The Ideal Free Distribution

as a game theoretical concept

Vlastimil Krivan

Biology Center
and
Faculty of Science
Ceske Budejovice
Czech Republic

vlastimil.krivan@gmail.com

www.entu.cas.cz/krivan

Ross Cressman

Department of Mathematics
Wilfrid Laurier University
Waterloo, Ontario
Canada

rcressman@wlu.ca

Talk outline:

1. The IFD as an ESS of the static Habitat selection game
2. Dispersal dynamics, but no population dynamics
3. The Habitat selection game as an example of a population game (both frequency and population dynamics combined)

The Habitat selection game

(Krivan, Cressman and Schneider, 2008)

1. Population(s) in a heterogeneous environment consisting of n patches

2. Each patch is characterized by its payoff V_i, $i = 1, \ldots, n$

3. Payoffs are negatively density dependent, i.e. $V_i(m_i)$ decreases with increasing abundance m_i in the $i-$th patch

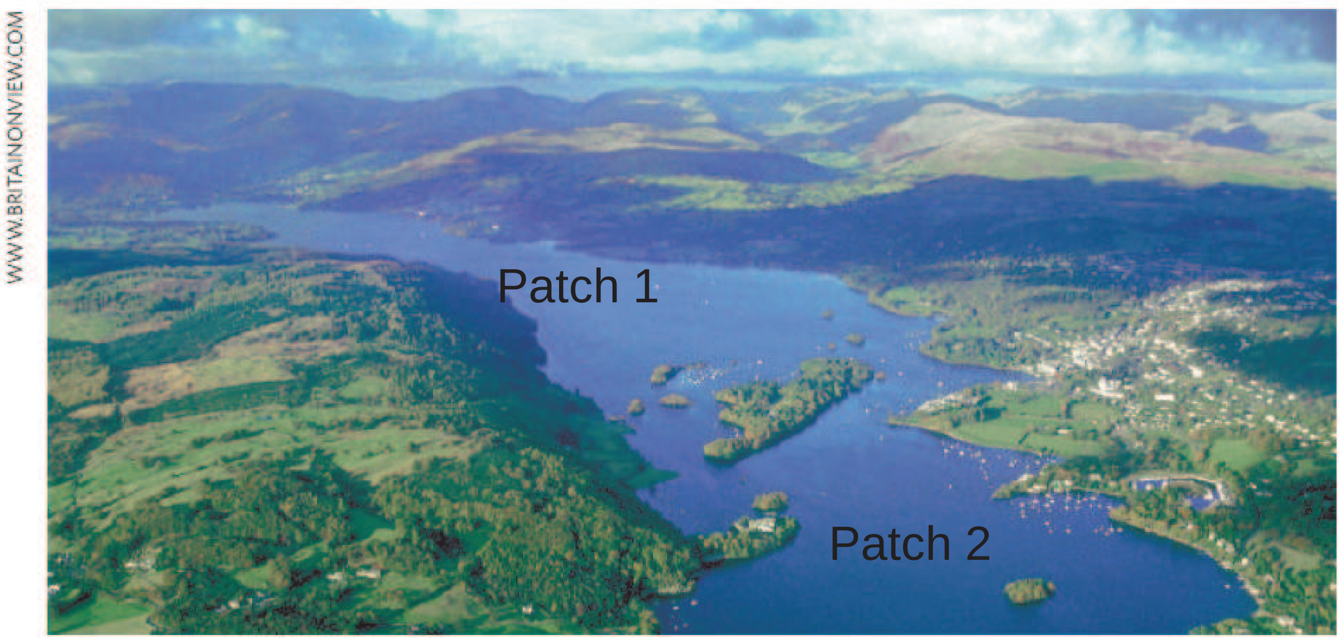


Figure 2 | Divided lake. Lake Windermere is separated by a shallow sill into two habitats for pike.

Individual pure strategy: Stay all your life in a single patch (e.g, sessile organisms)

Individual mixed strategy: Spend proportion p_i of the lifetime in patch i (vagile organism)

Population Monomorphism: All individuals in the population use the same strategy (either pure or mixed) $p = (p_1, \ldots, p_n)$. In this case p is also the population distribution among patches.

Population Polymorphism: The population consists of k behavioral phenotypes (with frequencies x_i) each of them characterized by a vector p_i that specifies the distribution of times an individual stays in different patches. Then population profile is given by $x_1 p_1 + \cdots + x_k p_k$ which specifies population distribution.

Fitness of a mutant with strategy $\tilde{p} = (\tilde{p}_1, \ldots, \tilde{p}_n)$ in a resident population where all individulas use strategy (distribution) $p = (p_1, \ldots, p_n)$:

$$G(\tilde{p}, p) = \tilde{p}_1 V_1(p_1) + \cdots + \tilde{p}_n V_n(p_n).$$

The Ideal Free Distribution

Definition 1 (Fretwell and Lucas 1969) *Population distribution* $p = (p_1, \ldots, p_n)$ *is called* the Ideal Free Distribution *if:*

(i) there exists index k *such that the first* k *habitats are occupied*

(i.e., $p_i > 0$ *for* $i = 1, \ldots, k$ *and* $p_j = 0$ *for* $j = k+1, \cdots, n$ *)*

(ii) payoffs in the occupied habitats are the same and maximal

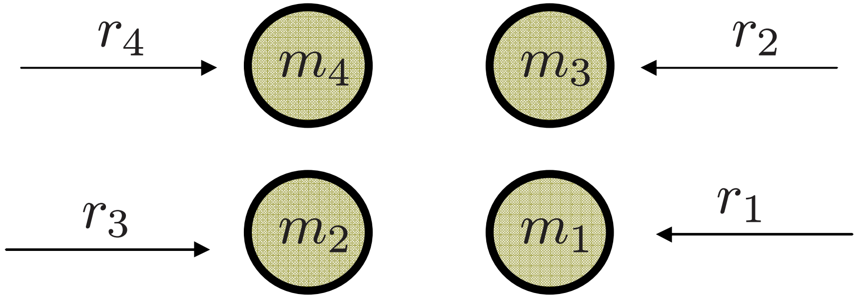
(i.e., $V_1(p_1) = \cdots = V_k(p_k) =: V^\star$ *and* $V_j(0) \le V^\star$ *for* $j = k+1, \cdots, n$*).*

Proposition 1 *The strategy corresponding to the Ideal Free Distribution is the Nash equilibrium of the Habitat selection game.*

Proposition 1 (Cressman and Krivan 2006) *The strategy corresponding to the IFD is an ESS of the Habitat selection game.*

Parkers matching principle

(Parker 1978)



m_i = abundance in the $i-$th patch

$M = m_1 + \cdots + m_n$ is the total (constant) population abundance

r_i = resource input rate in patch i

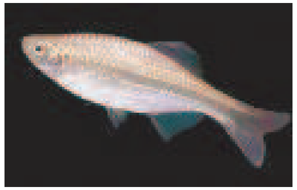
$$V_i = \frac{\text{resource input rate}}{\text{animal abundance in the patch}} = \frac{r_i}{m_i}$$

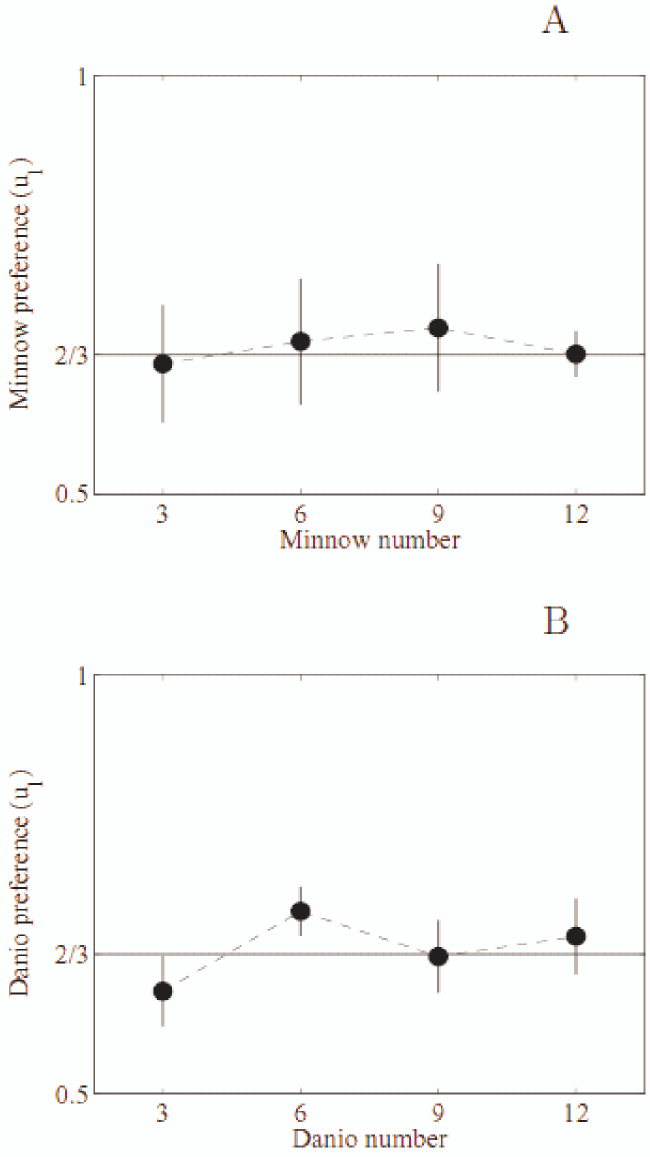
The corresponding IFD: $p_i = \frac{m_i}{M} = \frac{r_i}{r_1+\cdots+r_n}$

and all patches are occupied.

The IFD distribution of two fish species among two feeding sites

(Berec et al. 2006)



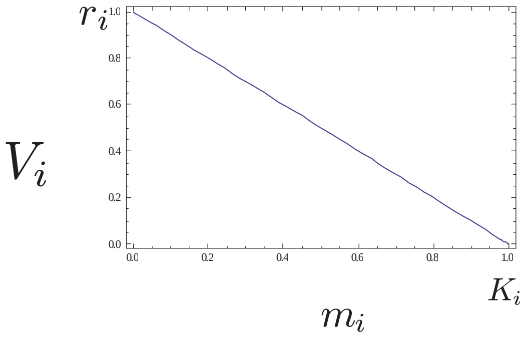


Patch payoff is a linear function of patch abundance

(Krivan and Sirot 2002, Cressman and Krivan 2010)

Patch payoff:

$$V_i = r_i \left(1 - \frac{m_i}{K_i}\right)$$



Fitness of a mutant with strategy $\tilde{p} = (\tilde{p}_1, \tilde{p}_2)$ in the resident population with distribution $p = (p_1, p_2)$ is:

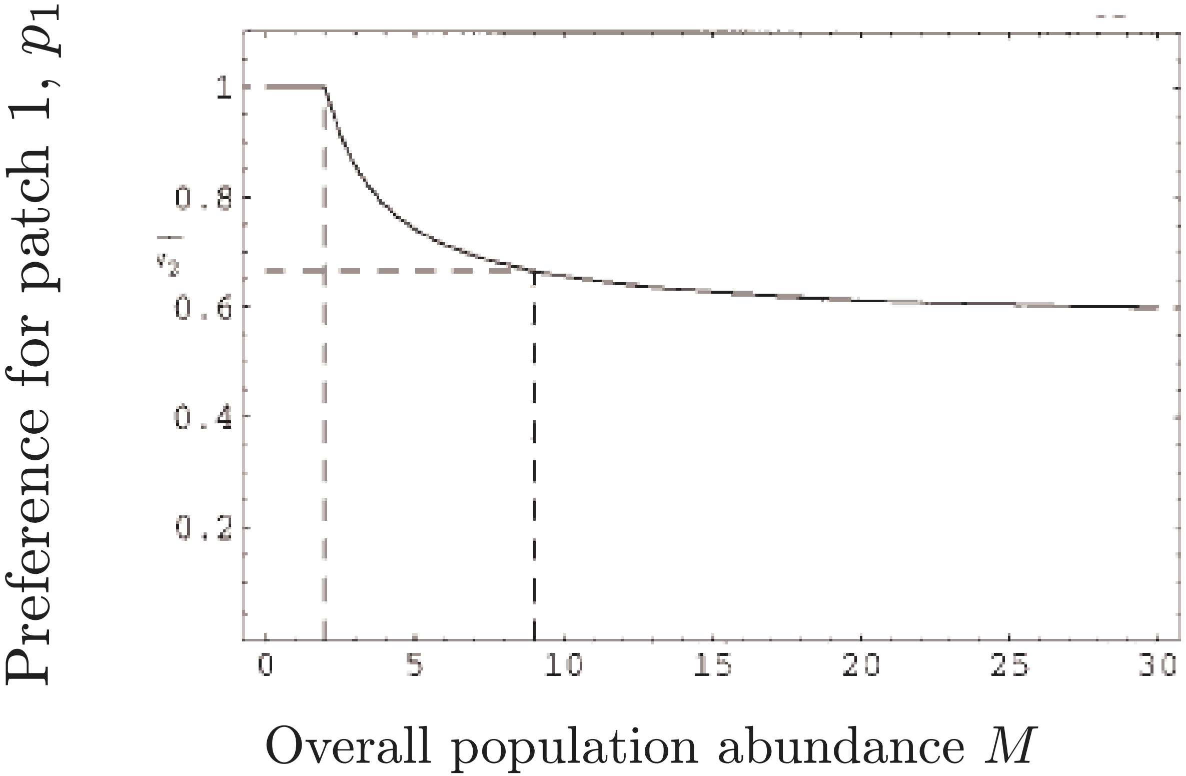
$$G(\tilde{p}, p) = \tilde{p}_1 V_1(p_1) + \tilde{p}_2 V_2(p_2) \qquad =: \langle \tilde{p}, Up \rangle$$

$$U = \begin{bmatrix} r_1(1 - \frac{M}{K_1}) & r_1 \\ r_2 & r_2(1 - \frac{M}{K_2}) \end{bmatrix}$$

The IFD for linear payoffs in 2 patches

Assuming $r_1 > r_2$, the IFD for the total population size $M = m_1 + m_2$ is:

$$p_1 = \begin{cases} 1 & \text{if } \; M < K_1 \frac{r_1 - r_2}{r_1} \\ \frac{r_2 K_1}{r_2 K_1 + r_1 K_2} + \frac{K_1 K_2 (r_1 - r_2)}{(r_2 K_1 + r_1 K_2) M} & \text{otherwise.} \end{cases}$$



Summary for the IFD as a static concept of the Habitat selection game

The Ideal Free Distribution is an ESS of the Habitat selection game.

It is static in the following sense:

1. It does not describe mechanistically how the distribution changes in time; it just predicts what the final distribution should be

2. It considers a single population only

3. It does not consider changes in population densities

Frequency dynamics for the Habitat selection game: Dispersal

(Cressman and Krivan, 2006)

D= dispersal matrix
D_{ij} = is the probability with which an individual will disperse from patch j to patch i in a unit of time

m_i=animal abundance in patch i

$M = m_1 + \cdots + m_n$ = overall (fixed) abundance

$$\frac{dm_i}{dt} = \sum_{j=1}^{n} \underbrace{D_{ij}(m)m_j}_{\uparrow} - \underbrace{D_{ji}(m)m_i}_{\uparrow} \qquad i = 1, \ldots, n$$

Immigration Emigration

Changes in population distribution: $p = (p_1, ..., p_n) = (\frac{m_1}{M}, \cdots, \frac{m_n}{M})$

$$\frac{dp}{dt} = D(p)p - p$$

Unconditional and balanced dispersal

Unconditional dispersal: $D_{ij} = \frac{1}{n}$

$$\frac{dm_i}{dt} = \frac{M}{n} - m_i, \quad i = 1, \cdots, n$$

with the corresponding uniform equilibrium distribution $m = (\frac{M}{n}, \cdots, \frac{M}{n})$.

Dispersal rates that lead to the IFD are called *balanced dispersal* (Holt 1985)

$$V_1(m_1) = \cdots = V_n(m_n).$$

For example, $D_{12} = \frac{1}{K_2}$ and $D_{21} = \frac{1}{K_1}$ are balanced at patch carrying capacities $m_1 = K_1$ and $m_2 = K_2$.

$$\begin{aligned} \frac{dm_1}{dt} &= r_1 m_1 (1 - \frac{m_1}{K_1}) + D_{12} m_2 - D_{21} m_1 \\ \frac{dm_2}{dt} &= r_2 m_2 (1 - \frac{m_2}{K_2}) + D_{21} m_1 - D_{12} m_2 \end{aligned}$$

Balanced dispersal rates

$$\frac{dm_i}{dt} = \sum_{j=1}^{n} D_{ij}(m)m_j - D_{ji}(m)m_i \quad \text{for } i = 1, \ldots, n.$$

Proposition 1 (Cressman and Krivan, 2006) *Let us assume that patch payoffs are negative density dependent. Let us assume that*

(i) individuals never disperse to patches with lower payoff, i.e.,

$$D_{ij} = 0 \ \text{ if } \ V_i < V_j$$

and
(ii) some individuals always disperse to a patch with the highest payoff, i.e.,

$$D_{ij} > 0 \quad for \quad some \;\; i, j \; with \, p_j > 0 \;\; \text{and} \;\; V_j < V_i = \max_{1 \le k \le H} V_k.$$

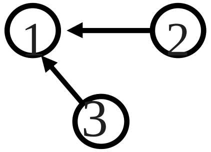
Then solutions of the dispersal dynamics converge to the IFD.

Dispersal Dynamics for Omniscient Animals

Assumptions: Animals are omniscient and they disperse to the patch(es) with the highest payoff.

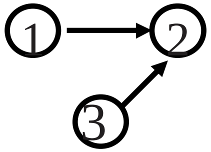
$$V_1(p_1 M) > \max\{V_2(p_2 M), V_3(p_3 M)\} : D^1 = \begin{pmatrix} 1 & 1 & 1 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

$$\begin{aligned} \frac{dp_1}{dt} &= 1 - p_1 \\ \frac{dp_2}{dt} &= -p_2 \\ \frac{dp_3}{dt} &= -p_3 \end{aligned}$$



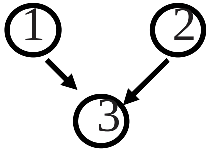
$$V_2(p_2 M) > \max\{V_1(p_1 M), V_3(p_3 M)\} : D^2 = \begin{pmatrix} 0 & 0 & 0 \\ 1 & 1 & 1 \\ 0 & 0 & 0 \end{pmatrix}$$

$$\begin{aligned} \frac{dp_1}{dt} &= -p_1 \\ \frac{dp_2}{dt} &= 1 - p_2 \\ \frac{dp_3}{dt} &= -p_3 \end{aligned}$$



$$V_3(p_3 M) > \max\{V_1(p_1 M), V_2(p_2 M)\} : D^3 = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 1 & 1 & 1 \end{pmatrix}$$

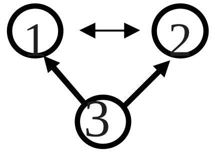
$$\begin{aligned} \frac{dp_1}{dt} &= -p_1 \\ \frac{dp_2}{dt} &= -p_2 \\ \frac{dp_3}{dt} &= 1 - p_3 \end{aligned}$$



$$V_1(p_1M) = V_2(p_2M) > V_3(p_3M) : D^{12} = \begin{pmatrix} u_1 & u_1 & u_1 \\ u_2 & u_2 & u_2 \\ 0 & 0 & 0 \end{pmatrix}$$

$$u_1 + u_2 = 1$$

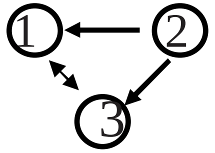
$$\begin{aligned} \frac{dp_1}{dt} &= u_1 - p_1 \\ \frac{dp_2}{dt} &= u_2 - p_2 \\ \frac{dp_3}{dt} &= -p_3 \end{aligned}$$



$$V_1(p_1M) = V_3(p_3M) > V_2(p_2M)\} : D^{13} = \begin{pmatrix} u_1 & u_1 & u_1 \\ 0 & 0 & 0 \\ u_3 & u_3 & u_3 \end{pmatrix}$$

$$u_1 + u_3 = 1$$

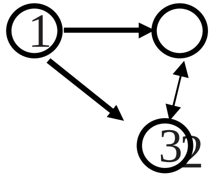
$$\begin{aligned} \frac{dp_1}{dt} &= u_1 - p_1 \\ \frac{dp_2}{dt} &= 1 - p_2 \\ \frac{dp_3}{dt} &= u_3 - p_3 \end{aligned}$$



$$V_2(p_2M) = V_3(p_3M) > V_1(p_1M) : D^{23} = \begin{pmatrix} 0 & 0 & 0 \\ u_2 & u_2 & u_2 \\ u_3 & u_3 & u_3 \end{pmatrix}$$

$$u_2 + u_3 = 1$$

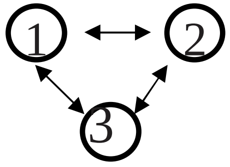
$$\begin{aligned} \frac{dp_1}{dt} &= -p_1 \\ \frac{dp_2}{dt} &= u_2 - p_2 \\ \frac{dp_3}{dt} &= u_3 - p_3 \end{aligned}$$



$$V_1(p_1M) = V_2(p_2M) = V_3(p_3M) : D^{123} = \begin{pmatrix} u_1 & u_1 & u_1 \\ u_2 & u_2 & u_2 \\ u_3 & u_3 & u_3 \end{pmatrix}$$

$$u_1 + u_2 + u_3 = 1$$

$$\begin{aligned} \frac{dp_1}{dt} &= u_1 - p_1 \\ \frac{dp_2}{dt} &= u_2 - p_2 \\ \frac{dp_3}{dt} &= u_3 - p_3 \end{aligned}$$



Filippov definition of a solution

(Filippov 1960, 1985)

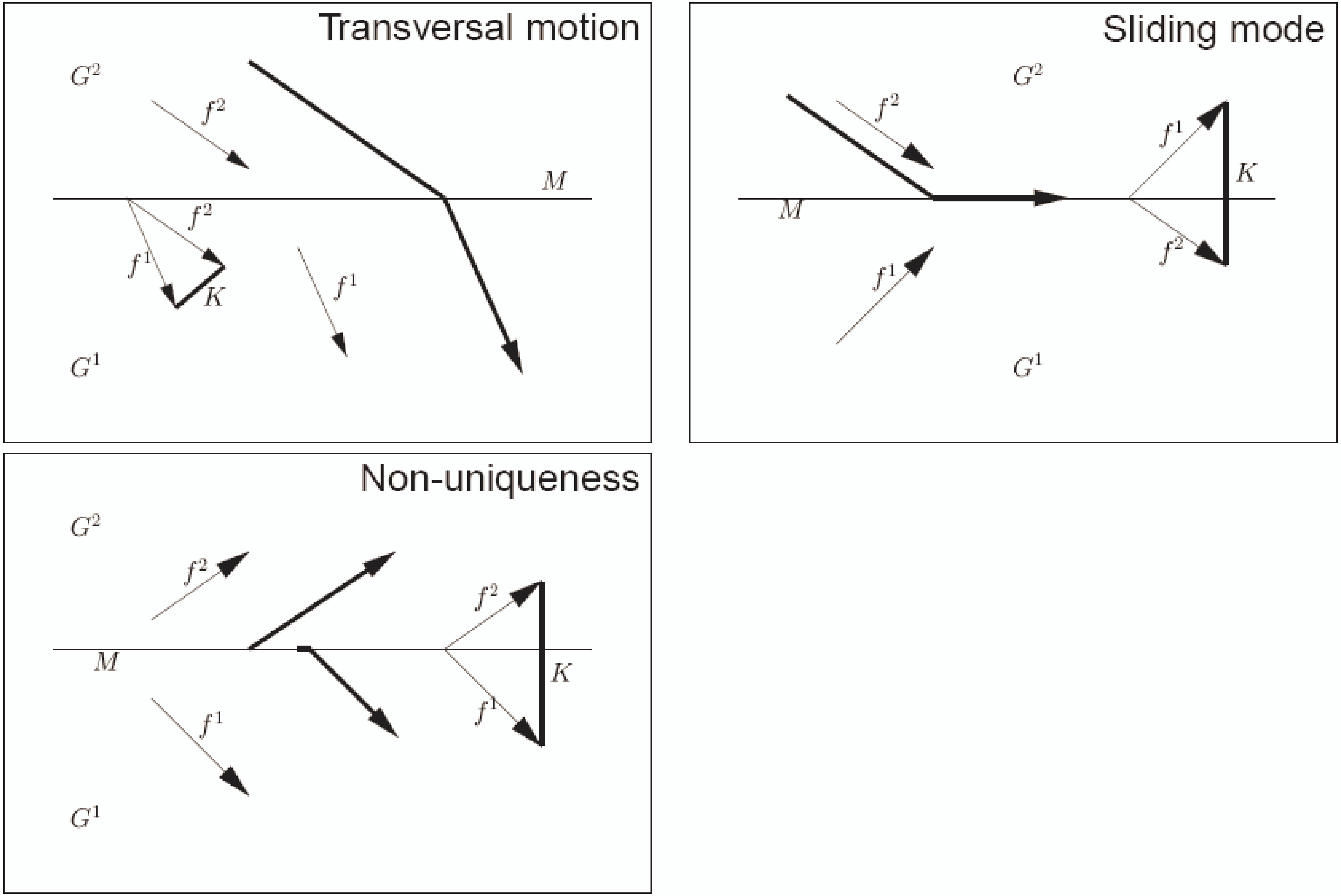
Let $\mathbf{R}^n = G^1 \cup G^2 \cup M$

$$\frac{dx}{dt} = \begin{cases} f^1(x) & x \in G^1 \\ f^2(x) & x \in G^2 \end{cases} \tag{DR}$$

$$F(x) \equiv \begin{cases} \{f^1(x)\} & x \in G^1 \\ \mathrm{conv}\{\lim_{\substack{y \in G^1 \\ y \to x}} f^1(y), \lim_{\substack{y \in G^2 \\ y \to x}} f^2(y)\} & x \in M \\ \{f^2(x)\} & x \in G^2 \end{cases}$$

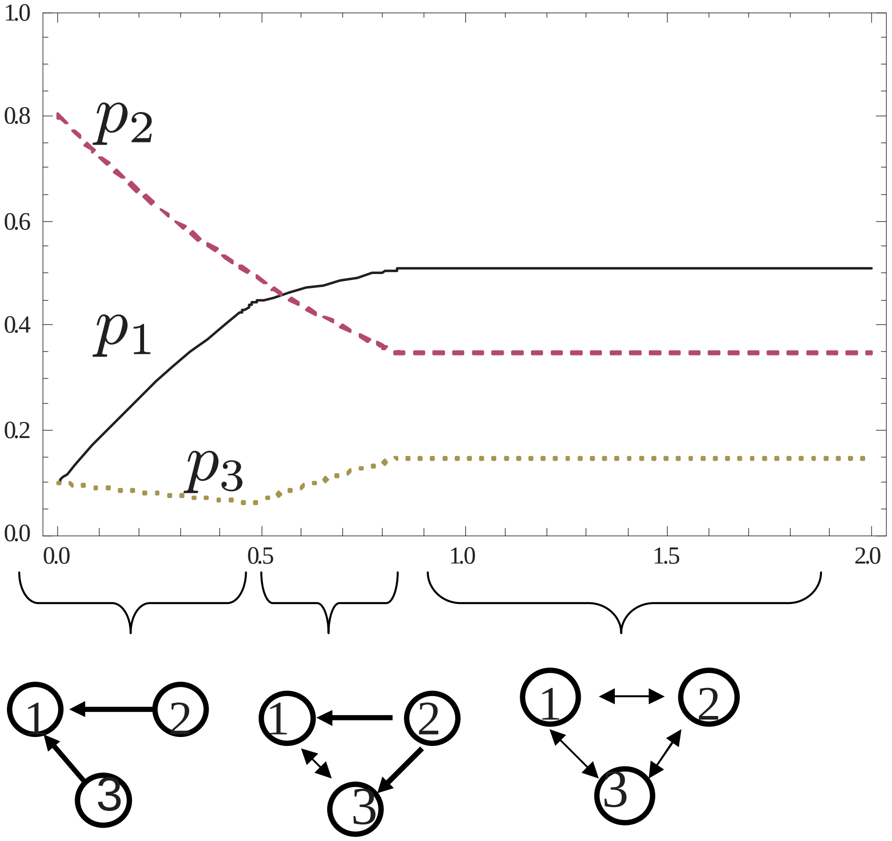
$$\frac{dx}{dt} \in F(x) \tag{DI}$$

Definition: Solutions of differential equation (DR) in the Filippov sense are solutions of differential inclusion (DI)

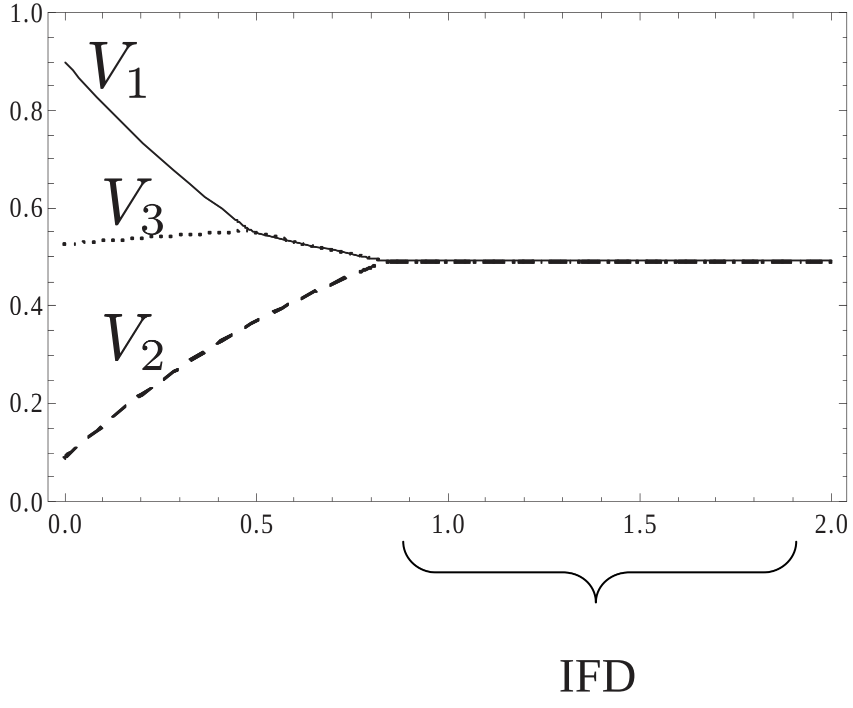

Transversal motion
G^2
f^2
M
f^2
f^1
K
f^1
G^1
Sliding mode
G^2
f^2
f^1
K
M
f^2
f^1
G^1
Non-uniqueness
G^2
f^2
f^2
M
K
f^1
f^1
G^1

Dispersal for omniscient animals

Distribution p_1, p_2, p_3



Payoffs V_1, V_2, V_3



Dispersal rates that lead to the replicator equation

$$D_{ij}(p) = \begin{cases} \mu p_i (V_i - V_j) & \text{if } V_i > V_j, \quad i \neq j \\ \\ 0 & \text{if } V_i \leq V_j, \quad i \neq j \end{cases}$$

Individuals are attracted to patches that are already occupied by their conspecifics, on the condition that the new patch payoff is larger than is the current payoff.

These dispersal rates lead to the replicator equation

$$\frac{dp_i}{dt} = \mu p_i \left(V_i(p_i M) - \overline{V}(p, M) \right), \quad i = 1, \ldots, n$$

Different conceptualizations of population and dispersal time scales

1. **Population dynamics very fast when compared to trait dynamics (***Adaptive dynamics*, e.g., U. Diekmann, R. Law, F. Dercole). Assumes that population dynamics are at an equilibrium at the current trait value. Changes in trait dynamics are described by the canonical equation. Typically assumes monomorphism, recently extended to measure valued traits (Cressman&Hofbauer 2004). Fitness functions typically non-linear.

2. **Trait dynamics are very fast when compared to population dynamics** (*Population game dynamics*). Assumes that traits are at an equilibrium at the current population abundance. The trait values are assumed to be evolutionary optimized. Can treat linear fitness functions (i.e., matrix games).

3. **Population dynamics and trait dynamics operate on a similar time scales** (P. Abrams, T. Vincent and J. Brown). Models explicitly both population and trait dynamics.

Logistic population growth in a two-patch environment

Payoff in habitat i: $V_i(m_i) = r_i(1 - \frac{m_i}{K_i})$ i=1,2

Population dynamics in patch i: $\frac{dm_i}{dt} = r_i m_i(1 - \frac{m_i}{K_i})$

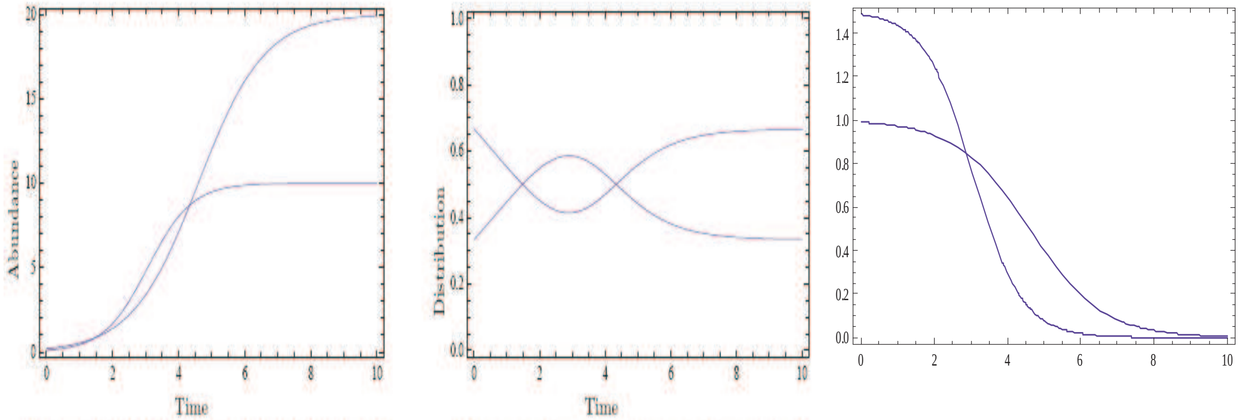
At the population equilibrium $V_1(K_1) = \cdots = V_n(K_n) = 0$, i.e., the IFD

Observation: At the population equilibrium the IFD is reached even when individuals do not disperse at all.

No dispersal

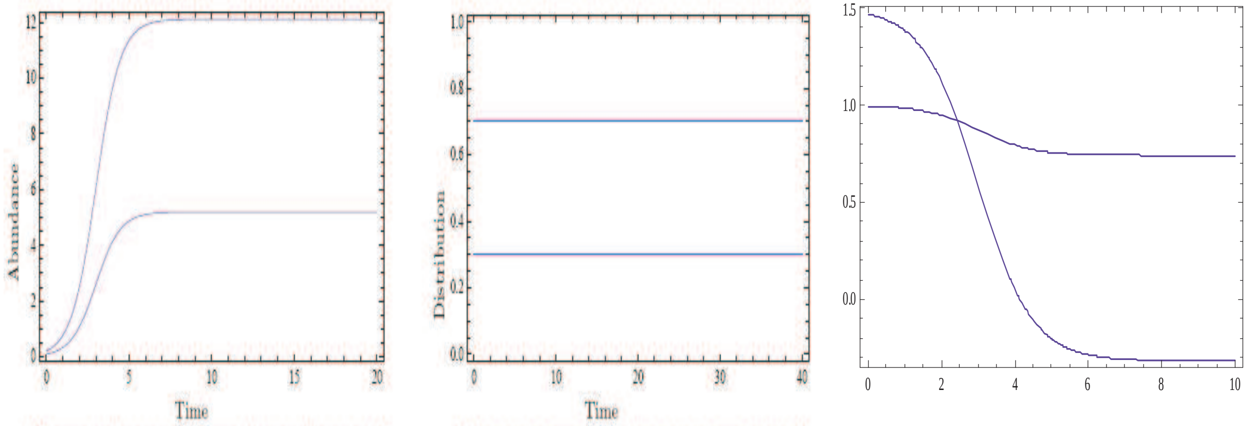
Population dynamics Distributional dynamics Patch payoffs

$$\begin{aligned}\frac{dm_1}{dt} &= r_1 m_1(1-\tfrac{m_1}{K_1})\\ \frac{dm_2}{dt} &= r_2 m_2(1-\tfrac{m_2}{K_2})\\ p_i &= \frac{m_i}{m_1+m_2}\end{aligned}$$



Unbalanced (random) dispersal

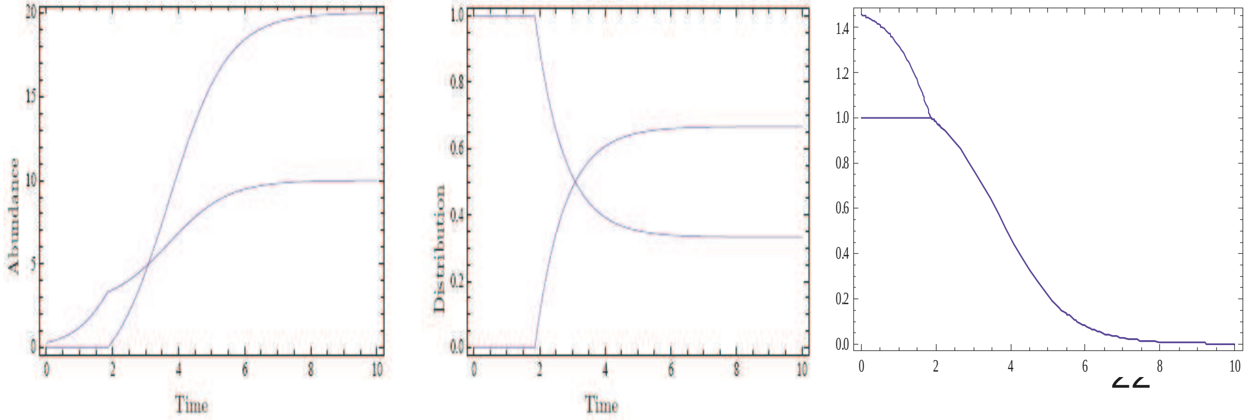
$$\begin{aligned}\frac{dM}{dt} &= r_1 p_1 M(1-\tfrac{p_1 M}{K_1})+\\ &\quad r_2 p_2 M(1-\tfrac{p_2 M}{K_2})\end{aligned}$$



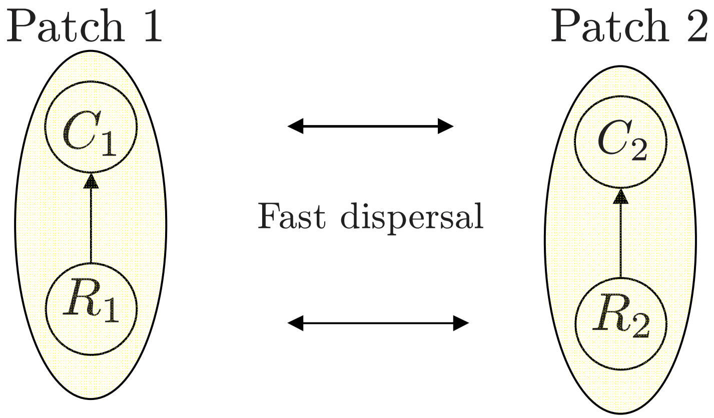
Balanced (fast) dispersal

$$\begin{aligned}\tfrac{dm_1}{dt} &= r_1 p_1(M)M(1-\tfrac{p_1(M)M}{K_1})\\ \tfrac{dm_2}{dt} &= r_2 p_2(M)M(1-\tfrac{p_2(M)M}{K_2})\end{aligned}$$

$$M = m_1 + m_2$$



The Habitat selection game for two-patch Lotka-Volterra predator-prey model



$$\begin{aligned} R &= R_1 + R_2 \\ C &= C_1 + C_2 \\ R_i &= u_i R \\ C_i &= v_i C \end{aligned}$$

$$\begin{aligned} \frac{dR}{dt} &= (r_1 - \lambda_1 v_1 C) u_1 R \quad &+& \quad (r_2 - \lambda_2 v_2 C) u_2 R \\ \frac{dC}{dt} &= (e_1 \lambda_1 u_1 R - m_1) v_1 C \quad &+& \quad (e_2 \lambda_2 u_2 R - m_2) v_2 C \end{aligned}$$

Fitness of a prey mutant with strategy $(\tilde{u}_1, \tilde{u}_2)$:

$$\mathrm{W}_R = \tilde{u}_1 (r_1 - \lambda_1 v_1 C) + \tilde{u}_2 (r_2 - \lambda_2 v_2 C)$$

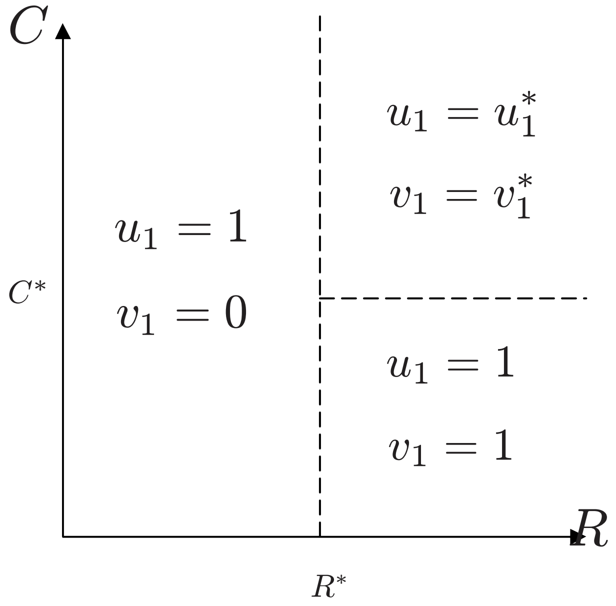
Fitness of a consumer mutant with strategy $(\tilde{v}_1, \tilde{v}_2)$:

$$\mathrm{W}_C = \tilde{v}_1 (e_1 \lambda_1 u_1 R - m_1) + \tilde{v}_2 (e_2 \lambda_2 u_2 R - m_2)$$

For $r_1 > r_2$ and $m_1 \geq m_2$ the Nash equilibria are

$$NE = \begin{cases} (u_1^*, v_1^*) & \text{if} \quad R > R^*,\ C > C^*, \\ (1,1) & \text{if} \quad R > R^*,\ C < C^*, \\ (1,0) & \text{if} \quad R < R^*, \\ \{(1, v_1) \mid v_1 \in [0, v_1^*]\} & \text{if} \quad R = R^*,\ C > C^*, \\ \{(1, v_1) \mid v_1 \in [0, 1]\} & \text{if} \quad R = R^*,\ C \leq C^*, \\ \{(u_1, 1) \mid u_1 \in [u_1^*, 1]\} & \text{if} \quad R > R^*,\ C = C^*. \end{cases}$$

$$v_1^* = \frac{m_1 - m_2 + e_2\lambda_2 R}{(e_1\lambda_1 + e_2\lambda_2)R}, \quad u_1^* = \frac{r_1 - r_2 + \lambda_2 C}{(\lambda_1 + \lambda_2)C}, \quad R^* = \frac{m_1 - m_2}{e_1\lambda_1}, \; C^* = \frac{r_1 - r_2}{\lambda_1}$$



ESS for the predator-prey model at fixed population densites

(Cressman 1992,2003)

Proposition 1 (Cressman 1992, 2003) *The interior predator-prey distribution for* $R > R^*$ *and* $C > C^*$

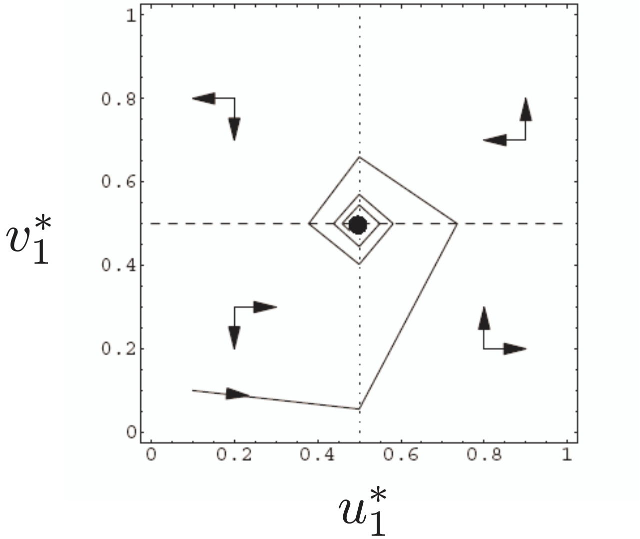
$$v_1^* = \frac{m_1 - m_2 + e_2\lambda_2 R}{(e_1\lambda_1 + e_2\lambda_2)R}, \quad u_1^* = \frac{r_1 - r_2 + \lambda_2 C}{(\lambda_1 + \lambda_2)C}$$

is a weak *ESS. This IFD is asymptotically stable for omniscient animals (best response) dynamics.*

Equal payoff lines:

Prey payoff in patch 1=Prey payoff in patch 2

Pred. payoff in patch 1=Pred. payoff in patch 2



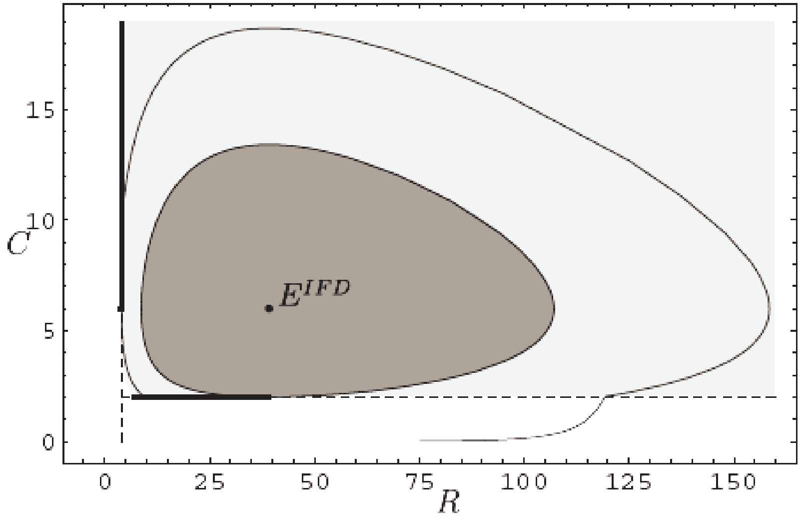
The arrows show in which direction prey fitness (horizontal arrow) and predator fitness (vertical arrow) increases.

Predator-prey population dynamics when distribution is at the IFD at each population densities

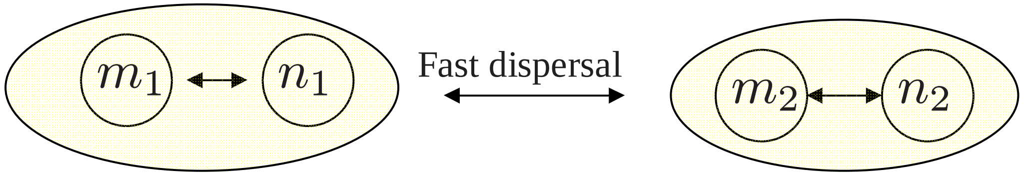
Proposition 1 (Krivan 1997,Boukal and Krivan 1999) *Trajectories of the prey-predator model with adaptive prey and predator dispersal converge to a global attractor that is formed by solutions of the Lotka-Volterra model*

$$\begin{aligned}\frac{dR}{dt} &= R\left(\frac{r_1\lambda_2 + r_2\lambda_1}{\lambda_1+\lambda_2} - \frac{\lambda_1\lambda_2}{\lambda_1+\lambda_2}C\right)\\ \frac{dC}{dt} &= C\left(\frac{e_1e_2\lambda_1\lambda_2}{e_1\lambda_1+e_2\lambda_2}R - \frac{e_1\lambda_1m_2+e_2\lambda_2m_1}{e_1\lambda_1+e_2\lambda_2}\right)\end{aligned}$$

that are contained in the region $\{(R,C) : R \geq \frac{m_1-m_2}{e_1\lambda_1},\ \ C \geq \frac{r_1-r_2}{\lambda_1}\}$.



The Habitat selection game for the two-patch Lotka-Volterra competition model



Patch 1 Patch 2

$$\frac{dM}{dt} = M\left[p_1 V_1(p,q;M,N) + p_2 V_2(p,q;M,N)\right]$$

$$\frac{dN}{dt} = N\left[q_1 W_1(p,q;M,N) + q_2 W_2(p,q;M,N)\right]$$

$$M = m_1 + m_2,\ N = n_1 + n_2,\ p_i = m_i/M,\ q_i = n_i/N$$

Species 1 payoff in habitat i : $V_i(p,q;M,N) = r_i\left(1 - \frac{p_i M}{K_i} - \frac{\alpha_i q_i N}{K_i}\right) \quad i = 1,2$

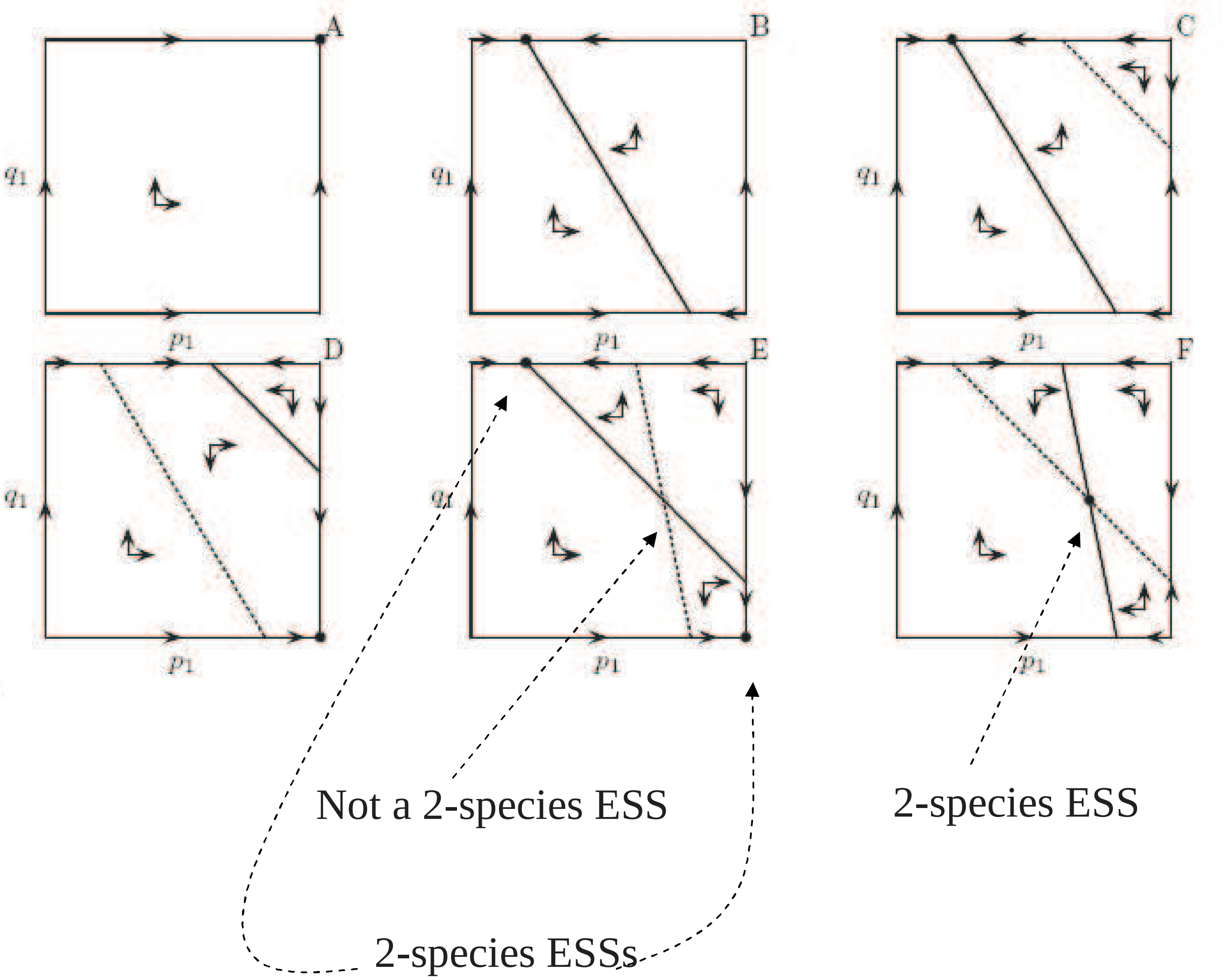
Species 2 payoff in habitat j: $W_j(p,q;M,N) = s_j\left(1 - \frac{q_j N}{L_j} - \frac{\beta_j p_j M}{L_j}\right) \quad j = 1,2.$

IFD at current population densities

Equal payoff lines:

$$V_1(p,q;M,N) = V_2(p,q;M,N)$$ Solid line

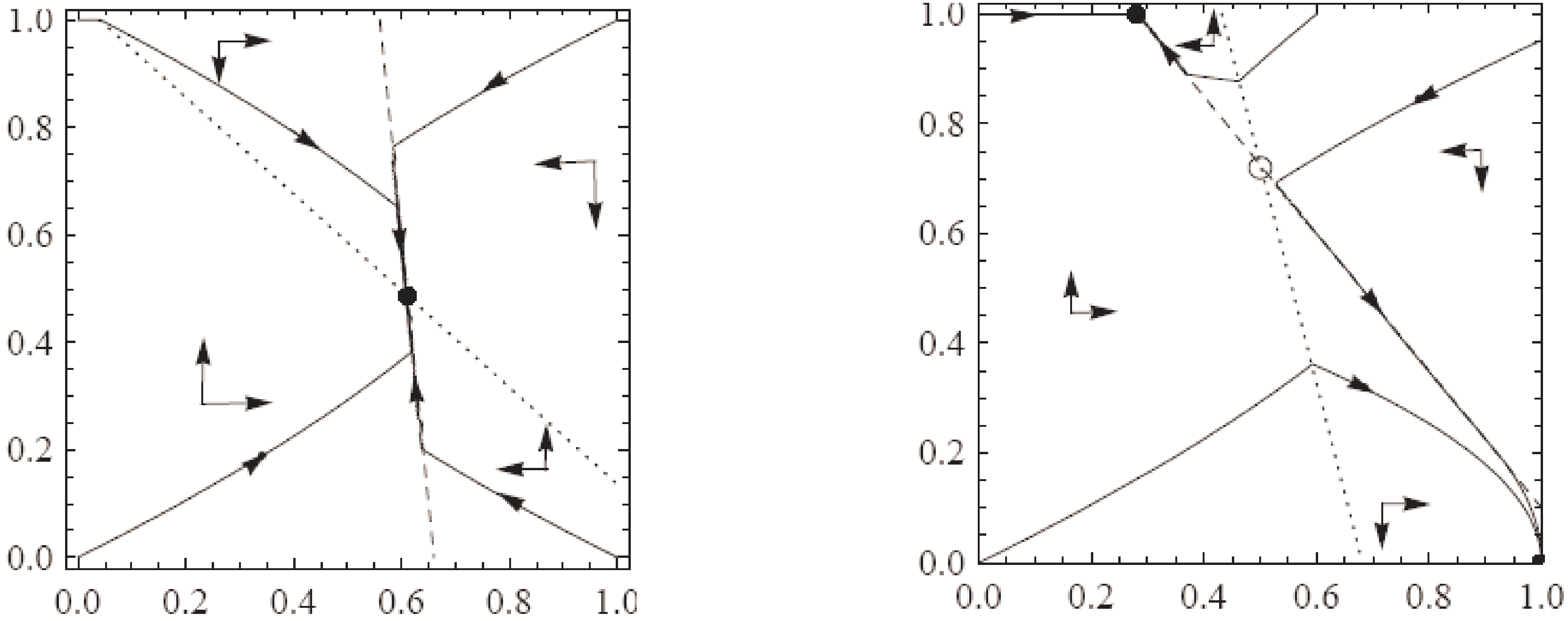
$$W_1(p,q;M,N) = W_2(p,q;M,N)$$ Dotted line



Not a 2-species ESS

2-species ESS

2-species ESSs



Proposition 1 (Cressman et al. 2004) *Let us assume that the interior Nash equilibrium for the distribution of two competing species at population densities M and N exists. If*

$$r_1 s_1 K_2 L_2 (1-\alpha_1\beta_1) + r_1 s_2 K_2 L_1 (1-\alpha_1\beta_2) + r_2 s_1 K_1 L_2 (1-\alpha_2\beta_1) + r_2 s_2 K_1 L_1 (1-\alpha_2\beta_2) > 0$$

Then this distributional equilibrium is a 2-species ESS.

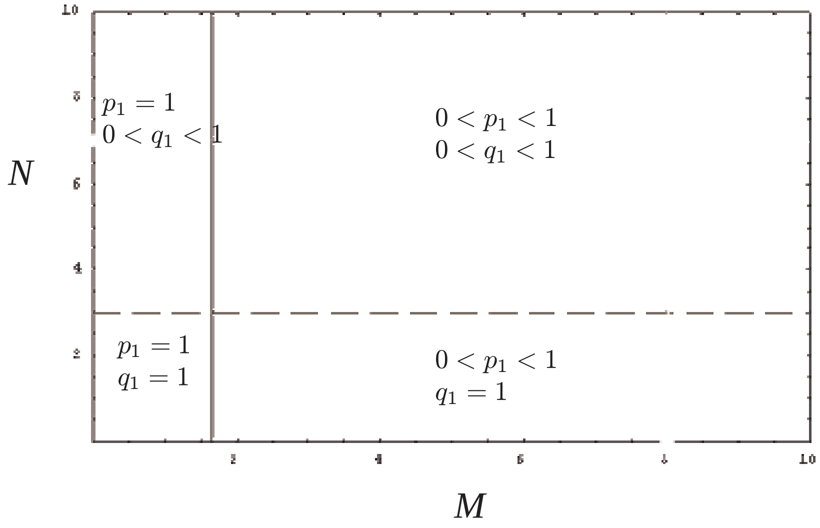
The habitat selection game for two competing species at fixed population densities

(Sirot and Krivan 2002, Cressman et al. 2004)

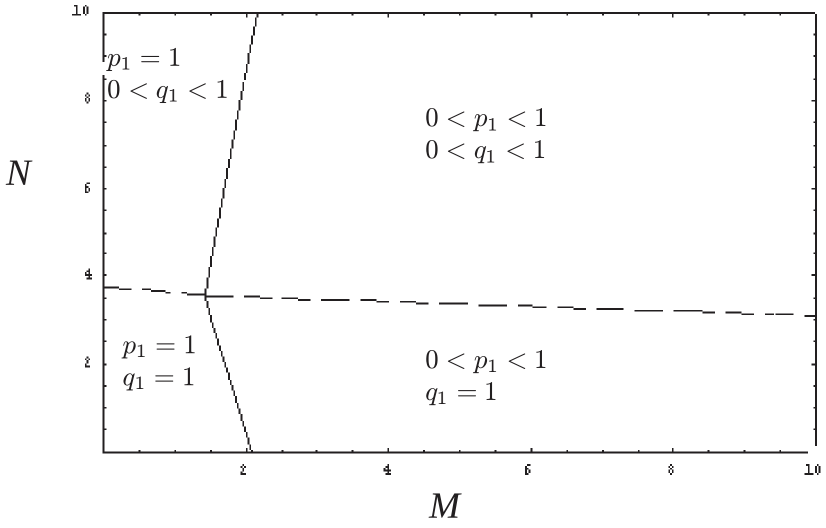
σ = the relative strength of intraspecific competition to interspecific competition
σ=0: interspecific competition only;
σ=1: intraspecific competition only

$$\begin{aligned} V_i(p,q;M,N) &= r_i\left(1-\tfrac{p_i\sigma M}{K_i}-\tfrac{\alpha_i q_i(1-\sigma)N}{K_i}\right) \quad i=1,2 \\ W_j(p,q;M,N) &= s_j\left(1-\tfrac{q_j\sigma N}{L_j}-\tfrac{\beta_j p_j(1-\sigma)M}{L_j}\right) \quad j=1,2. \end{aligned}$$

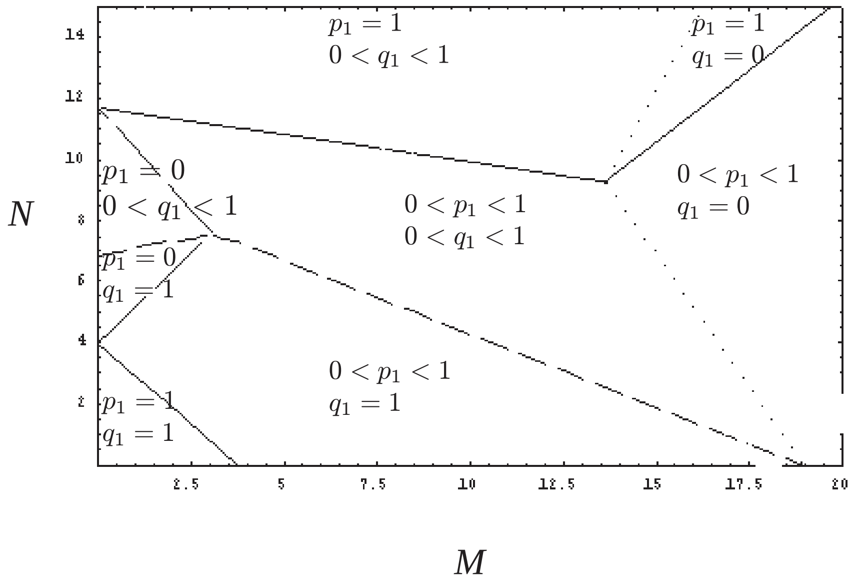
$\sigma = 1$ (Intraspec.comp.only)



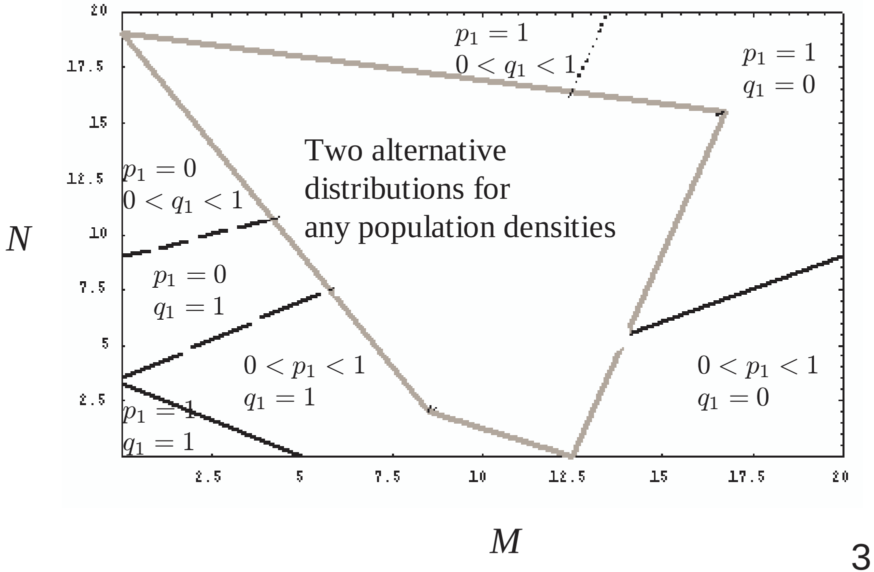
$\sigma = 0.8$



$\sigma = 0.44$



$\sigma = 0.33$



Population dynamics for competing species

Population dynamics without dispersal:

$$\begin{cases} \dfrac{dm_i}{dt} = m_i r_i \left(1 - \dfrac{m_i}{K_i} - \dfrac{\alpha_i n_i}{K_i}\right) & i = 1, 2 \\ \dfrac{dn_j}{dt} = n_j s_j \left(1 - \dfrac{n_j}{L_j} - \dfrac{\beta_j m_j}{L_j}\right) & j = 1, 2. \end{cases}$$

Population dynamics under balanced dispersal:

$$\begin{cases} \dfrac{dM}{dt} = M\left[p_1 V_1(p, q; M, N) + p_2 V_2(p, q; M, N)\right] \\ \\ \dfrac{dN}{dt} = N\left[q_1 W_1(p, q; M, N) + q_2 W_2(p, q; M, N)\right] \end{cases}$$

Population equilibrium: $m_i^* = \dfrac{K_i - \alpha_i L_i}{1 - \alpha_i \beta_i}, \;\; n_i^* = \dfrac{L_i - \beta_i K_i}{1 - \alpha_i \beta_i} \quad i = 1, 2.$

Question: *How the stability of the model without dispersal compares to the model with dispersal?*

Interplay between population and dispersal stability

1. Conditions for population stability in the two patches without dispersal:

$$1 - \alpha_1\beta_1 > 0 \text{ and } 1 - \alpha_2\beta_2 > 0$$

2. Condition for distributional stability of the IFD:

$$r_1s_1K_2L_2(1-\alpha_1\beta_1)+r_1s_2K_2L_1(1-\alpha_1\beta_2)+r_2s_1K_1L_2(1-\alpha_2\beta_1)+r_2s_2K_1L_1(1-\alpha_2\beta_2) > 0$$

Thus, population equilibrium stability of the model without dispersal does not imply distributional stability of the model with dispersal.

$$\begin{aligned}
\frac{dm_1}{dt} &= m_1V_1(m_i, n_i) + I_{12}(m, n)m_2 - I_{21}(m, n)m_1 \\
\frac{dm_2}{dt} &= m_2V_2(m_2, n_2) + I_{21}(m, n)m_1 - I_{12}(m, n)m_2 \\
\frac{dn_1}{dt} &= n_1W_1(m_1, n_1) + J_{12}(m, n)m_2 - J_{21}(m, n)m_1 \\
\frac{dn_2}{dt} &= n_2W_2(m_2, n_2) + J_{21}(m, n)m_1 - J_{12}(m, n)m_2
\end{aligned}$$

Dispersal can destabilizes population dynamics

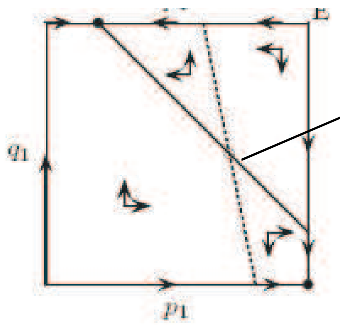
(Abrams et al. 2007)

1. $1 - \alpha_1\beta_1 > 0$ and $1 - \alpha_2\beta_2 > 0$

2. Distributional instability of the interior IFD:

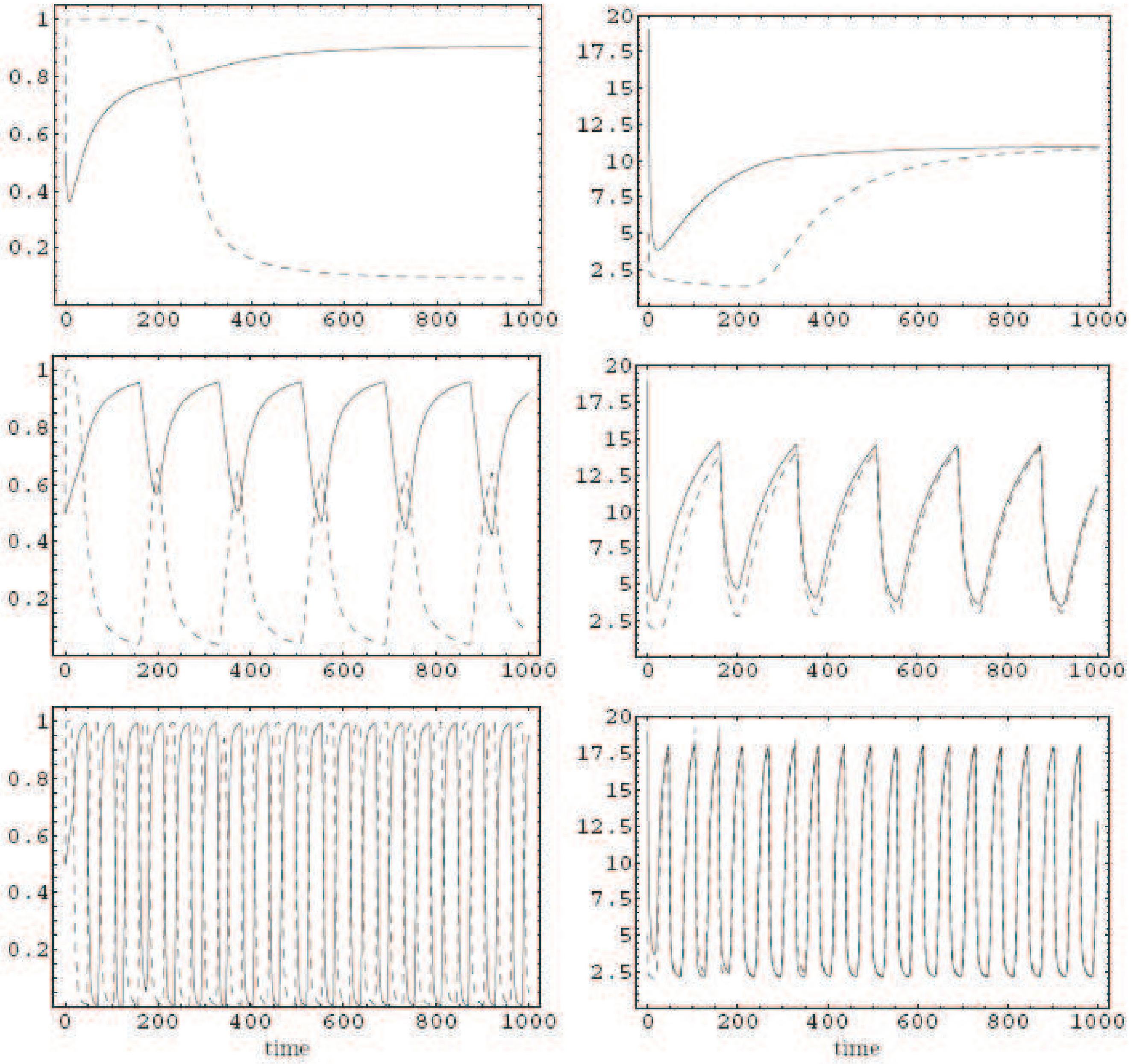
$$r_1 s_1 K_2 L_2(1-\alpha_1\beta_1)+r_1 s_2 K_2 L_1(1-\alpha_1\beta_2)+r_2 s_1 K_1 L_2(1-\alpha_2\beta_1)+r_2 s_2 K_1 L_1(1-\alpha_2\beta_2) < 0$$

Table 1: Candidate population-distributional equilibria (Abrams et al. 2007)



M	N	p_1	q_1	payoffs
11	11	$\frac{10}{11}$	$\frac{1}{11}$	$V_1 = V_2 = W_1 = W_2 = 0$
20	10	$\frac{19}{20}$	0	$V_1 = V_2 = W_2 = 0, W_1 > 0$
12	1	$\frac{5}{6}$	1	$V_1 = V_2 = W_1 = 0, W_2 > 0$
10	20	1	$\frac{1}{20}$	$V_1 = V_1 = W_2 = 0, V_2 > 0$
1	10	0	0	$V_2 = W_2 = 0, V_1 > 0, W_1 > 0$
19	19	1	0	$V_1 = W_2 = 0, V_2 > 0, W_1 > 0$
2	2	0	1	$V_2 = W_1 = 0, V_1 > 0, W_2 > 0$
10	1	1	1	$V_1 = W_1 = 0, V_2 > 0, W_2 > 0$

Species distributions p_1, q_1 Total Population dynamics M, N



No dispersal

Intermediate dispersal

Fast dispersal

Mathematical conceptualization of population game dynamics

Population dynamics $$\frac{dx_i}{dt} = x_i f_i(x,u), \qquad i = 1, \ldots, n$$

Controls (animal strategies, or phenotypic plastic traits):

$$u = (u_1, \ldots, u_k) \in U{=}U^1 \times \cdots \times U^k$$

Fitness of the i-th individuals: $G_i(u_i; u, x) = f_i(x,u)$

Strategies that maximize animal fitness are the Nash equilibria (or ESS) at current population numbers:

$$N(x) = \Big\{ u \in U \mid G_i(u_i; u, x) \geq G_i(v; u, x) \ \text{ for any } \ v \in U^i, \ \ i = 1, \ldots, k \Big\}.$$

Feedback control: $u \in N(x)$

This approach assumes time scale separtion: Behavioral processes operate on a much faster time scale than do population dynamics

Mathematical conceptualization of the mutant-resident system

$$\begin{aligned}
\frac{dx_i}{dt} &= x_i G_i(u_i; u, x, \tilde{u}, \tilde{x}), \quad i = 1, \ldots, k \\
\frac{d\tilde{x}_i}{dt} &= \tilde{x}_i G_i(\tilde{u}_i; u, x, \tilde{u}, \tilde{x}), \quad i = 1, \ldots, k
\end{aligned}$$

$$u \in N(x, \tilde{x}, \tilde{u})$$

Optimal resident behavior when mutants are present:

$$N(x, \tilde{x}, \tilde{u}) = \{u \in U \mid G_i(u_i; u, x, \tilde{u}, \tilde{x}) \geq G_i(v; u, x, \tilde{u}, \tilde{x}) \text{ for any } v\}$$

Proposition 1 (Cressman and Krivan, 2009) *The proportion of mutants to residents* ($\tilde{x}/x$) *cannot increase in time, but mutants can survive in the population mix.*

Resident-mutant system for single species logistic growth

Resident population x with strategy u and fitness:

$$G(u;\tilde{u},x,\tilde{x}) = u_1 r_1 \left(1 - \tfrac{u_1 x + \tilde{u}_1 \tilde{x}}{K_1}\right) + u_2 r_2 \left(1 - \tfrac{u_2 x + \tilde{u}_2 \tilde{x}}{K_2}\right)$$

Mutant population $\tilde{x}$ with strategy $\tilde{u}$ and fitness:

$$G(\tilde{u};\tilde{u},x,\tilde{x}) = \tilde{u}_1 r_1 \left(1 - \tfrac{u_1 x + \tilde{u}_1 \tilde{x}}{K_1}\right) + \tilde{u}_2 r_2 \left(1 - \tfrac{u_2 x + \tilde{u}_2 \tilde{x}}{K_2}\right)$$

$$\begin{aligned} \frac{dx}{dt} &= x \;\; G(u;\tilde{u},x,\tilde{x}) = x\langle u, U(x,\tilde{x},\tilde{u})u\rangle \\ \frac{d\tilde{x}}{dt} &= \tilde{x} \;\; G(\tilde{u};\tilde{u},x,\tilde{x}) = \tilde{x}\langle \tilde{u}, U(x,\tilde{x},\tilde{u})u\rangle \end{aligned}$$

$$U(x,\tilde{x},\tilde{u}) = \begin{pmatrix} r_1(1 - \frac{x+\tilde{u}_1\tilde{x}}{K_1}) & r_1(1 - \frac{\tilde{u}_1\tilde{x}}{K_1}) \\ r_2(1 - \frac{\tilde{u}_2\tilde{x}}{K_2}) & r_2(1 - \frac{x+\tilde{u}_2\tilde{x}}{K_2}) \end{pmatrix}$$

Resident-mutant system for single species logistic growth

$$\begin{aligned}\frac{dx}{dt} &= x\langle u, U(x,\tilde{x},\tilde{u})u\rangle = (r_1u_1+r_2u_2)x\left(1-\tfrac{x}{k_1}-\tfrac{\alpha}{k_1}\tilde{x}\right)\\ \frac{d\tilde{x}}{dt} &= \tilde{x}\langle \tilde{u}, U(x,\tilde{x},\tilde{u})u\rangle = (r_1\tilde{u}_1+r_2\tilde{u}_2)\tilde{x}\left(1-\tfrac{\tilde{x}}{k_2}-\tfrac{\beta}{k_2}x\right)\end{aligned}$$

$$k_1 = \frac{K_1K_2(r_1u_1+r_2u_2)}{K_2r_1u_1^2+K_1r_2u_2^2},\quad k_2 = \frac{K_1K_2(r_1\tilde{u}_1+r_2\tilde{u}_2)}{K_2r_1\tilde{u}_1^2+K_1r_2\tilde{u}_2^2}$$

$$\alpha = \frac{K_2r_1u_1\tilde{u}_1+K_1r_2u_2\tilde{u}_2}{K_2r_1u_1^2+K_1r_2u_2^2},\quad \beta = \frac{K_2r_1u_1\tilde{u}_1+K_1r_2u_2\tilde{u}_2}{K_2r_1\tilde{u}_1^2+K_1r_2\tilde{u}_2^2}$$

Proposition 1 (Cressman and Krivan, 2010) *When resident and mutant strategies* $u = (u_1, u_2)$ *and* $v = (v_1, v_2)$ *are* fixed *then:*

1. *When residents and mutants show distinct preferences for patches* $(u_1 - K_1/(K_1+K_2))(\tilde{u}_1 - K_1/(K_1+K_2)) < 0$*) then residents and mutants co-exists at a globally asymptotically stable equilibrium.*
2. *When residents and mutants show the same preferences for patches* $(u_1 - K_1/(K_1+K_2))(\tilde{u}_1 - K_1/(K_1+K_2)) > 0$*) then the population with strategy that better matches the IFD will survive and outcompete the other population.*

Resident-mutant system for logistic growth: Residents follow the IFD

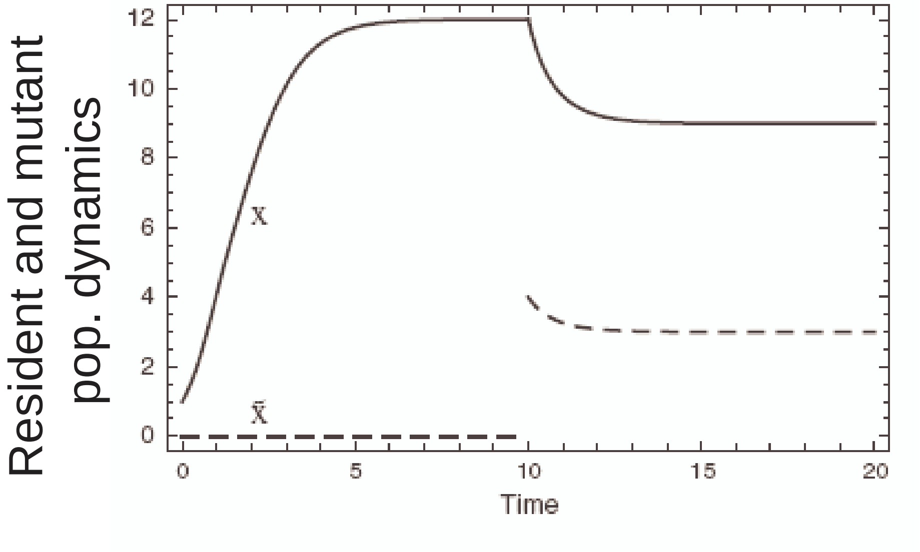
$$
\begin{aligned}
\frac{dx}{dt} &= x\langle u, U(x,\tilde{x},\tilde{u})u\rangle = (r_1u_1+r_2u_2)x\left(1-\tfrac{x}{k_1}-\tfrac{\alpha}{k_1}\tilde{x}\right)\\
\frac{d\tilde{x}}{dt} &= \tilde{x}\langle \tilde{u}, U(x,\tilde{x},\tilde{u})u\rangle = (r_1\tilde{u}_1+r_2\tilde{u}_2)\tilde{x}\left(1-\tfrac{\tilde{x}}{k_2}-\tfrac{\beta}{k_2}x\right)
\end{aligned}
$$

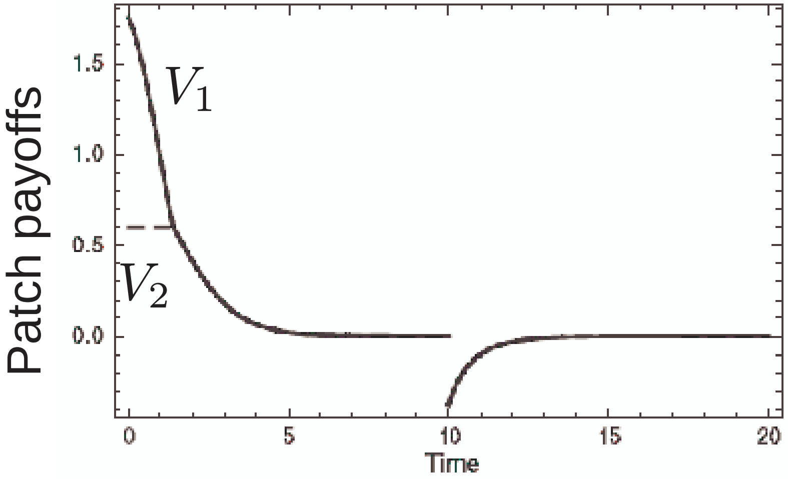
$$
u_1 = \begin{cases} 1 & x \le x_1 \\ \frac{r_2K_1}{r_2K_1+r_1K_2} + \frac{K_1K_2(r_1-r_2)}{(r_2K_1+r_1K_2)x} + \frac{(K_1r_2-\tilde{u}_1(K_1r_2+K_2r_1))\tilde{x}}{(K_1r_2+K_2r_1)x} & x > x_1 \end{cases}
$$

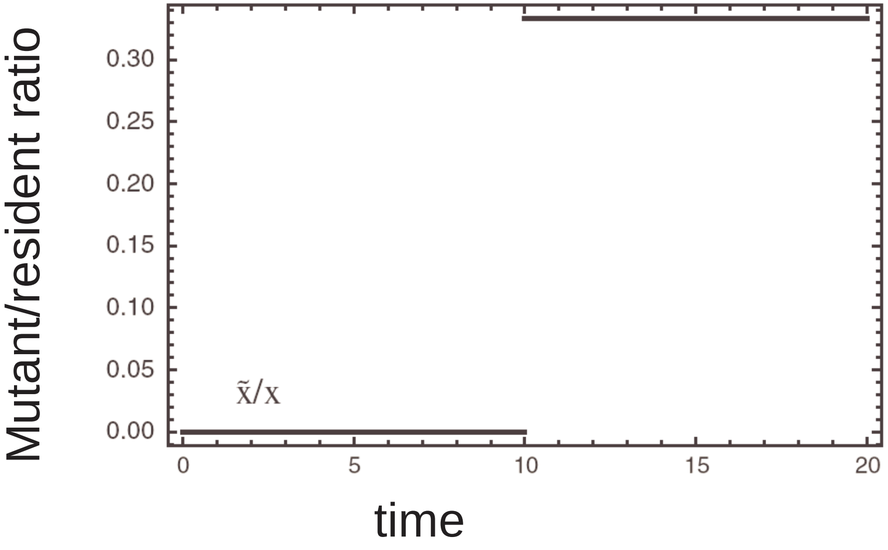
$$
x_1 = \frac{K_1(r_1-r_2)}{r_1} + \frac{(r_2K_1-\tilde{u}_1(K_2r_1+K_1r_2))\tilde{x}}{r_1K_2}
$$

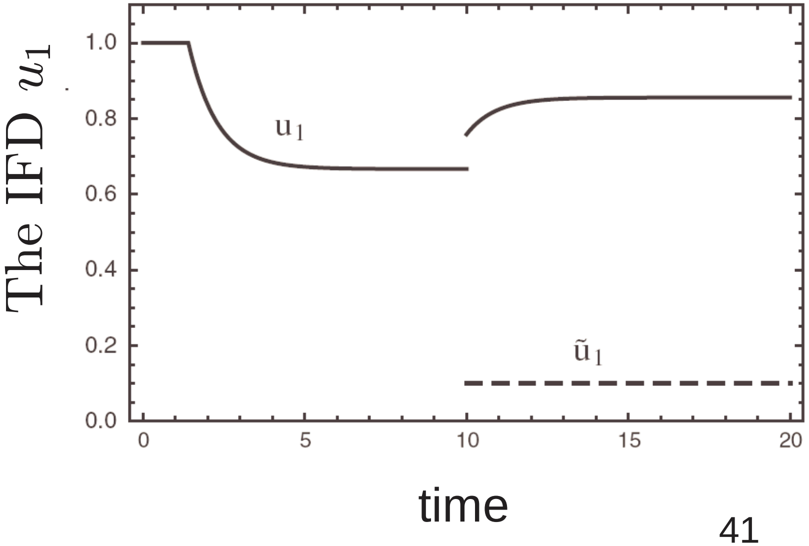
Proposition 1 (Cressman and Krivan, 2010) *When residents follow the IFD strategy, population densities in both patches converge to their carrying capacities and mutants survive with residents.*

Resident-mutant system for logistic growth: Residents follow the IFD









Prediction: If at the population dynamics attractor the animal distribution equalizes patch payoffs, there is no selection against mutants. Thus, mutants can survive with residents, and polymorphism can occur.

Dispersal and predator-prey population dynamics operate on a similar time scales

$$
\begin{aligned}
\frac{dx_1}{dt} &= x_1 f_1(x_1, y_1) + \alpha(f_1(x_1, y_1) - f_2(x_2, y_2)) \\
\frac{dx_2}{dt} &= x_2 f_2(x_2, y_2) + \alpha(f_2(x_2, y_2) - f_1(x_1, y_1)) \\
\frac{dy_1}{dt} &= y_1 g_1(x_1) + \beta(g_1(x_1) - g_2(x_2)) \\
\frac{dy_2}{dt} &= y_2 g_2(x_2) + \beta(g_2(x_2) - g_1(x_1)).
\end{aligned}
$$

Proposition 1 (Cressman, Krivan, in prep.) *Let* $\frac{\partial f_i}{\partial x_i} < 0$, $\frac{\partial f_i}{\partial y_i} < 0$, $g_i'(x_i) > 0$, *and there exists an interior equilibrium of predator-prey population dynamics without any dispersal* (x^*, y^*). *Then this equilibrium is locally asymptotically stable for any dispersal rates* $\alpha \geq 0$ *and* $\beta \geq 0$.

Dispersal and competition population dynamics operate on a similar time scales

$$\begin{aligned}
\frac{dx_1}{dt} &= x_1 f_1(x_1,y_1) + \alpha(f_1(x_1,y_1) - f_2(x_2,y_2)) \\
\frac{dx_2}{dt} &= x_2 f_2(x_2,y_2) + \alpha(f_2(x_2,y_2) - f_1(x_1,y_1)) \\
\frac{dy_1}{dt} &= y_1 g_1(x_1,y_1) + \beta(g_1(x_1,y_1) - g_2(x_2,y_2)) \\
\frac{dy_2}{dt} &= y_2 g_2(x_2,y_2) + \beta(g_2(x_2,y_2) - g_1(x_1,y_1)).
\end{aligned}$$

Proposition 1 (Cressman, Krivan, in prep.) *Let* $\frac{\partial f_i}{\partial x_i} < 0$, $\frac{\partial f_i}{\partial y_i} < 0$, $\frac{\partial g_i}{\partial x_i} < 0$, $\frac{\partial g_i}{\partial y_i} < 0$ *and without any dispersal* $(\alpha = \beta = 0)$*the two species do coexists at an stable equilibrium in both patches. If, in addition*

$$\frac{\partial f_1}{\partial x_1}\frac{\partial g_2}{\partial y_2} - \frac{\partial f_1}{\partial y_1}\frac{\partial g_2}{\partial x_2} > 0, \quad \frac{\partial f_2}{\partial x_2}\frac{\partial g_1}{\partial y_1} - \frac{\partial f_2}{\partial y_2}\frac{\partial g_1}{\partial x_1} > 0,$$

Then the interior equilibrium is locally asymptotically stable for any dispersal rates $\alpha \geq 0$ *and* $\beta \geq 0$.

References

Abrams, P., Cressman, R., Krivan, V. 2007. The role of behavioral dynamics in determining the patch distributions of interacting species. American Naturalist 169:505-518.

Cressman, R., Krivan, V., Garay, J. 2004. Ideal free distributions, evolutionary games and population dynamics in multiple species environments. The American Naturalist, 164:473-489

Cressman, R., Krivan, V. 2006. Migration dynamics for the Ideal Free Distribution. American Naturalist 168:384-397

Krivan, V. 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. American Naturalist 149:164-178.

Krivan, V. 2008. Dispersal dynamics: Distribution of lady beetles. European Journal of Entomology 105:405-409.

Krivan, V., Sirot, E. 2002. Habitat selection by two competing species in a two-habitat environment. American Naturalist 160:214-234.

Krivan, V., Cressman, R., Schneider, C. 2008. The Ideal Free Distribution: A review and synthesis of the game theoretic perspective. Theoretical Population Biology 73:403-425.

More at www.entu.cas.cz/krivan