

Community Assembly and Complex Life Cycles

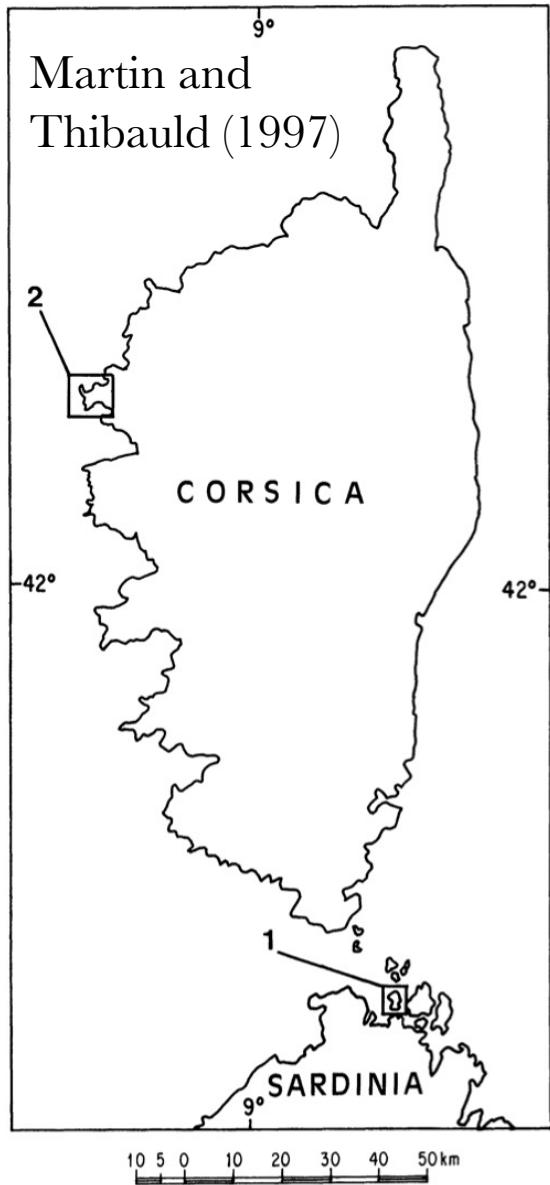
Marco Saltini, Paula Vasconcelos and Claus Rueffler



UPPSALA
UNIVERSITET

Department of Ecology and Genetics
Animal Ecology
Uppsala University

Coexistence of similar species – *Sylvia* warblers



Moltoni's Warbler
Sylvia subalpina



Sardinian Warbler
Sylvia melanocephala



Marmora's Warbler
Sylvia sarda

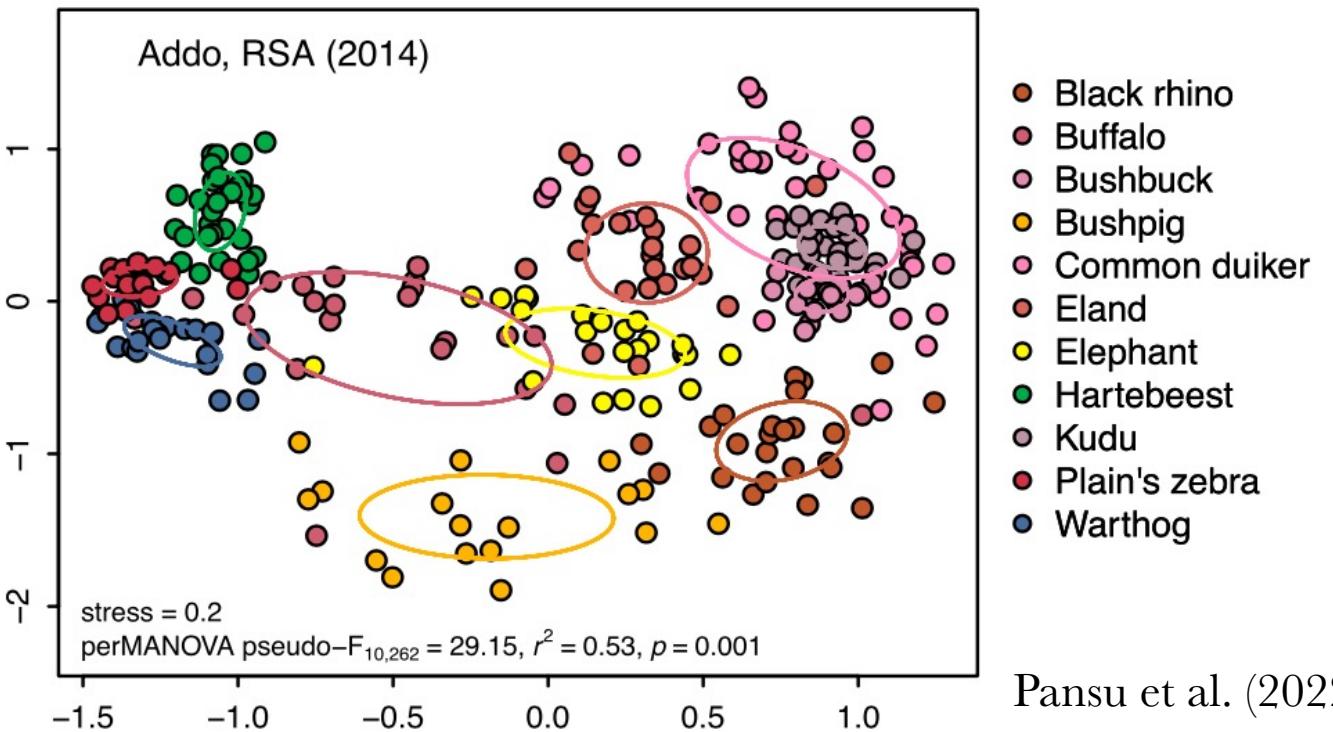


Dartford Warbler
Sylvia undata

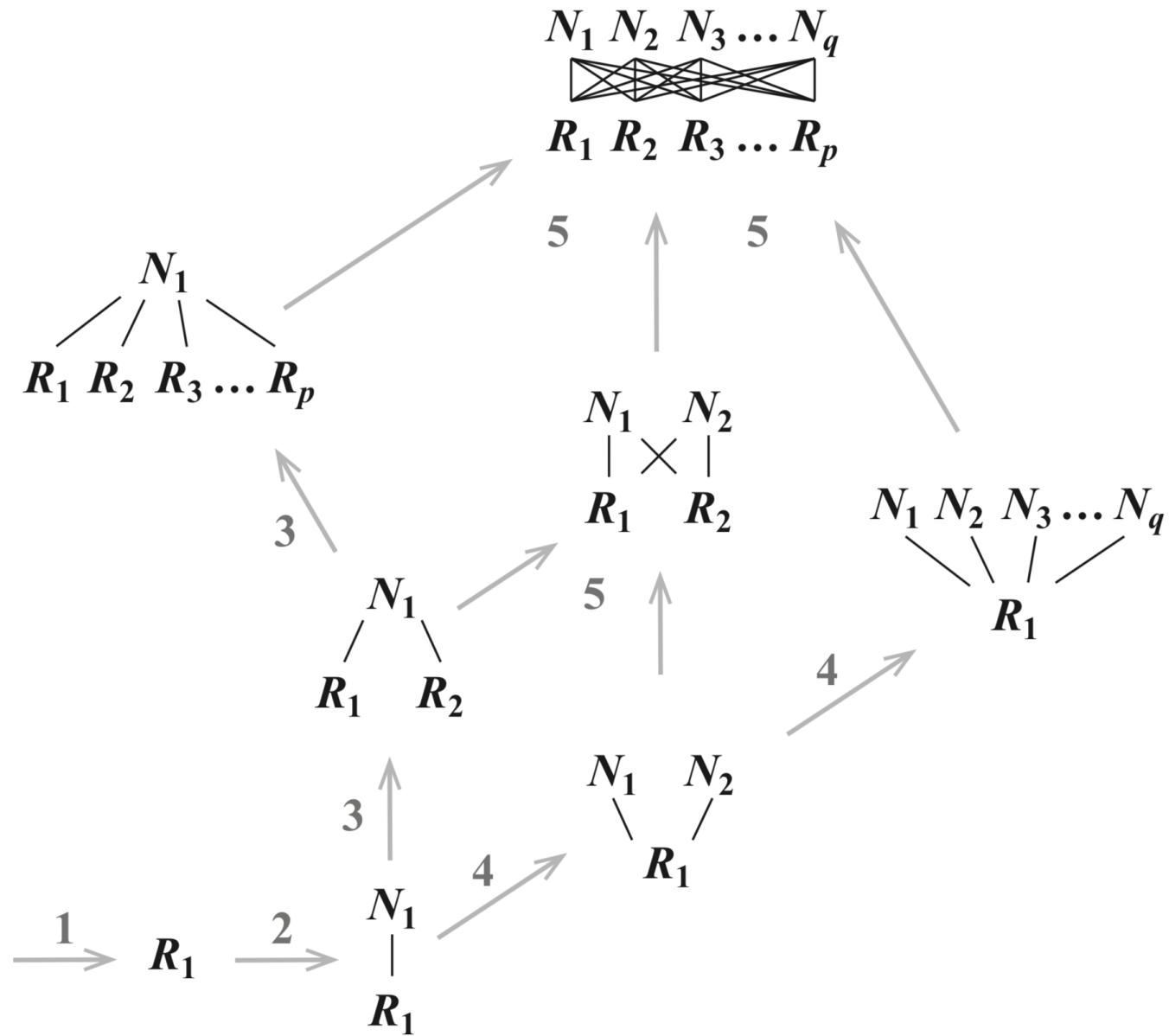
Coexistence of large herbivores



Diet analysis
based on DNA
metabarcoding
of fecal
samples



Theory of Community Ecology

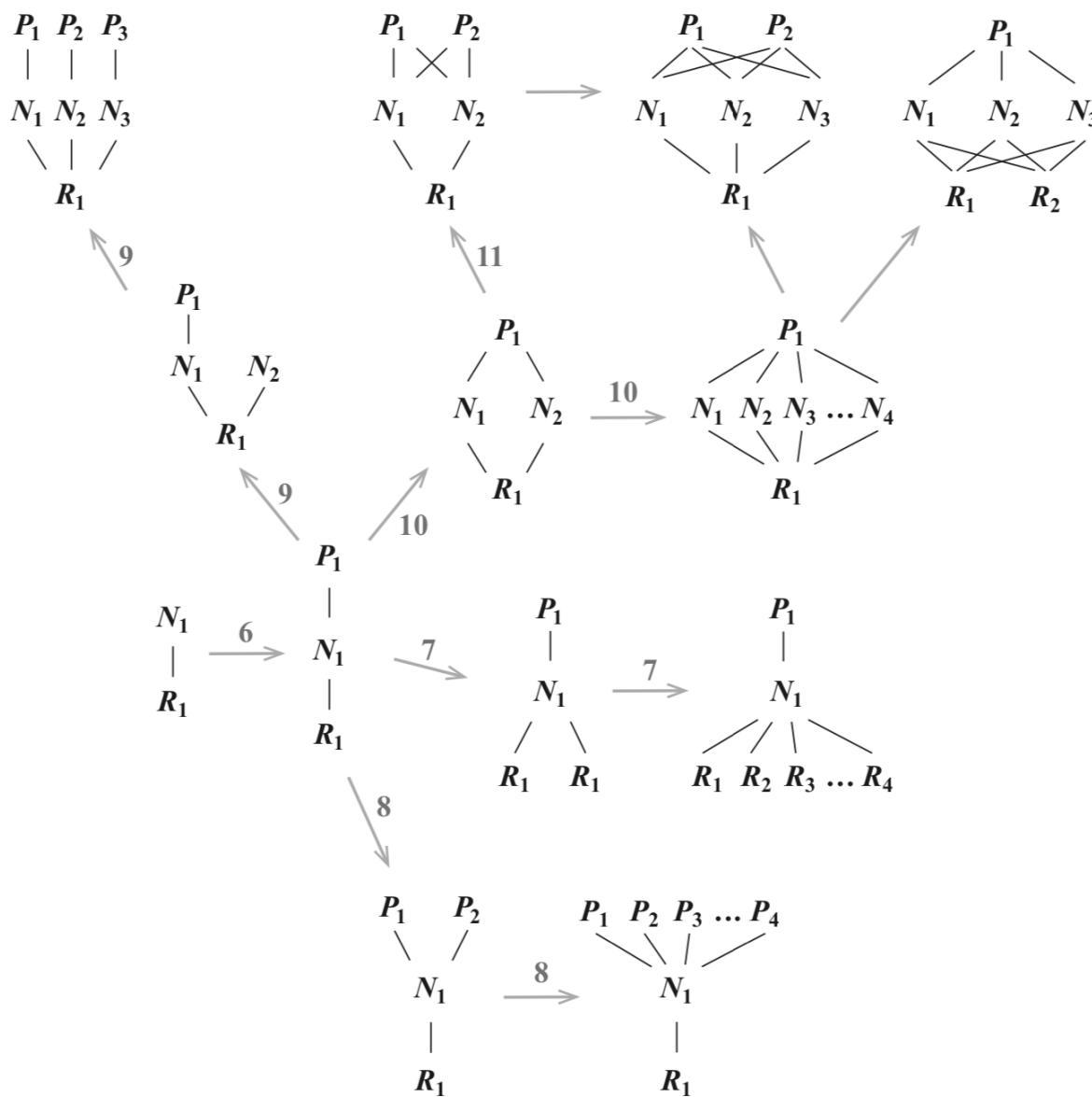


Coexistence in Ecology
A MECHANISTIC PERSPECTIVE

Mark A. McPeek

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Theory of Community Ecology



Coexistence in Ecology
A MECHANISTIC PERSPECTIVE

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Theory of Community Ecology

$$\frac{N(t)b(N, E)}{N(t)d(N, E)}$$

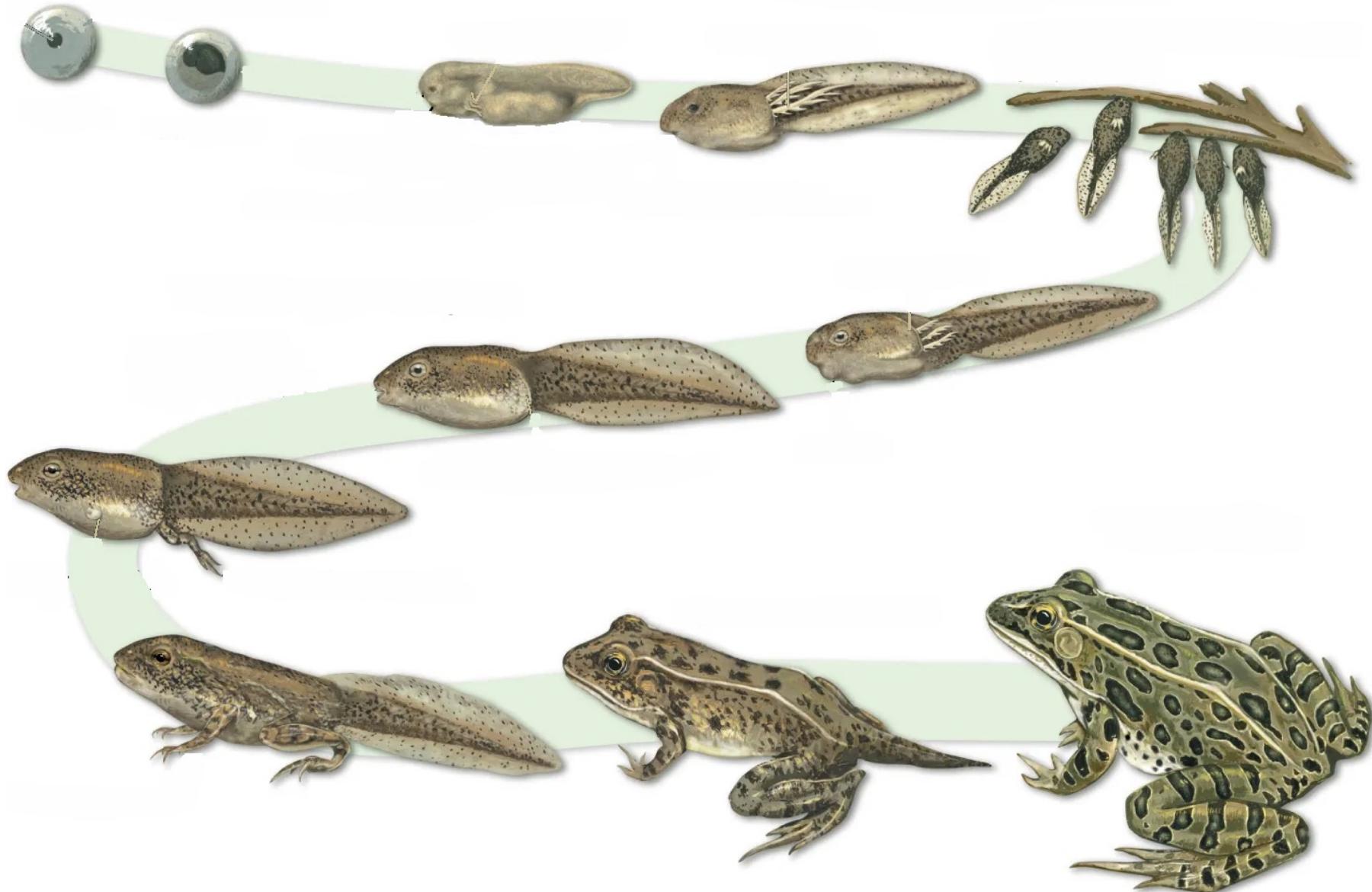
$$\frac{dN(t)}{dt} = N(t)(b(N, E) - d(N, E))$$

All individuals belonging to a species are *indistinguishable*

Complex life cycles and ontogenetic niche shift



Complex life cycles and ontogenetic niche shift



Complex life cycles and ontogenetic niche shift

Size, Scaling, and the Evolution of Complex Life Cycles

E. E. WERNER

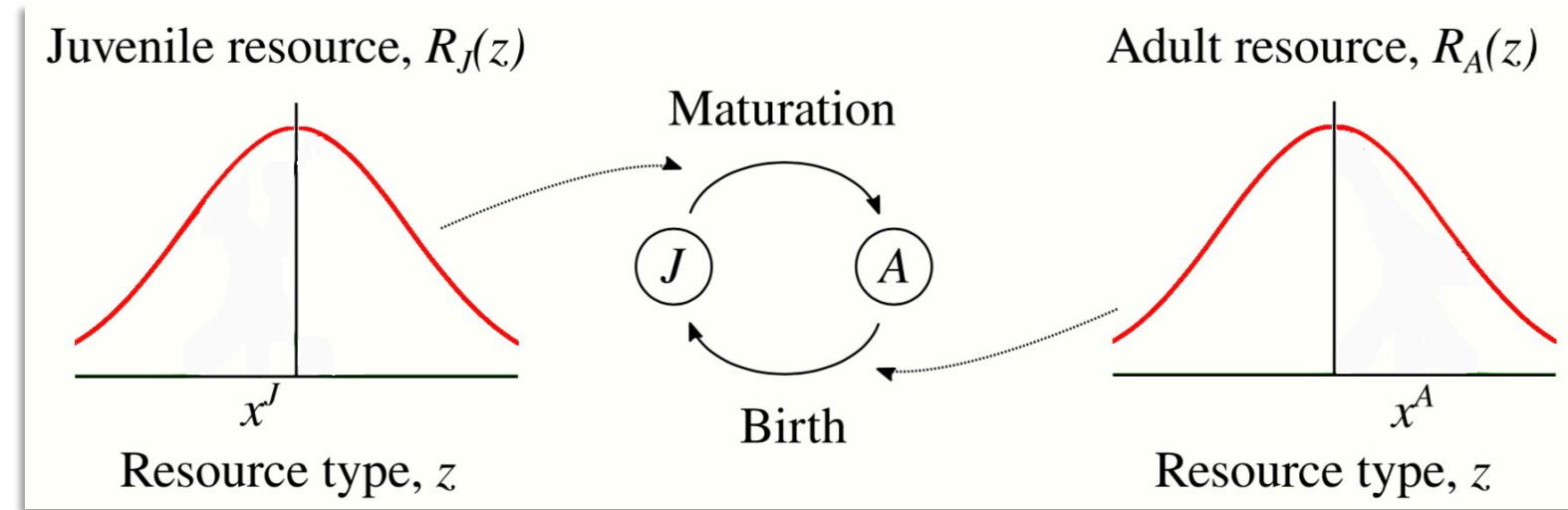
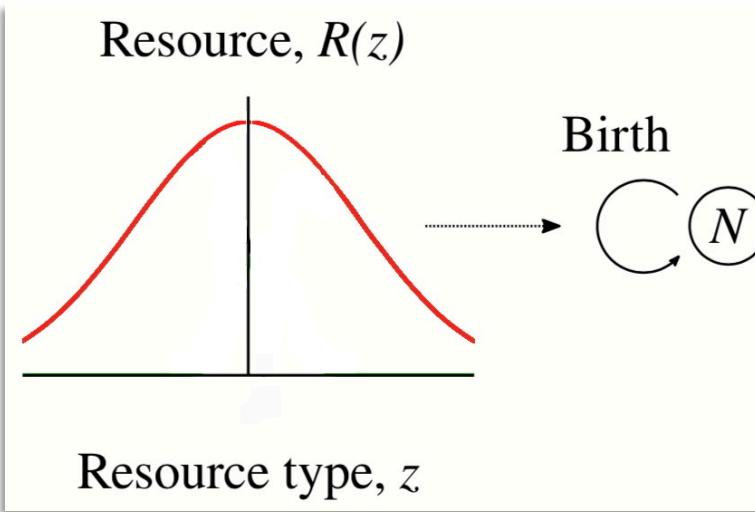
Size-Structured Populations

B. Ebenman and L. Persson (Eds.)

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How pervasive are these modes of development in animal life cycles? Pearse et al. (1987) list some 33 phyla in the kingdom Animalia. In 25 of these phyla metamorphosis is a major life cycle feature, or at least important classes undergo a metamorphosis (Table 1). Of the seven phyla that appear not to exhibit metamorphosis, only the Nematoda is speciose. Due to the dominance of insects and the marine phyla, I have estimated that perhaps 80% of animal species undergo a metamorphosis during the life cycle! Additionally, a large proportion of direct developing species exhibit marked shifts in niche during ontogeny and therefore effectively have complex life histories (Werner and Gilliam 1984). Clearly, complex life cycles are the norm among animals, and ontogenetic shifts in ecology and attendant changes in body plan represent a pervasive and characteristic element of life history structure.

How does adding a larval life-stage affect community assembly driven by competition for shared resources?



Simple life cycle

competition for resources
affects birth rate

Complex life cycle

competition for juvenile resources affects maturation rate
and competition for adult resources affects birth rate
(*ontogenetic niche shift*)

From LV predatory-prey to LV competition (Robert MacArthur)

$$\frac{dR(z)}{dt} = R(z)r \left(1 - \frac{R(z)}{K(z)}\right) - R(z) \sum_{i=1}^n a(z, x_i) N_i$$

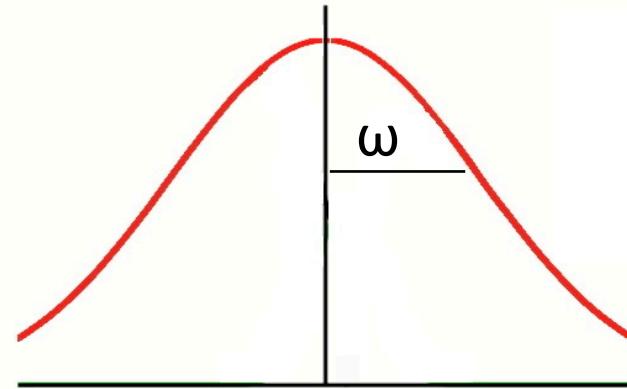
$$\frac{dN_i}{dt} = N_i c \int_{-\infty}^{+\infty} a(z, x_i) R(z) dz - N_i d$$

From LV predatory-prey to LV competition (Robert MacArthur)

$$\frac{dR(z)}{dt} = R(z)r \left(1 - \frac{R(z)}{K(z)} \right) - R(z) \sum_{i=1}^n a(z, x_i) N_i$$

$$\frac{dN_i}{dt} = N_i c \int_{-\infty}^{+\infty} a(z, x_i) R(z) dz - N_i d$$

Resource, $R(z)$



Resource type, z

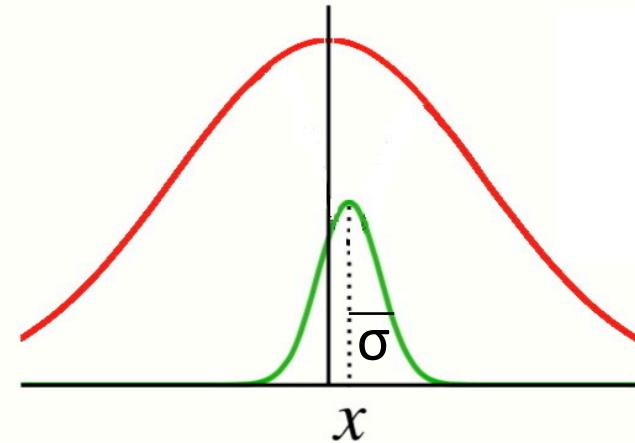
— Carrying capacity, K

From LV predatory-prey to LV competition (Robert MacArthur)

$$\frac{dR(z)}{dt} = R(z)r \left(1 - \frac{R(z)}{K(z)} \right) - R(z) \sum_{i=1}^n a(z, x_i) N_i$$

$$\frac{dN_i}{dt} = N_i c \int_{-\infty}^{+\infty} a(z, x_i) R(z) dz - N_i d$$

Resource, $R(z)$



Resource type, z

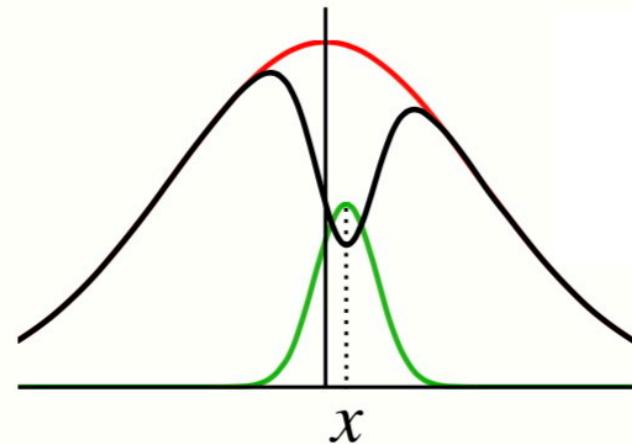
- Carrying capacity, K
- Resource utilization, a

From LV predatory-prey to LV competition (Robert MacArthur)

$$\frac{dR(z)}{dt} = R(z)r \left(1 - \frac{R(z)}{K(z)}\right) - R(z) \sum_{i=1}^n a(z, x_i) N_i$$

$$\frac{dN_i}{dt} = N_i c \int_{-\infty}^{+\infty} a(z, x_i) R(z) dz - N_i d$$

Resource, $R(z)$



Resource type, z

- Carrying capacity, K
- Resource utilization, a
- Resources at equilibrium, \hat{R}

From LV predatory-prey to LV competition (Robert MacArthur)

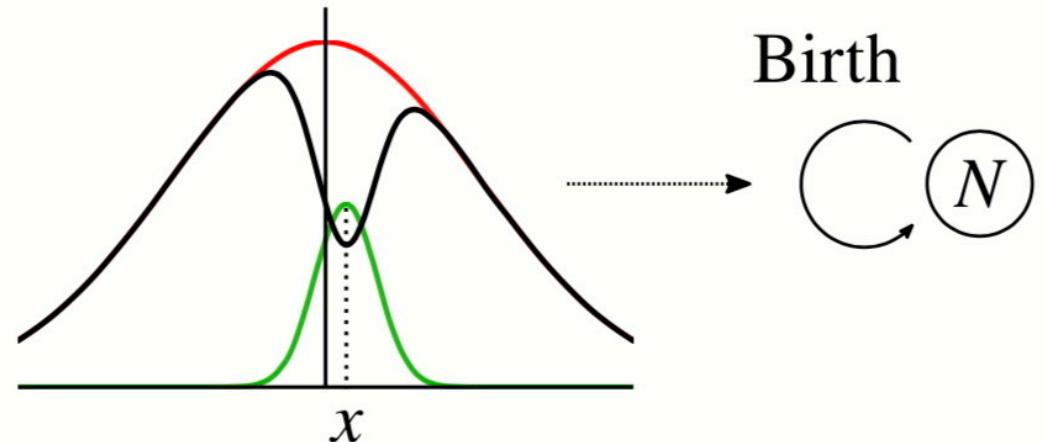
$$\frac{dR(z)}{dt} = R(z)r \left(1 - \frac{R(z)}{K(z)}\right) - R(z) \sum_{i=1}^n a(z, x_i) N_i$$

$$\frac{dN_i}{dt} = N_i c \int_{-\infty}^{+\infty} a(z, x_i) R(z) dz - N_i d$$

$$\frac{dN_i}{dt} = b(x_i, \mathbf{X}, \mathbf{N}) N_i - dN_i$$

$$b(x_i, \mathbf{X}, \mathbf{N}) = b_0(x_i) \left(1 - \sum_{j=1}^n \alpha(x_i, x_j) N_j\right)$$

Resource, $R(z)$



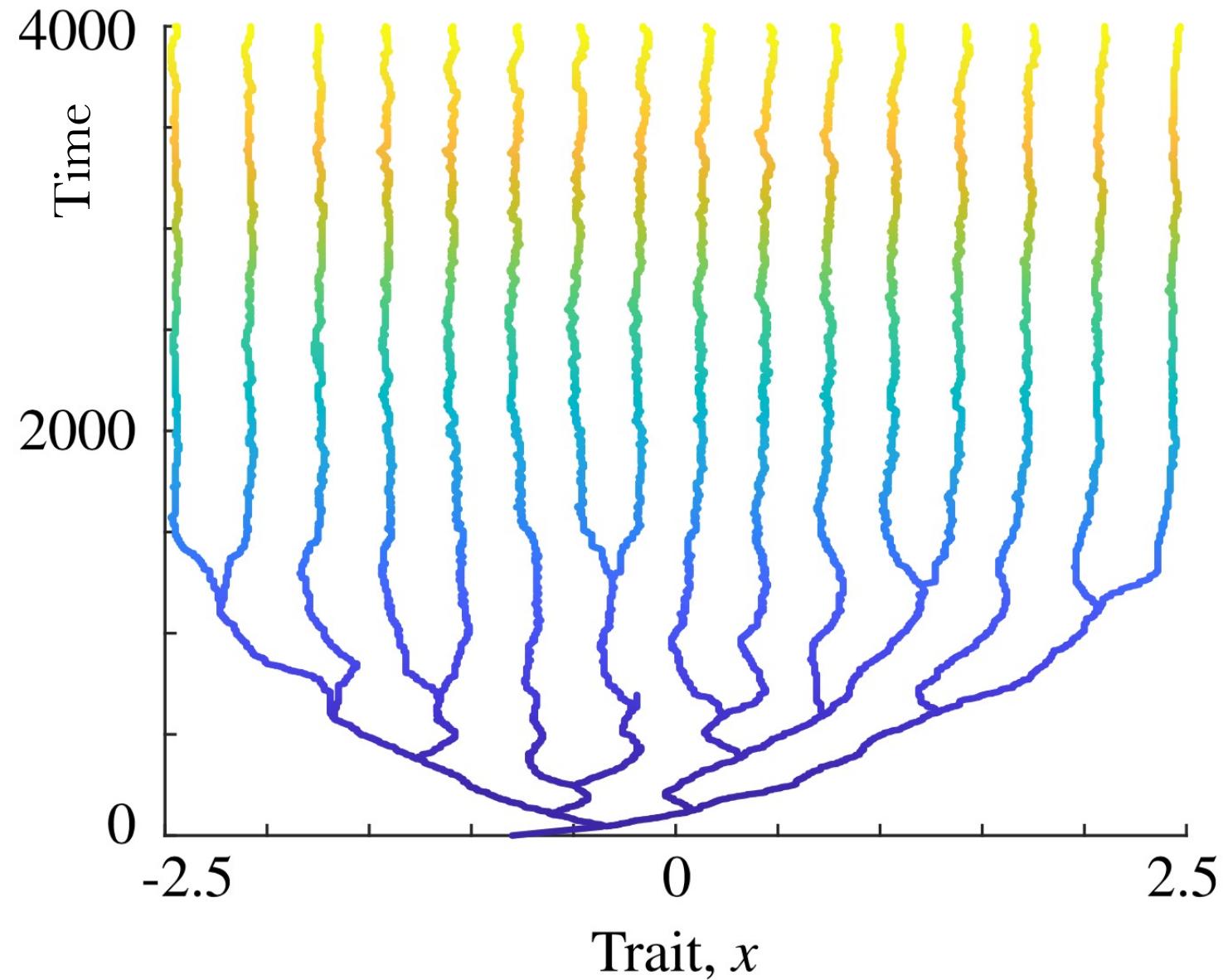
Resource type, z

— Carrying capacity, K

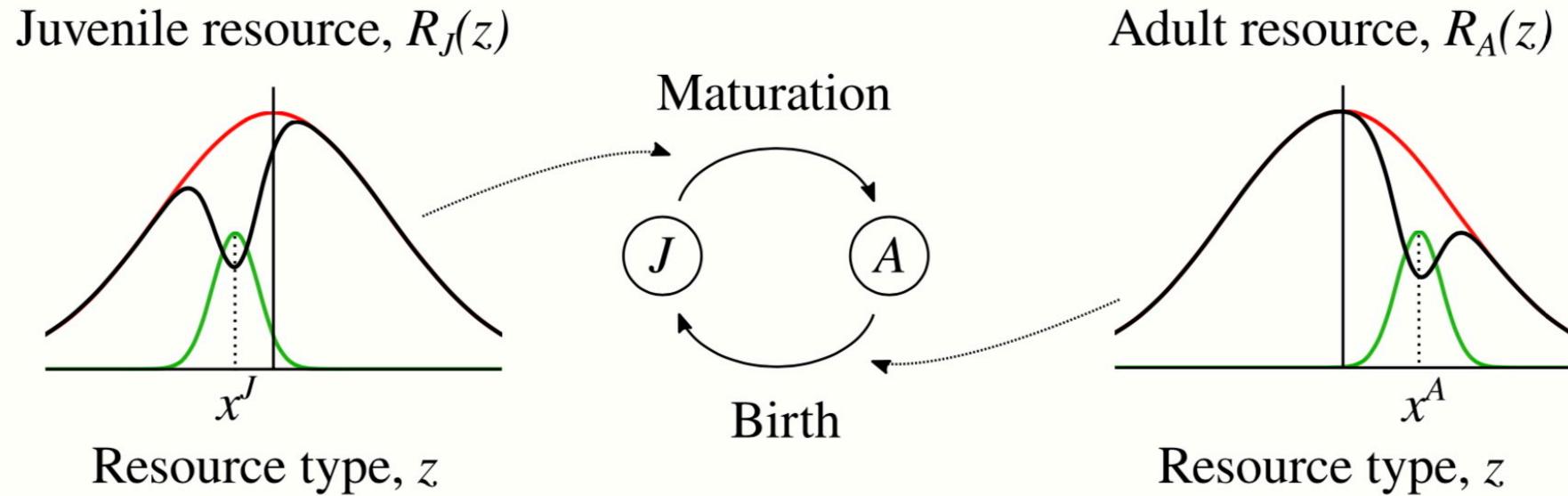
— Resource utilization, a

— Resources at equilibrium, \hat{R}

Gradual diversification driven by competition for resources



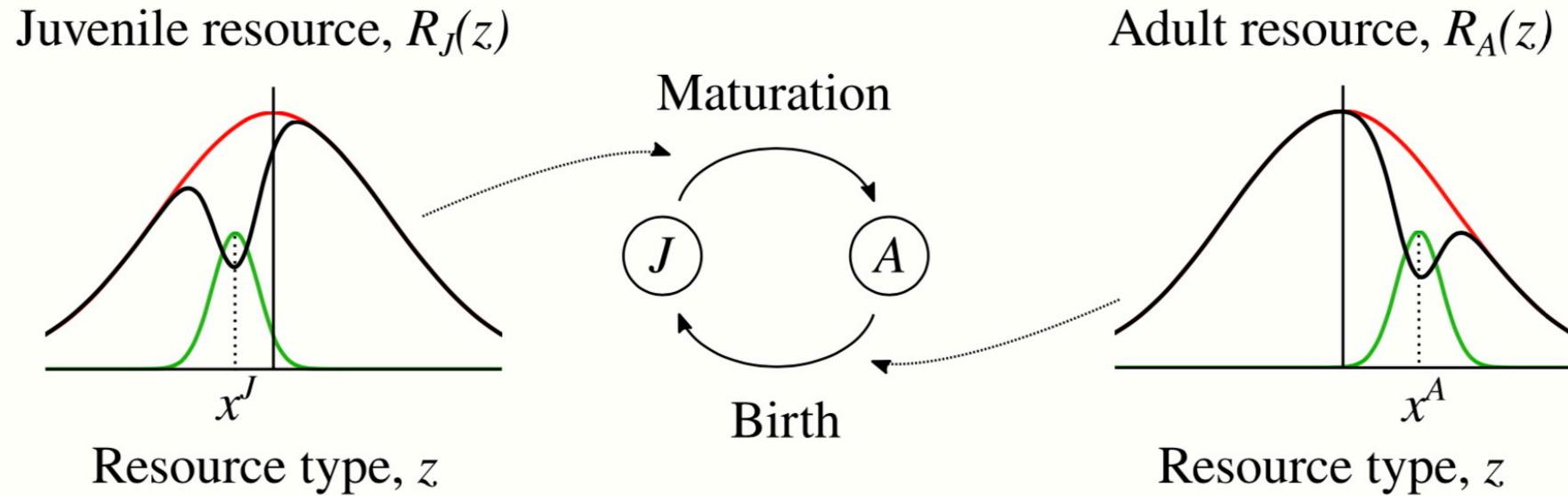
From LV predatory-prey to LV competition – with ontogenetic niche shift



$$\frac{dJ_i}{dt} = b(x_i^A, \mathbf{X}^A, A)A_i - m(x_i^J, \mathbf{X}^J, J)J_i - d_J J_i$$

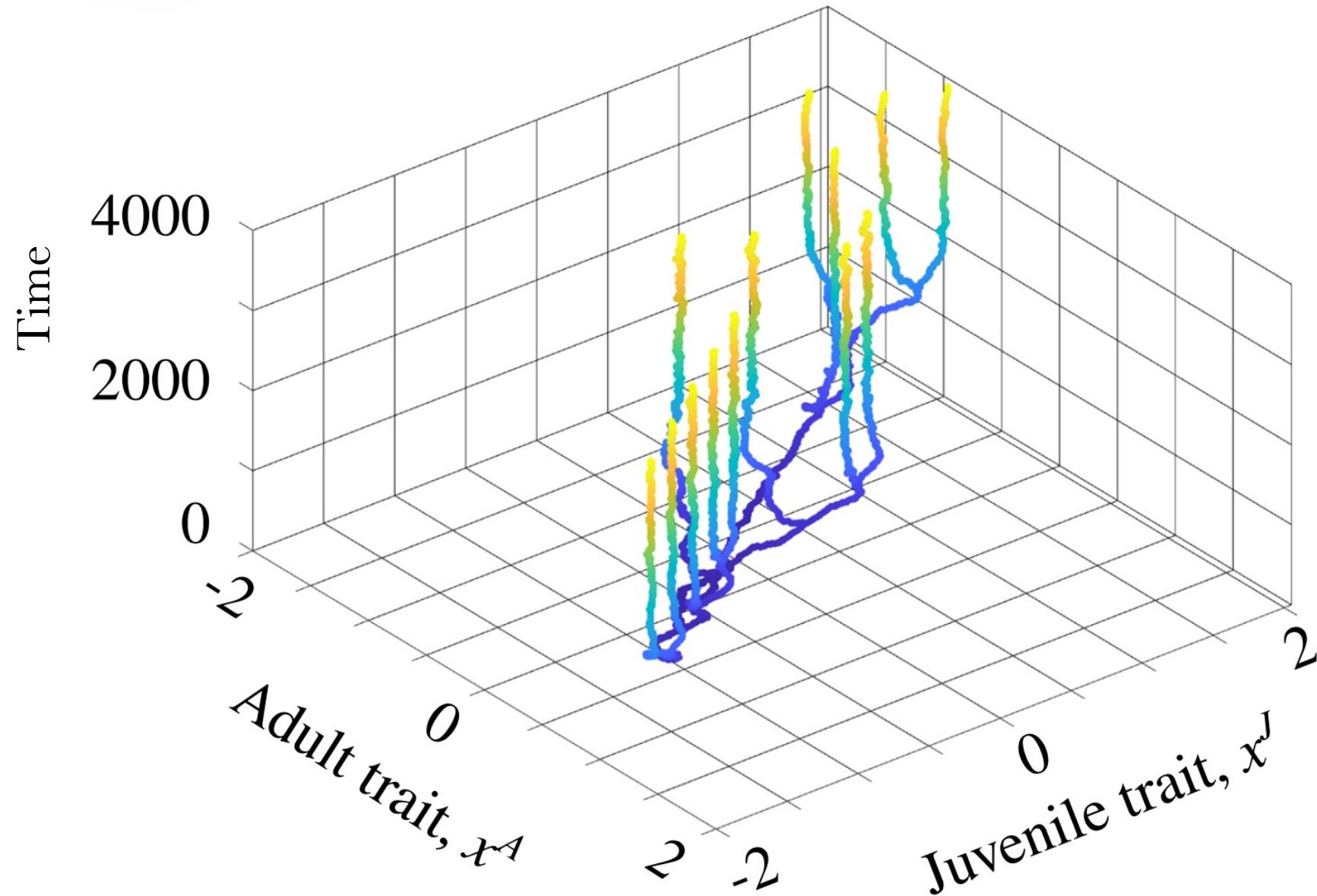
$$\frac{dA_i}{dt} = m(x_i^J, \mathbf{X}^J, J)J_i - d_A A_i,$$

From LV predatory-prey to LV competition – with ontogenetic niche shift

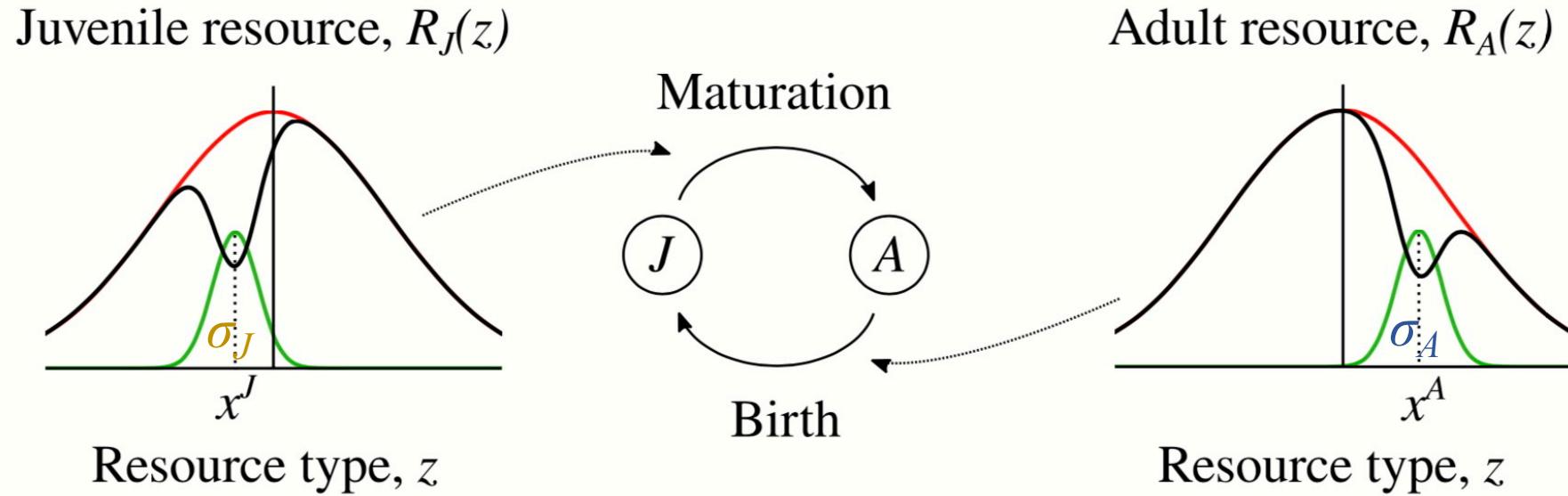


$$\begin{aligned} \frac{dJ_i}{dt} &= b(x_i^A, \mathbf{X}^A, A) A_i - m(x_i^J, \mathbf{X}^J, J) J_i - d_J J_i \\ \frac{dA_i}{dt} &= m(x_i^J, \mathbf{X}^J, J) J_i - d_A A_i, \end{aligned}$$

Gradual diversification driven by competition for resources at two life stages

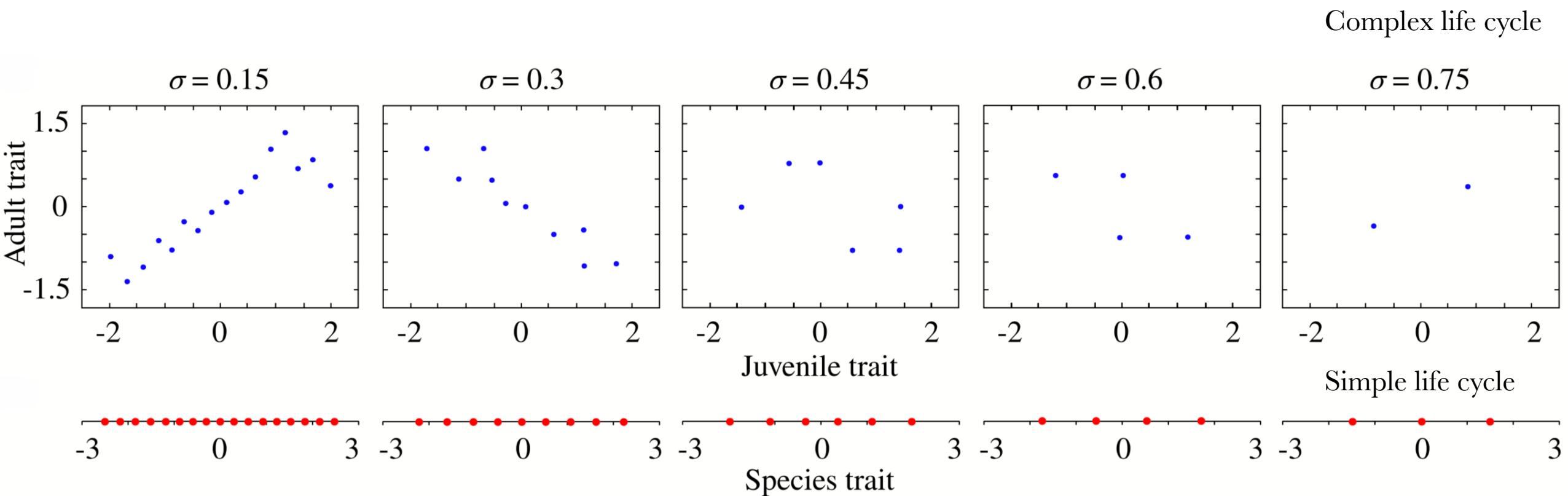


From LV predatory-prey to LV competition – with ontogenetic niche shift

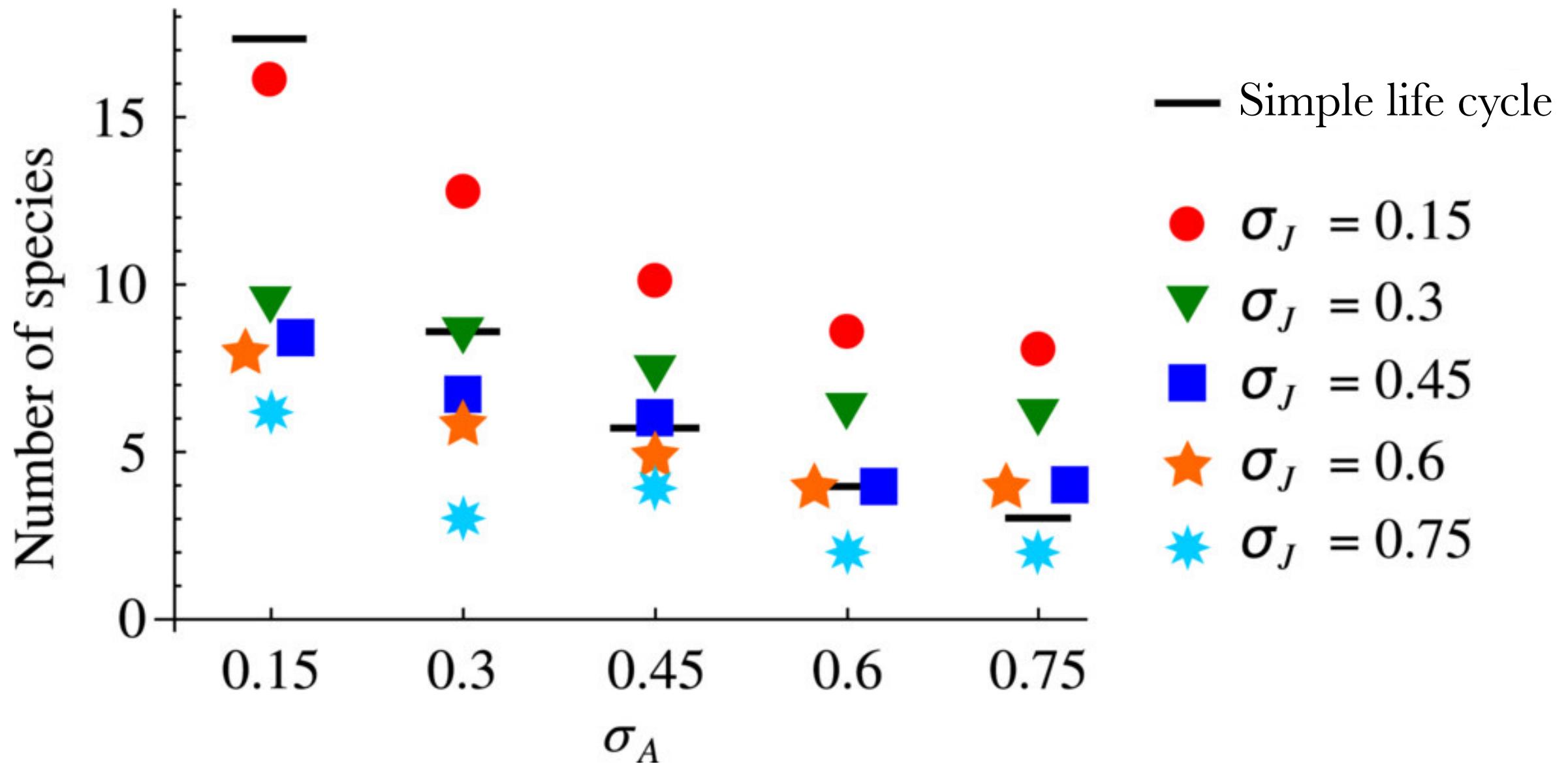


$$\begin{aligned} \frac{dJ_i}{dt} &= b(x_i^A, \mathbf{X}^A, A)A_i - m(x_i^J, \mathbf{X}^J, J)J_i - d_J J_i \\ \frac{dA_i}{dt} &= m(x_i^J, \mathbf{X}^J, J)J_i - d_A A_i, \end{aligned}$$

Results: Gradual evolution

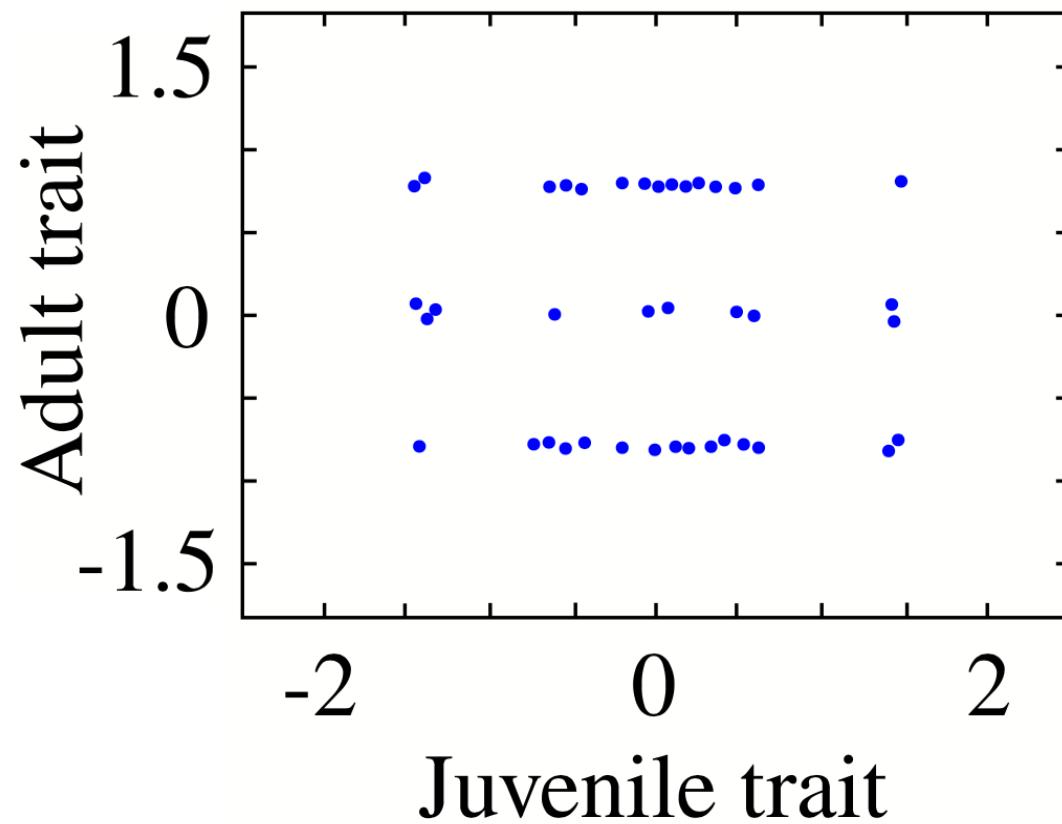


Results: Gradual evolution

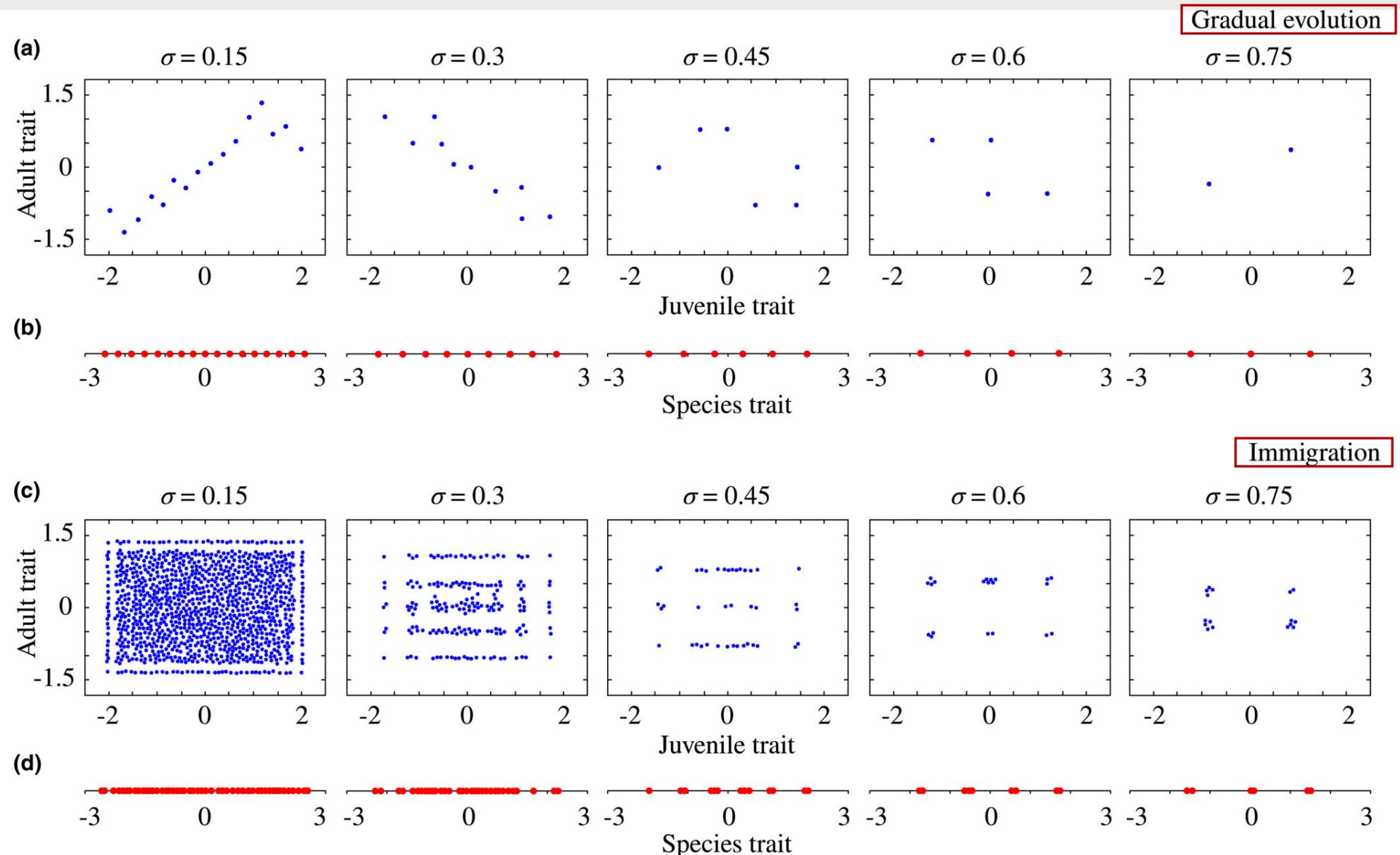


Results: Immigration

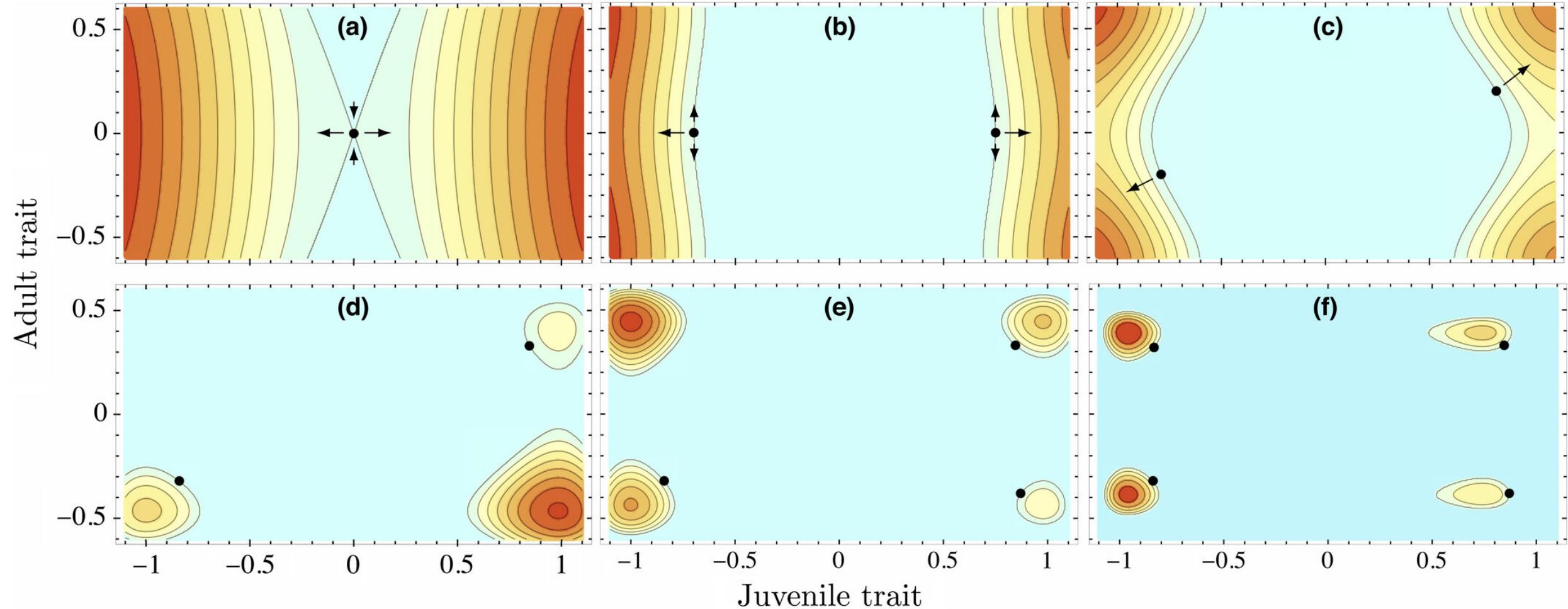
Addition of randomly selected phenotypes until community is saturated.



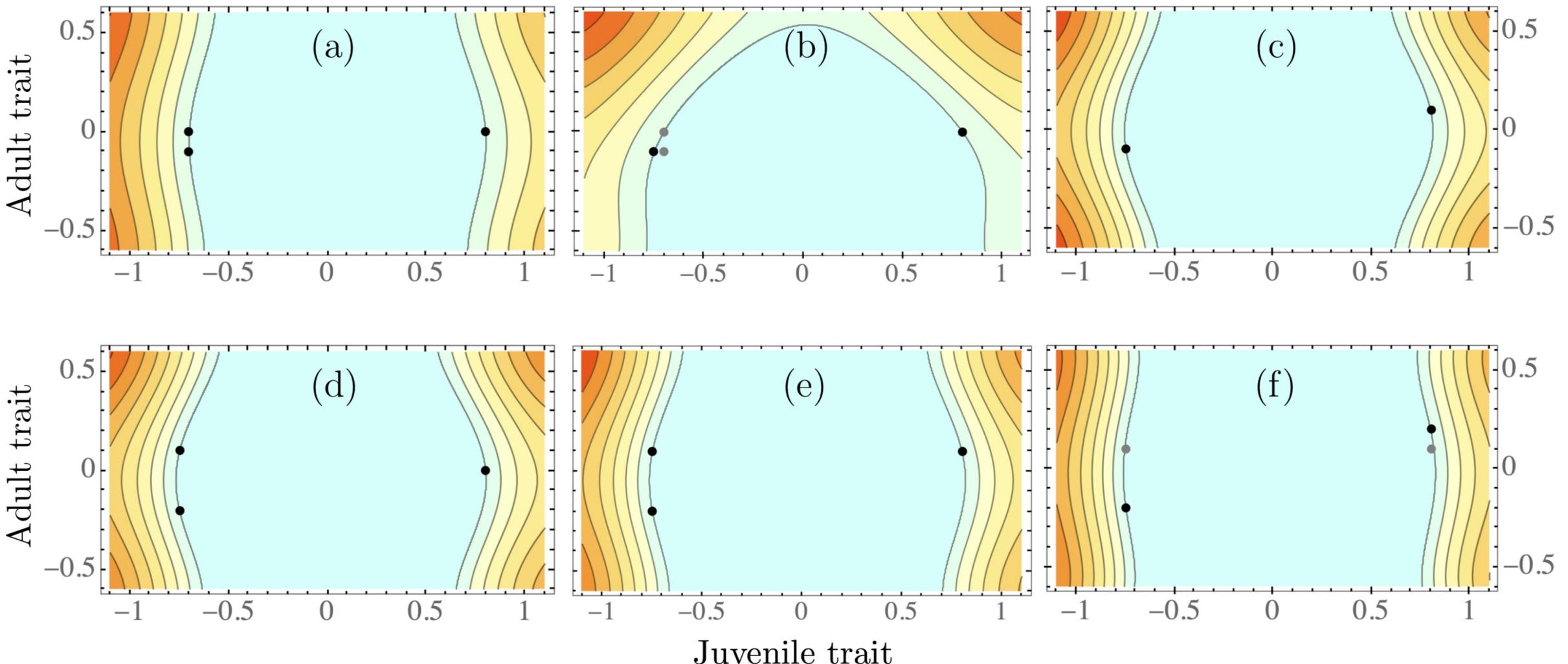
Gradual evolution vs. Immigration



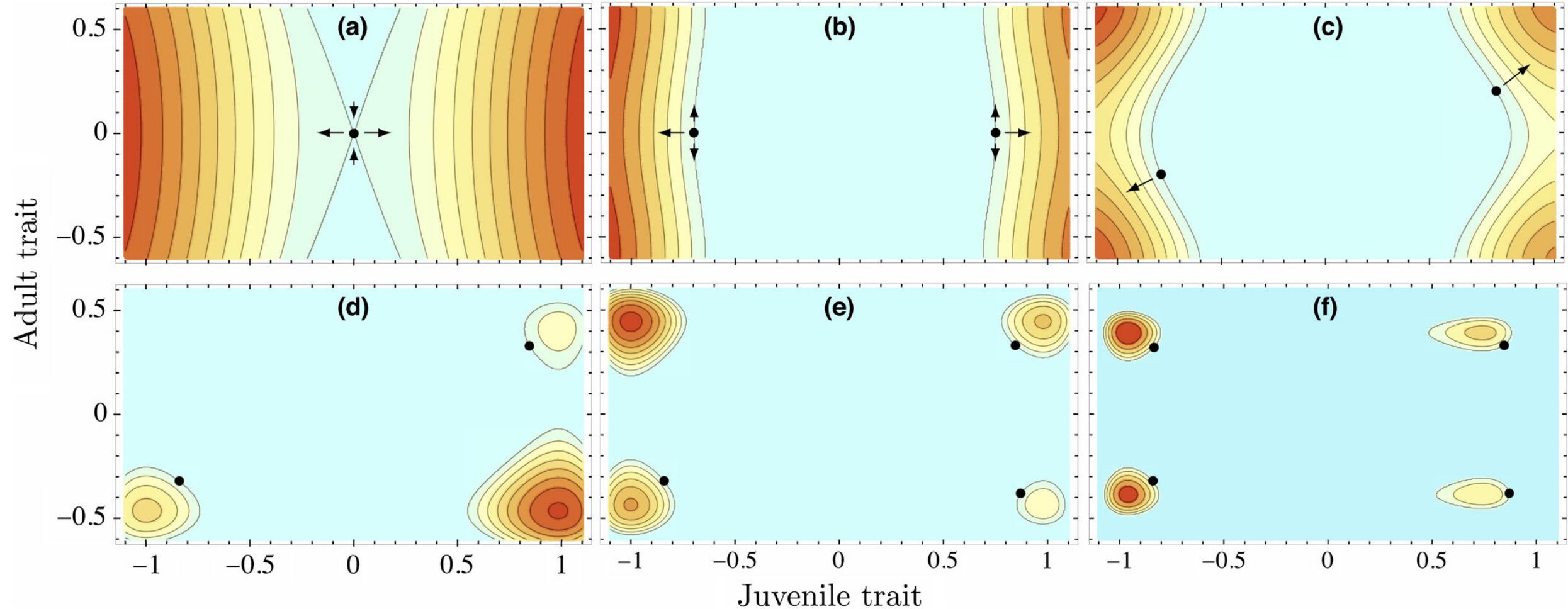
Gradual evolution vs. Immigration



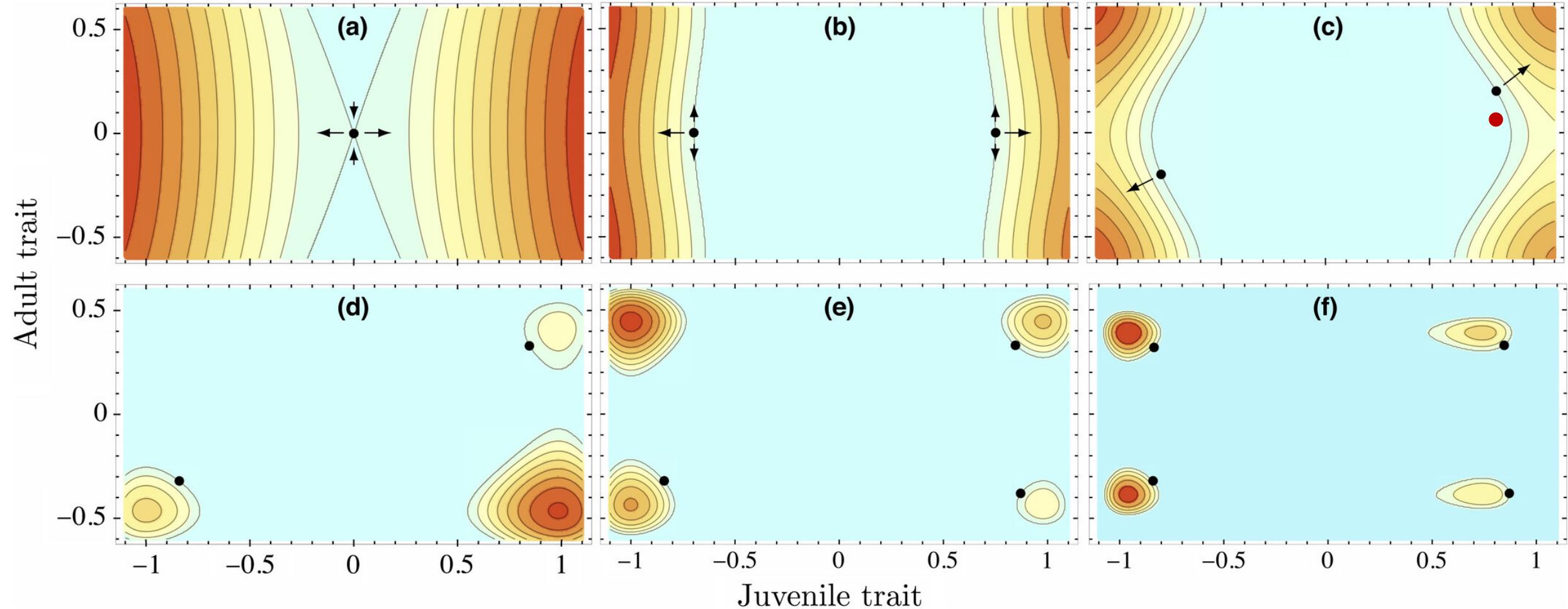
Symmetry breaking under gradual evolution



Gradual evolution vs. Immigration



Gradual evolution vs. Immigration



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LETTER

ECOLOGY LETTERS

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Complex life cycles drive community assembly through immigration and adaptive diversification

Marco Saltini^{1,2}  | Paula Vasconcelos¹ | Claus Rueffler¹



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Consequences of life-cycle complexity to the potential for evolutionary branching

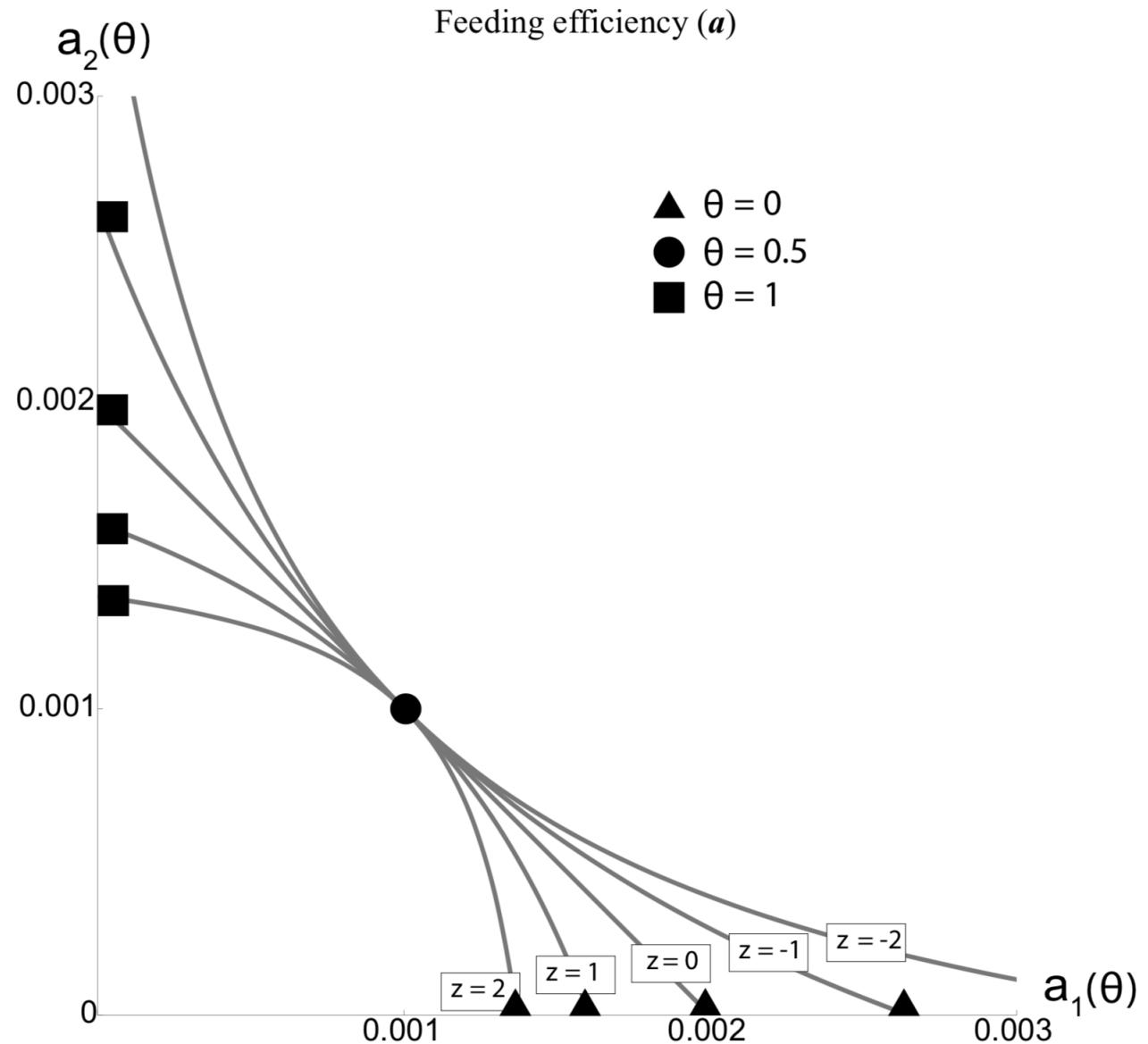
 Paula Vasconcelos,  Marco Saltini,  Claus Rueffler

doi: <https://doi.org/10.1101/2022.08.31.506002>

A version with two resources per stage

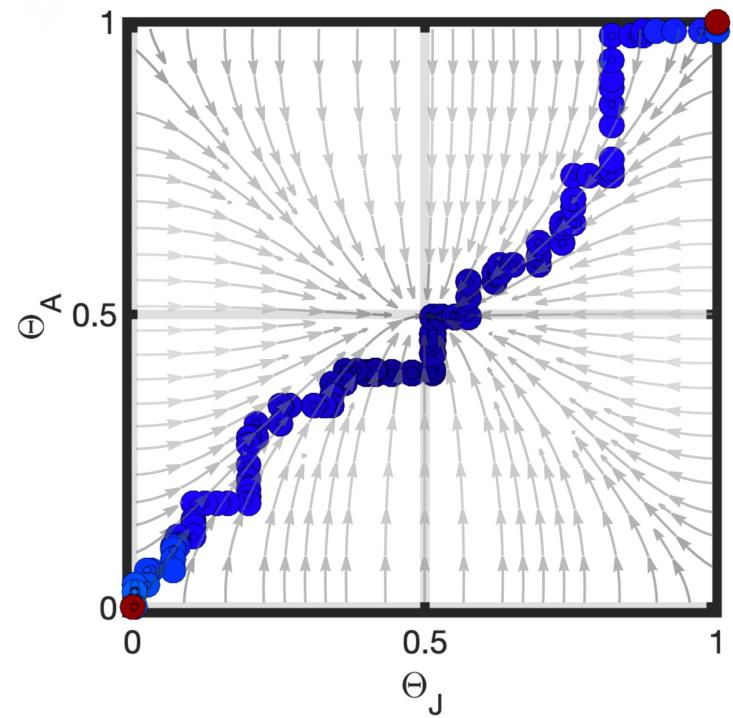
$$\begin{aligned}
 \frac{dR_{1,J}}{dt} &= R_{1,J}r_{1,J} \left(1 - \frac{R_{1,J}}{K_{1,J}}\right) - JR_{1,J}a_{1,J} \\
 \frac{dR_{2,J}}{dt} &= R_{2,J}r_{2,J} \left(1 - \frac{R_{2,J}}{K_{2,J}}\right) - JR_{2,J}a_{2,J} \\
 \frac{dR_{1,A}}{dt} &= R_{1,A}r_{1,A} \left(1 - \frac{R_{1,A}}{K_{1,A}}\right) - AR_{1,A}a_{1,A} \\
 \frac{dR_{2,A}}{dt} &= R_{2,A}r_{2,A} \left(1 - \frac{R_{2,A}}{K_{2,A}}\right) - AR_{2,A}a_{2,A} \\
 \frac{dJ}{dt} &= A(c_{1,A}a_{1,A}R_{1,A} + c_{2,A}a_{2,A}R_{2,A}) - J(c_{1,J}a_{1,J}R_{1,J} + c_{2,J}a_{2,J}R_{2,J}) - Jd_J \\
 \frac{dA}{dt} &= J(c_{1,J}a_{1,J}R_{1,J} + c_{2,J}a_{2,J}R_{2,J}) - Ad_A.
 \end{aligned}
 \quad \left. \begin{array}{l} \\ \\ \\ \end{array} \right\} \text{juvenile resources} \quad \left. \begin{array}{l} \\ \\ \end{array} \right\} \text{adult resources} \quad \left. \begin{array}{l} \\ \\ \end{array} \right\} \text{juveniles} \quad \left. \begin{array}{l} \\ \\ \end{array} \right\} \text{adults}$$

Stage specific trade-off in resource feeding efficiencies



Results: Joint gradual evolution

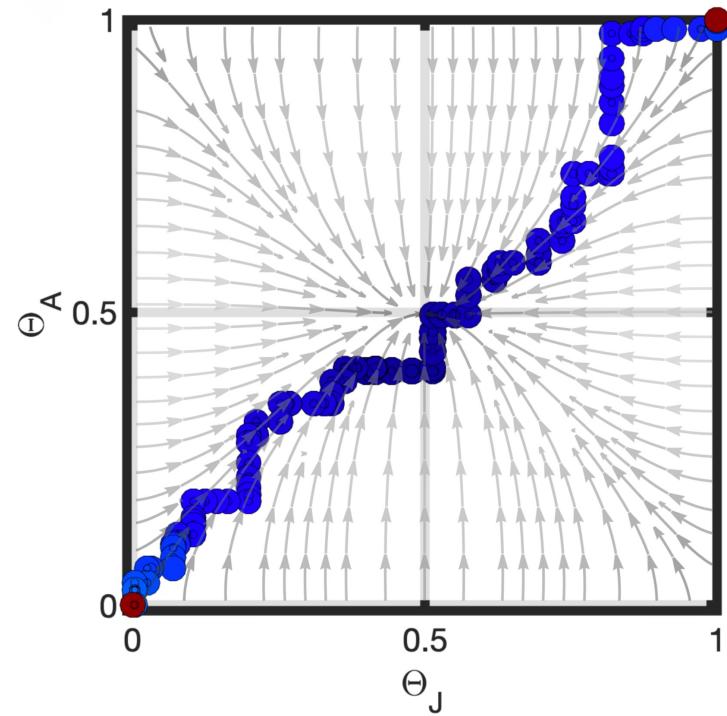
Symmetric resource
growth rates



diagonal community
(as in model with infinitely many resources)

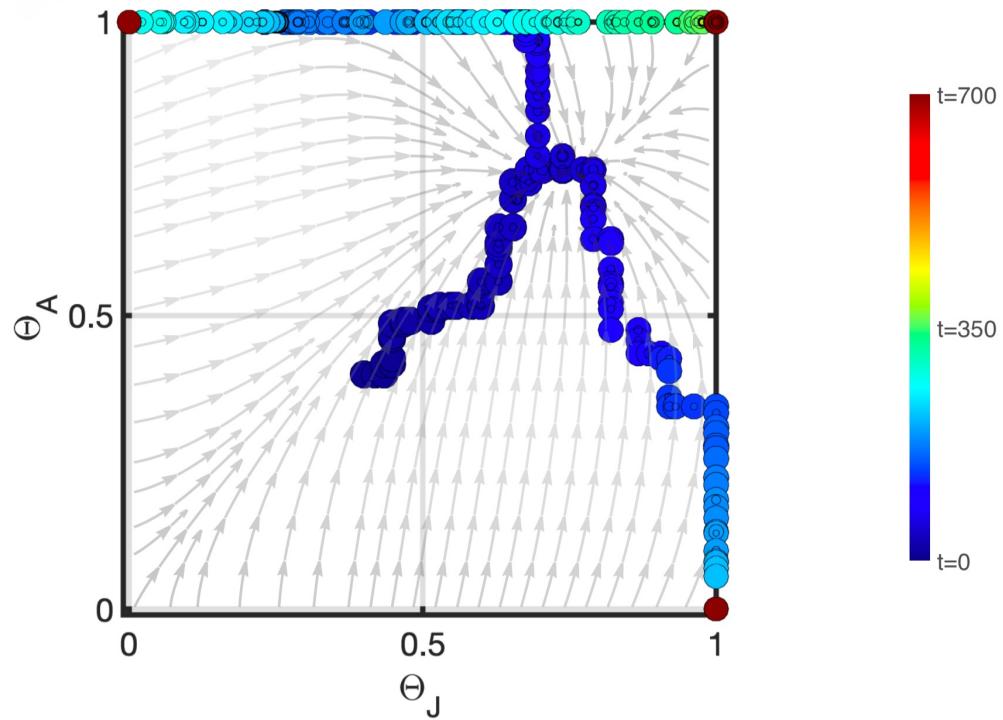
Results: Joint gradual evolution

Symmetric resource
growth rates



diagonal community
(as in model with infinitely many resources)

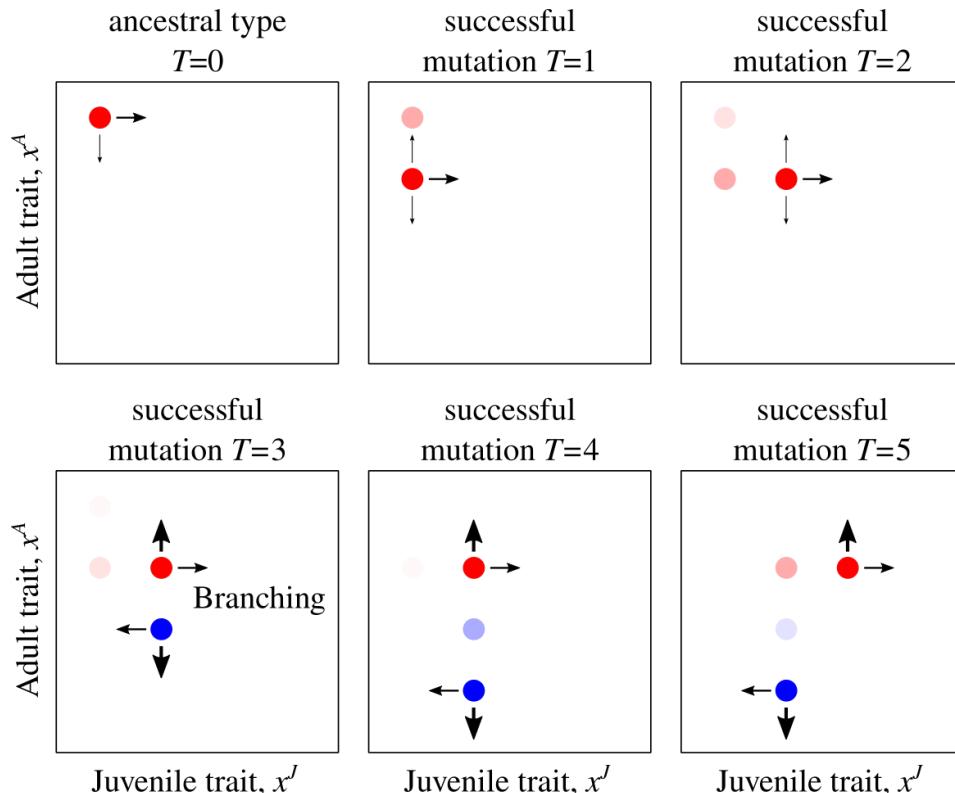
Asymmetric resource
growth rates



three coexisting types possible
(but never four)

The End

Simulation algorithm: jump process



Dieckmann and Law (1996)
Champagnat *et al.* (2006)

Trait substitution rate: per-capita mutation rate times population birth rate times establishment probability

$$g(\mathbf{y}_i, \mathbf{X}) = \mu \hat{A}_i b(\mathbf{x}_i, \mathbf{X}) p_{\text{est}}(\mathbf{y}_i, \mathbf{X})$$

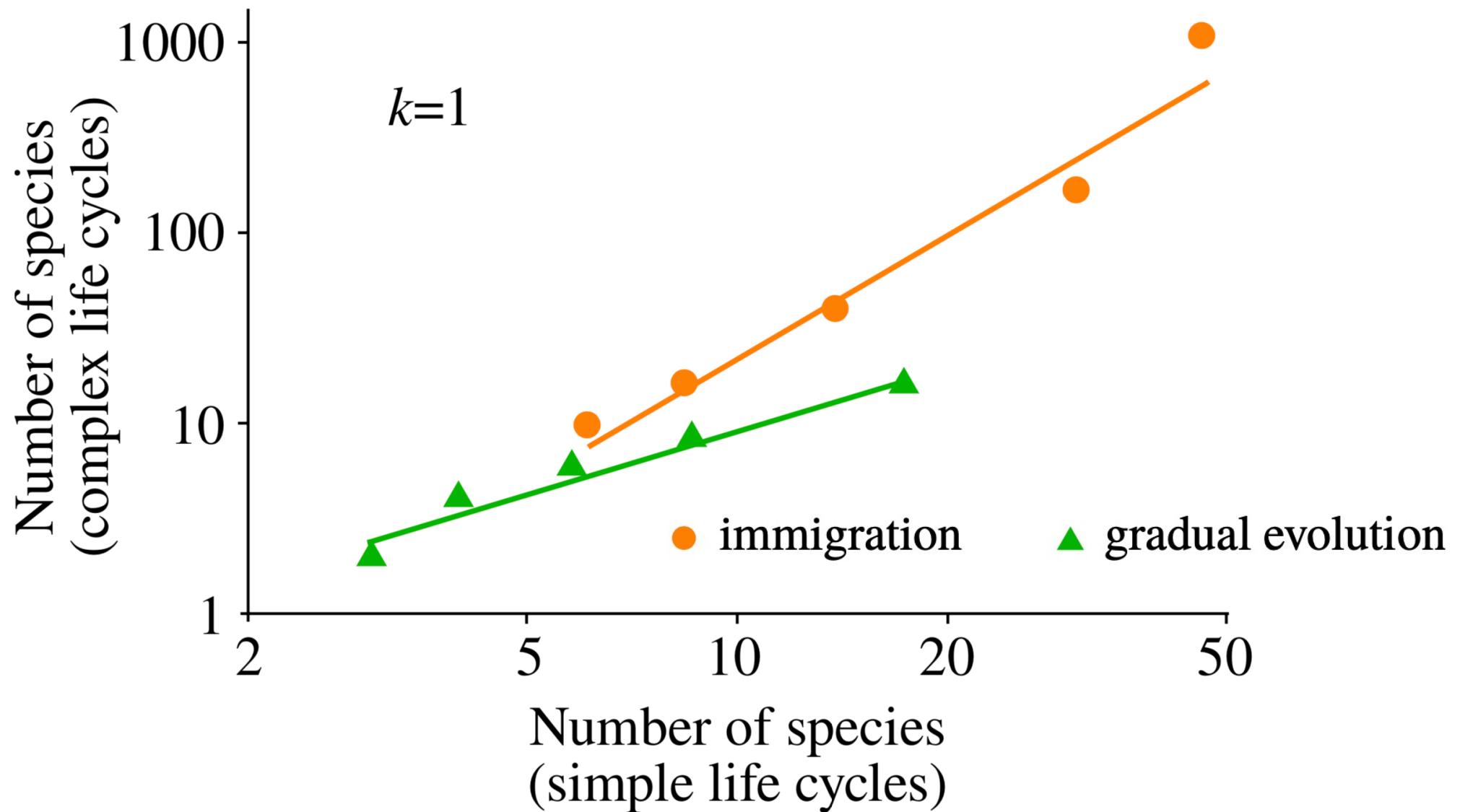
Establishment probability: probability of a beneficial mutation to escape extinction due to demographic stochasticity

$$p_{\text{est}}(\mathbf{y}_i, \mathbf{X}) = \frac{m(\mathbf{y}_i, \mathbf{X})}{m(\mathbf{y}_i, \mathbf{X}) + d_J} - \frac{d_A}{b(\mathbf{y}_i, \mathbf{X})}$$

Polymorphic trait substitution sequence: next trait substitution given by relative trait substitution rate

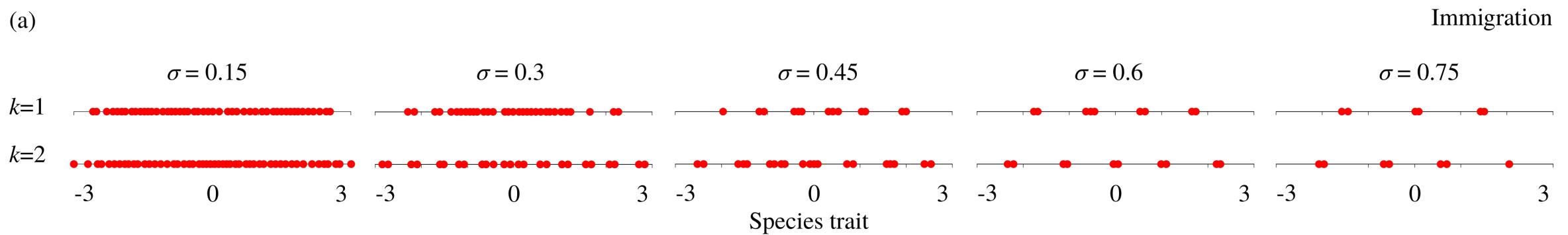
$$g(\mathbf{y}_i, \mathbf{X}) / \sum_{\{\mathbf{y}\}} g(\mathbf{y}, \mathbf{X})$$

Gradual evolution vs. Immigration

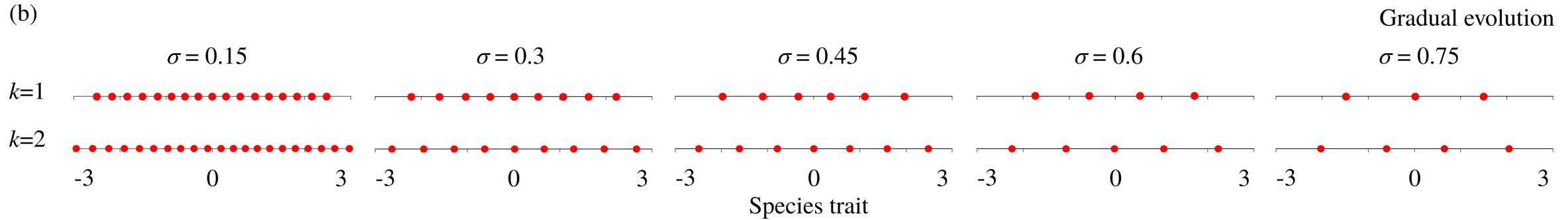


$k=1$ vs. $k=2$

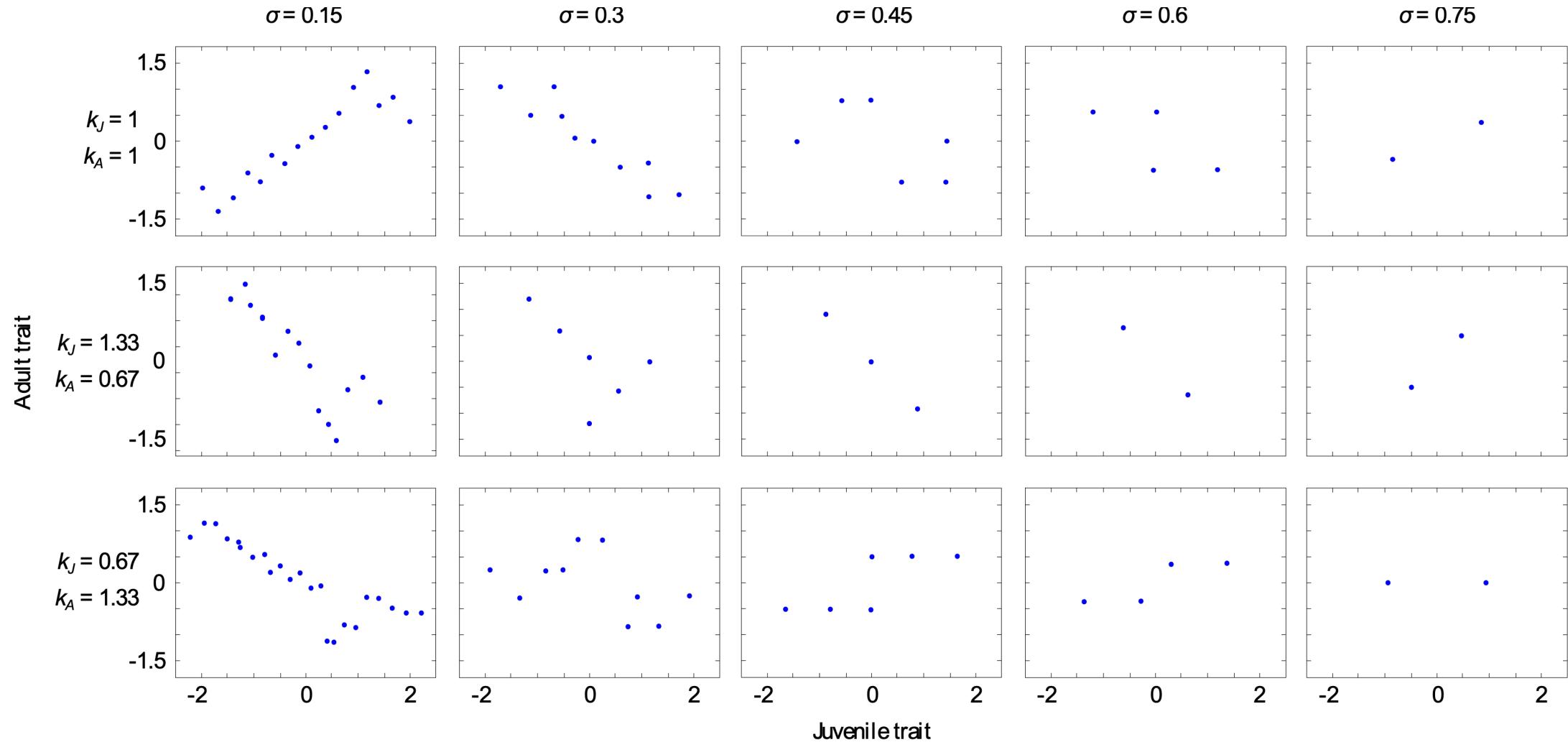
(a)



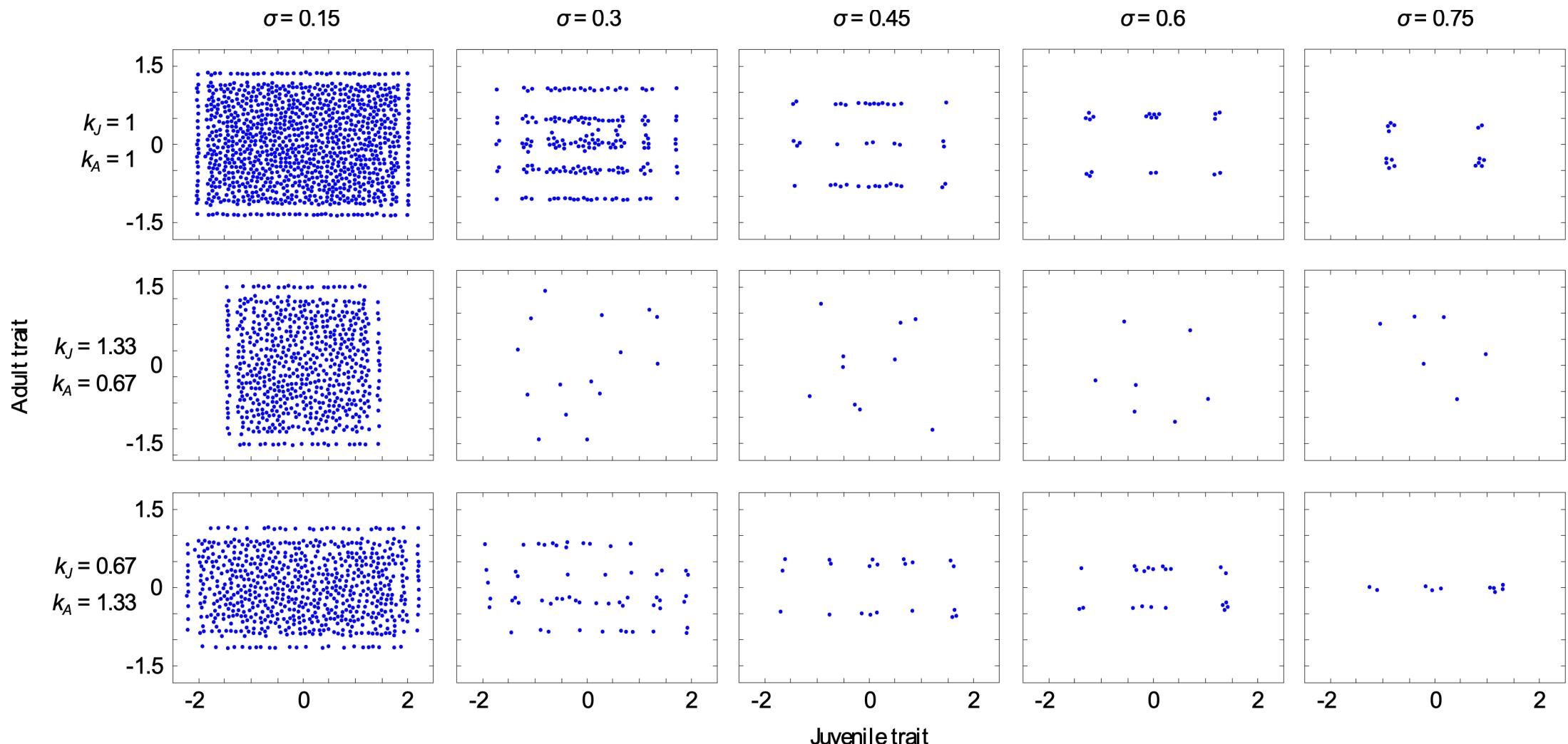
(b)



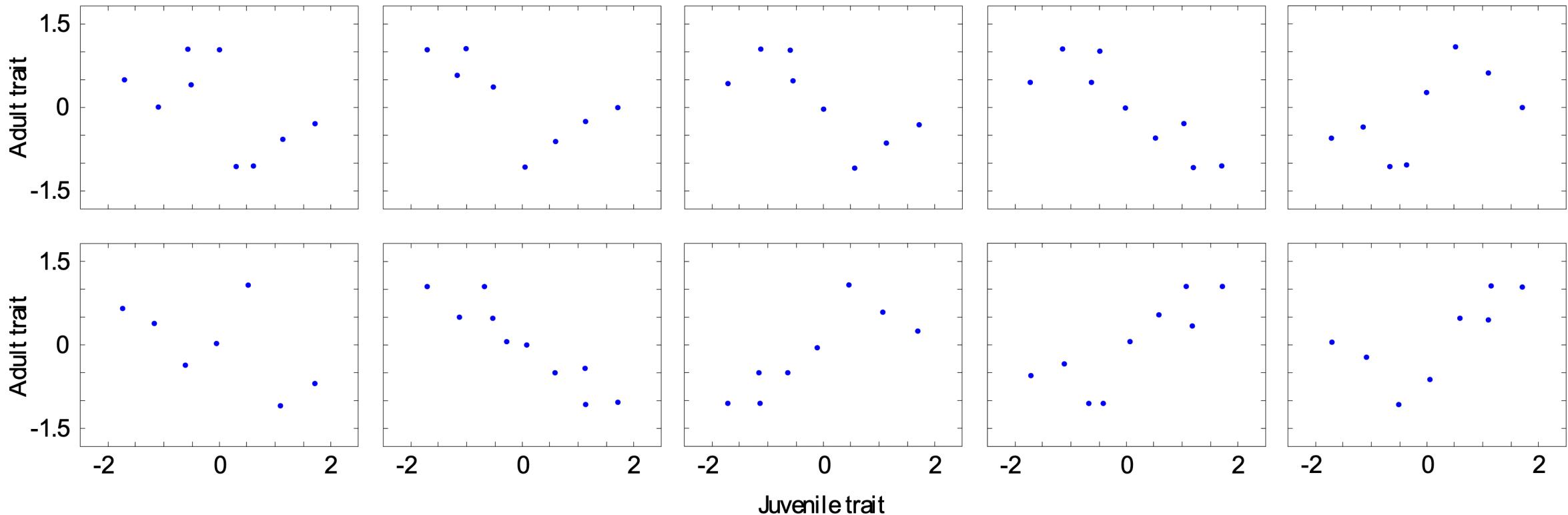
Asymmetry in resource abundance – Gradual evolution



Asymmetry in resource abundance - Immigration

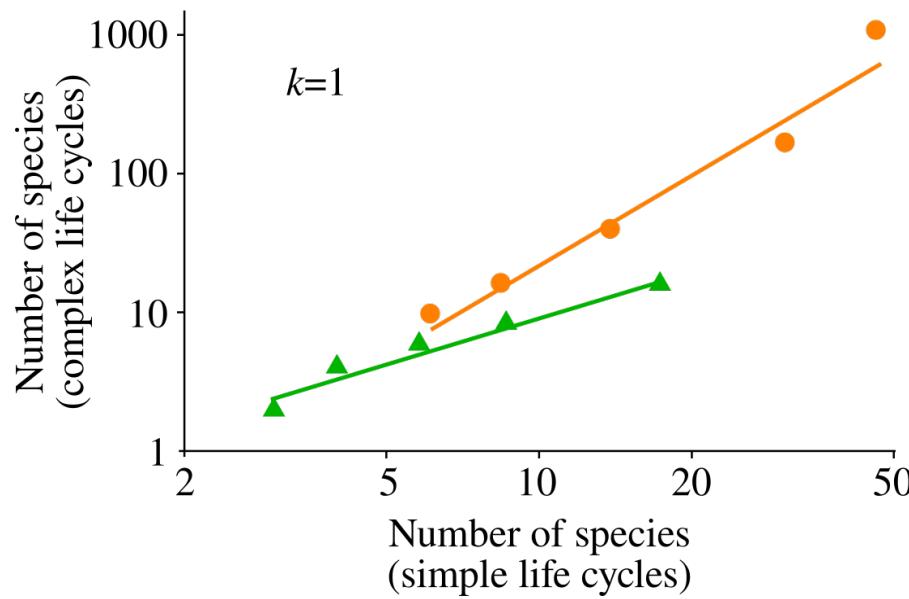


Gradual evolution – ten simulation runs

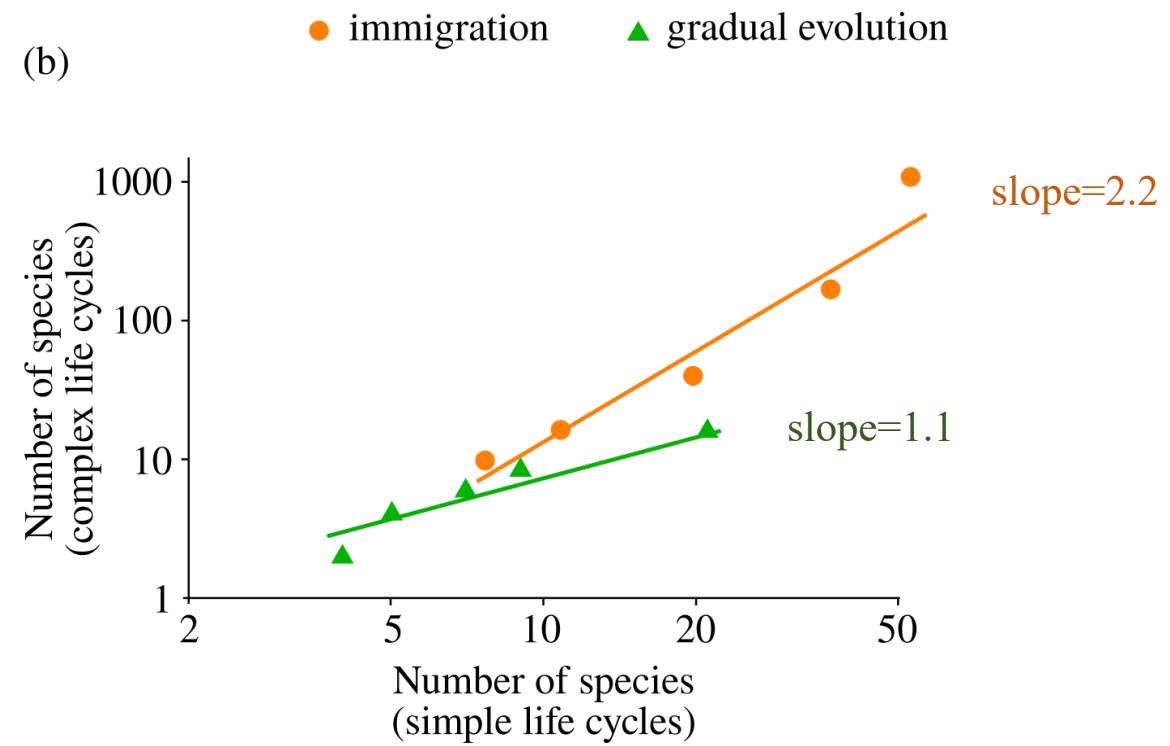


Complex life cycles facilitate species richness through immigration

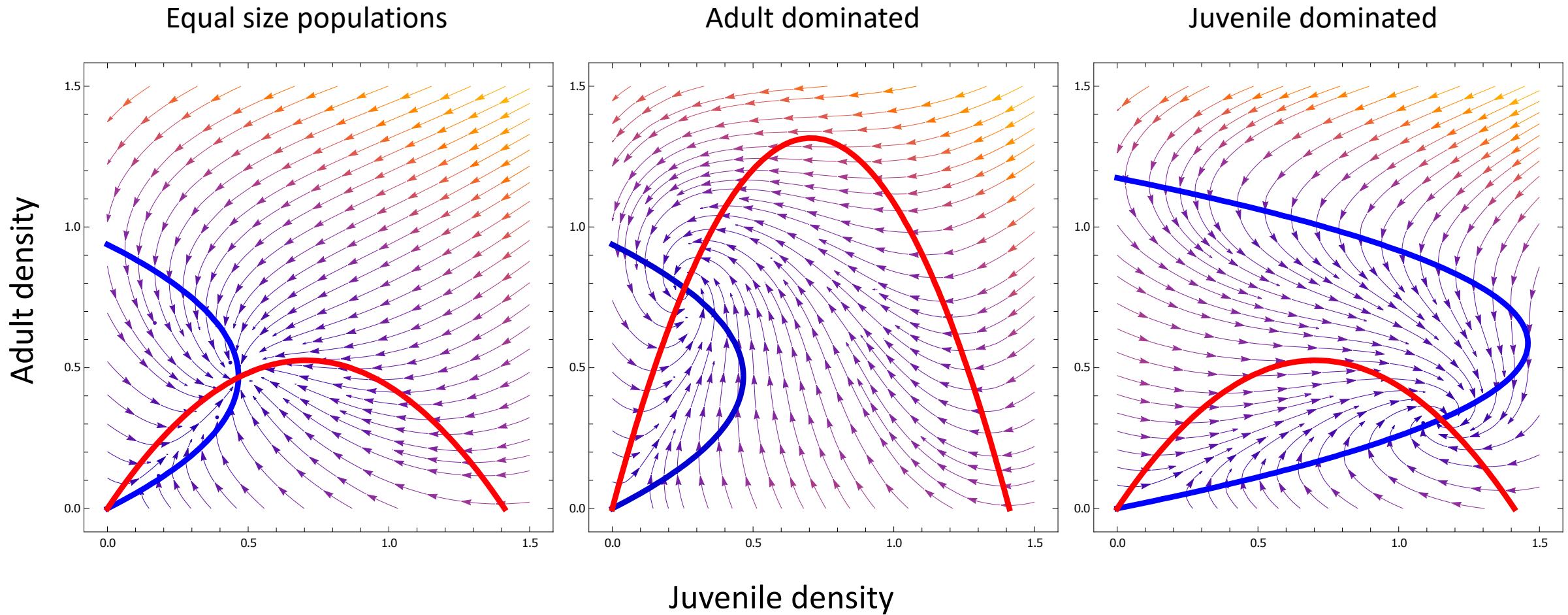
(a)



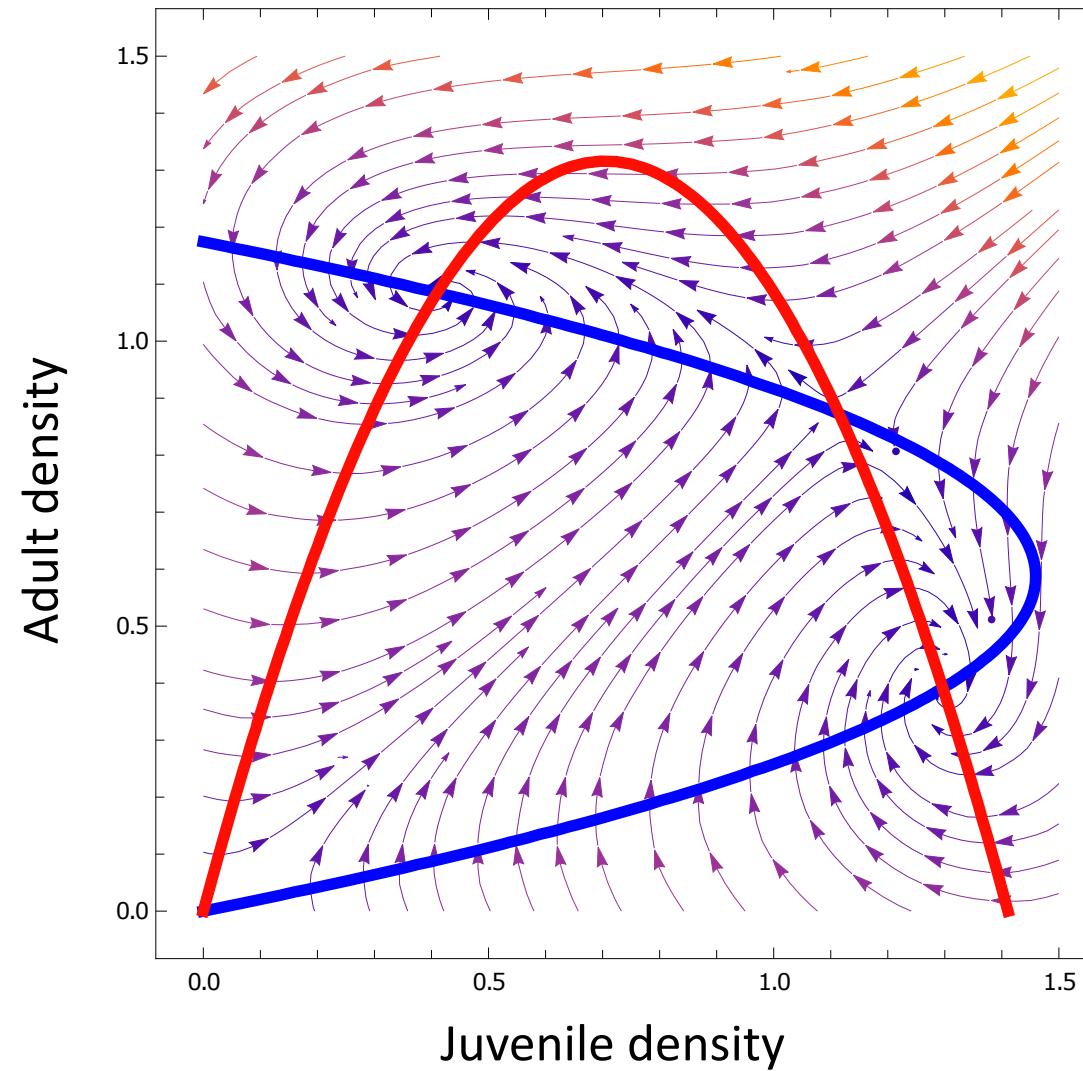
(b)



Population dynamics



Population dynamics



From LV predatory-prey to LV competition – Complex life cycles

$$\frac{dR_J(z)}{dt} = R_J(z) \left[r \left(1 - \frac{R_J(z)}{K(z)} \right) - \sum_i a_J(z, x_i^J) J_i \right]$$

$$\frac{dR_A(z)}{dt} = R_A(z) \left[r \left(1 - \frac{R_A(z)}{K(z)} \right) - \sum_i a_A(z, x_i^A) A_i \right]$$

$$\frac{dJ_i}{dt} = A_i c \int_{-\infty}^{+\infty} a_A(z, x_i^A) R_A(z) dz - J_i c \int_{-\infty}^{+\infty} a_J(z, x_i^J) R_J(z) dz - J_i d$$

$$\frac{dA_i}{dt} = J_i c \int_{-\infty}^{+\infty} a_J(z, x_i^J) R_J(z) dz - A_i d$$

From LV predatory-prey to LV competition – Complex life cycles

$$\frac{dJ_i}{dt} = A_i b_i - J_i m_i - J_i d$$

$$\frac{dA_i}{dt} = J_i m_i - A_i d$$

$$m_i = m_0(x_i) \left(1 - \sum_j \alpha(x_i, x_j) J_j \right)$$

$$b_i = b_0(x_i) \left(1 - \sum_j \alpha(x_i, x_j) A_j \right)$$

Intrinsic maturation and birth rate

$$m_0(x_i^J) = c_J \frac{\omega k}{\sqrt{\sigma_J^2 + \omega^2}} \exp \left[-\frac{(x_i^J)^2}{2(\sigma_J^2 + \omega^2)} \right],$$

$$b_0(x_i^A) = c_A \frac{\omega k}{\sqrt{\sigma_A^2 + \omega^2}} \exp \left[-\frac{(x_i^A)^2}{2(\sigma_A^2 + \omega^2)} \right].$$

Competition coefficients

$$\alpha_J(x_i^J, x_j^J) = \frac{1}{\sqrt{2\pi}r} \sqrt{\frac{\sigma_J^2 + \omega^2}{\sigma_J^2 + 2\omega^2}} \exp \left[-\frac{\omega^2 (x_i^J - x_j^J)^2 + \sigma_J^2 \left((x_i^J)^2 + (x_j^J)^2 \right)}{2\sigma_J^2 (\sigma_J^2 + 2\omega^2)} + \frac{(x_i^J)^2}{2(\sigma_J^2 + \omega^2)} \right], \quad (\text{S5a})$$

$$\alpha_A(x_i^A, x_j^A) = \frac{1}{\sqrt{2\pi}r} \sqrt{\frac{\sigma_A^2 + \omega^2}{\sigma_A^2 + 2\omega^2}} \exp \left[-\frac{\omega^2 (x_i^A - x_j^A)^2 + \sigma_A^2 \left((x_i^A)^2 + (x_j^A)^2 \right)}{2\sigma_A^2 (\sigma_A^2 + 2\omega^2)} + \frac{(x_i^A)^2}{2(\sigma_A^2 + \omega^2)} \right]. \quad (\text{S5b})$$