frac{N_{B,i}}{N_{A,i}}\left(V_{B,i} - V_{A,i} + \left(x_{B,i} - x_{A,i}\right)^2\right)$$

$$\frac{dV_{B,i}}{dt} = M - 2V_{B,i}^2 + D\,\frac{N_{A,i}}{N_{B,i}}\left(V_{A,i} - V_{B,i} + \left(x_{A,i} - x_{B,i}\right)^2\right)$$

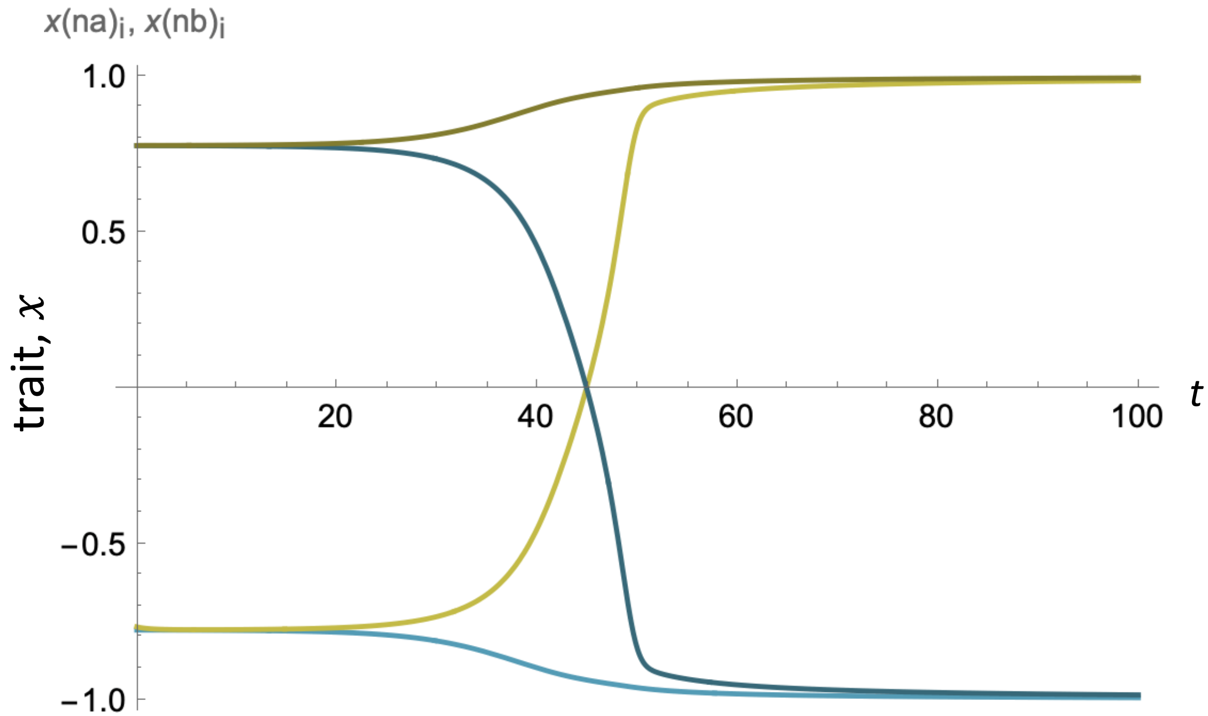
Example: Two-Patch Model

$(\mathcal{N} = 1, D = 0.1, M = 0)$



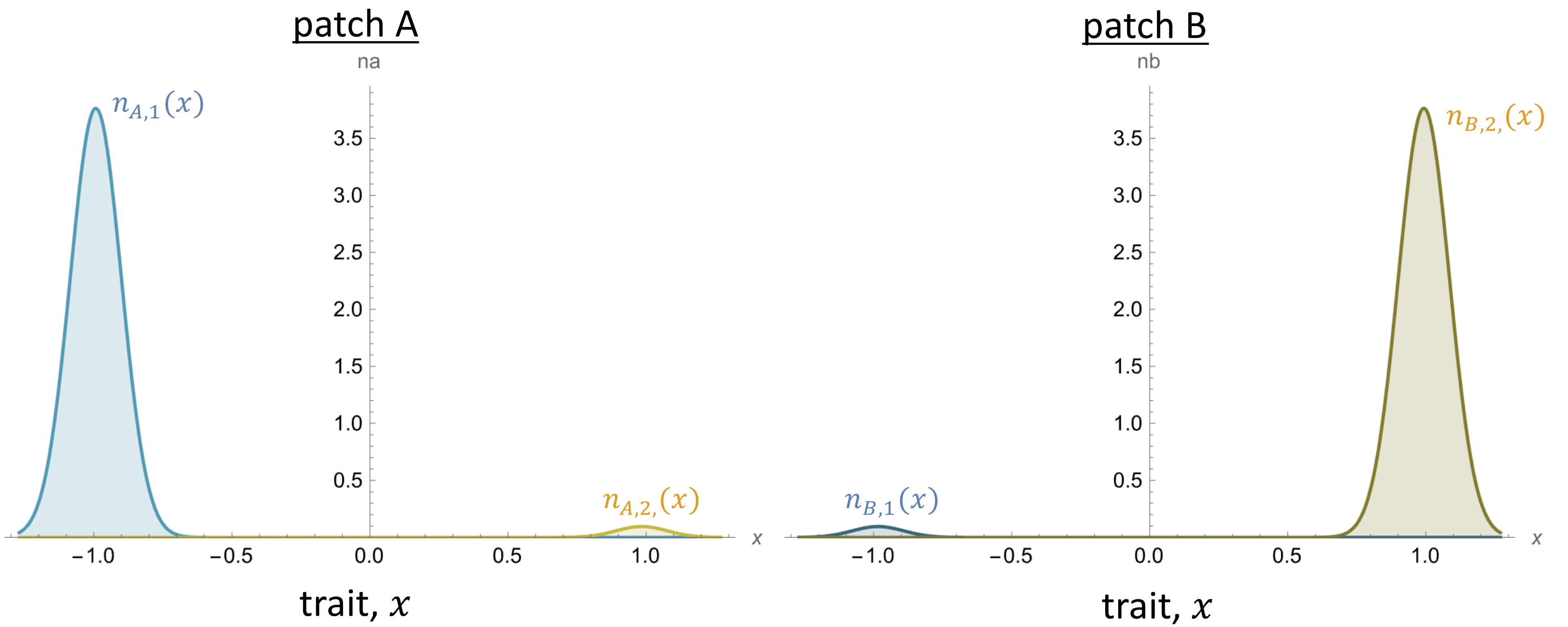
Example: Two-Patch Model

$(\mathcal{N} = 2, D = 0.1, M = 0)$



Example: Two-Patch Model

$(\mathcal{N} = 2, D = 0.1, M = 0)$



IV. Conclusions

- Multi-species moment equations provide an efficient and intuitive way to model eco-evolutionary dynamics, including the causes and consequences of intraspecific trait variation
- Invasion criteria can be calculated by evolving the trait mean and variance of a rare invader, along with branching point conditions
- Intraspecific trait variation decreases species richness
- Spatial models can result in local adaptation and species sorting in heterogeneous environments
- See also: Lion S, Boots M, Sasaki A. 2022. Multimorph eco-evolutionary dynamics in structured populations. *American Naturalist* 200: 345–372

(Wickman, Koffel & Klausmeier *Am Nat* 2023)

Overall Conclusions

- Diversity is an essential feature of complex systems such as ecological communities
- Trait-based eco-evolutionary modeling is a mature field that provides tools to understand the origin & maintenance of diversity
- Diversity is key to understanding ecological resilience

Competitive communities

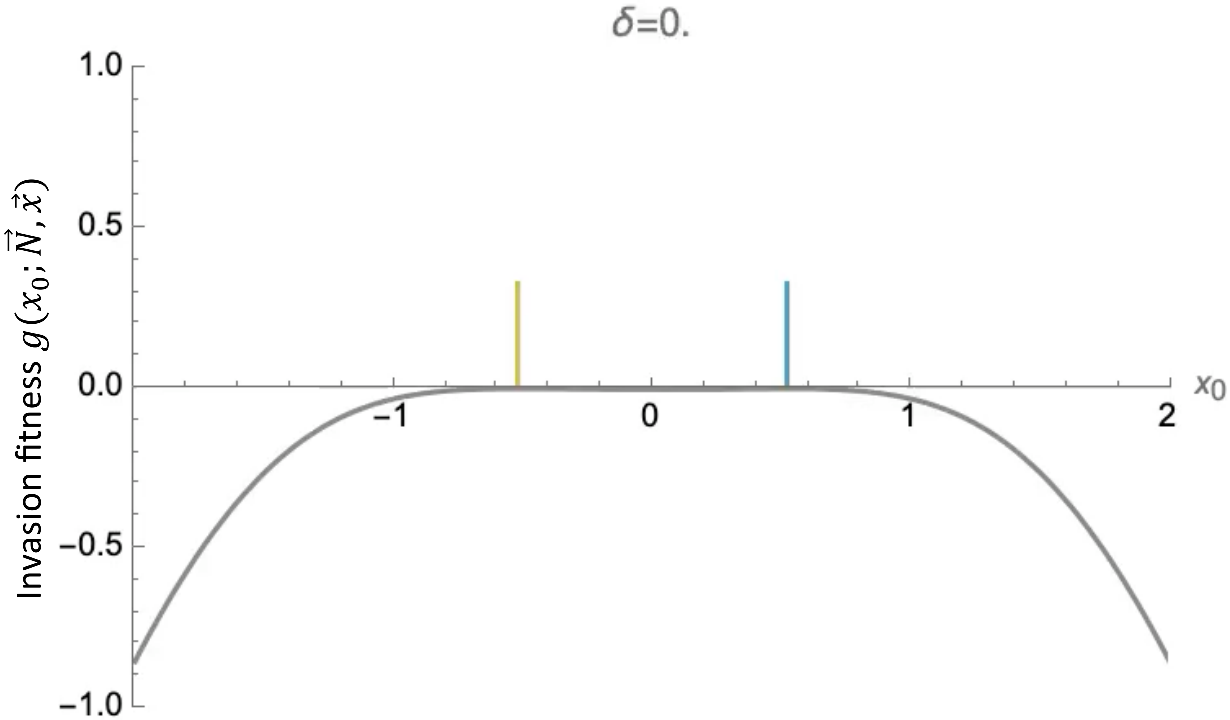
Evolutionary quantitative genetics framework:

$$\frac{dN_i}{dt} = g(x_i; \vec{N}, \vec{x})N_i$$
$$\frac{dx_i}{dt} = V\,\frac{\partial g}{\partial x}(x_i; \vec{N}, \vec{x}) - \delta$$

Trait-based Lotka-Volterra competition model:

$$g(x_i; \vec{N}, \vec{x}) = r(x_i) - \sum_{j=1}^{\mathcal{N}} \alpha(x_i, x_j)N_j$$

Competitive communities



Competitive communities