ADAPTIVE DYNAMICS BUDAPEST JUNE 14 - 18 2004

TOWARDS A MORE COMPLETE BIFURCATION ANALYSIS OF ADAPTIVE DYNAMICS

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OUTLINE

I. THE LOTKA-VOLTERRA FRAMEWORK

II. GENERALIZATIONS I

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IV. IMPLICATIONS FOR BIFURCATION ANALYSIS

TRAIT-DEPENDENT

LOTKA-VOLTERRA DIFFERENTIAL EQUATIONS

FOR k POPULATIONS $i = 1, \ldots, k$:

POPULATION i: DENSITY n_i AND TRAIT $x_i \in \mathbb{T}$

COMMUNITY STATE SPACE:

$\mathbb{R}_+^k = \{n = (n_1, \ldots, n_k) \in \mathbb{R}^k : n_i \geq 0$ **for all** $i = 1, \ldots, k\}$

$$\boxed{\frac{d}{dt} n_i = n_i \left(r(x_i) + \sum_{j=1}^{k} a(x_i, x_j) n_j \right), i = 1, \ldots, k.}$$

WITH $a(x_i, x_i) = -1$ FOR ALL $i = 1, \ldots, k$

TERMINOLOGY:

- **INTERACTION MATRIX** $A(x_1, \ldots, x_k) =$

$$\begin{pmatrix} -1 & a(x_1,x_2) & . & . & . & a(x_1,x_k) \\ a(x_2,x_1) & -1 & a(x_2,x_3) & . & . & a(x_2,x_k) \\ . & . & . & . & . & . \\ . & . & . & . & . & . \\ . & . & . & . & . & . \\ a(x_k,x_1) & . & . & . & a(x_k,x_{k-1}) & -1 \end{pmatrix}$$

- $R(\mathbb{T}^k) = \{(x_1, \ldots, x_k) \in \mathbb{T}^k : |A(x_1, \ldots, x_k)| \neq 0\}$**:**

THE NON-DEGENERATE CASES

$D(\mathbb{T}^k) = \{(x_1, \ldots, x_k) \in \mathbb{T}^k : |A(x_1, \ldots, x_k)| = 0\}$**:**

THE DEGENERATE CASES

$$LV_k(x_1, \ldots, x_k)$$

REDUCED BY $x_i \Downarrow$ $\Uparrow$ **AUGMENTED BY** x_i

$$LV_{k-1}(x_1, \ldots, x_k \setminus x_i)$$

$$\triangle^k_{i,j} = \{(x_1, \ldots, x_k) \in \mathbb{T}^k : x_i = x_j\},$$

THE DIAGONAL HYPERPLANE $x_i = x_j$

FITNESS OF MUTANTS' PHENOTYPE TRAIT y ON COMMUNITY-DYNAMICAL ATTRACTOR $\langle x_1, \ldots, x_k \rangle \in R(\mathbb{T}^k)$:

$$s_{\langle x_1,\ldots,x_k\rangle}(y) = \lim_{T\to+\infty} \frac{1}{T} \int_0^T \left(\frac{1}{n_y(t)} \frac{d}{dt} n_y(t) \right) \Big|_{n_y=0} dt =$$

$$\lim_{T\to+\infty} \frac{1}{T} \int_0^T \left(r(y) + \sum_{i=1}^k a(y, x_i) n_i(t) \right) dt =$$

$$r(y) + \sum_{i=1}^k a(y, x_i) \overline{n}_i$$

NEUTRALITY: $s_{\langle x_1,\ldots,x_k\rangle}(x_i) = 0, i = 1, \ldots, k \Rightarrow$

$$\overline{n}_i = \hat{n}_i, i = 1, \ldots, k$$

$$s_{\langle x_1,\ldots,x_k\rangle}(y) = r(y) + \sum_{i=1}^k a(y, x_i) \hat{n}_i$$

THUS: C-ATTRACTOR $\langle x_1, \ldots, x_k \rangle \in R(\mathbb{T}^k)$

$$\Downarrow$$

UNIQUE EQUILIBRIUM POINT $(\hat{n}_1, \ldots, \hat{n}_k) \in \mathbb{R}^k_+$

FOR $(x_1, \ldots, x_k) \in R(\mathbb{T}^k)$:

$$s_{(x_1,\ldots.x_k)}(y) = r(y) + \sum_{i=1}^{k} a(y, x_i)\hat{n}_i(x_1, \ldots, x_k)$$

WITH n_i FROM

$$s_{(x_1,\ldots,x_k)}(x_i) = 0,\ i = 1, \ldots, k$$

A STRAIGHTFORWARD RESULT

LET $(x_1, \ldots, x_k) \in R(\mathbb{T}^k)$ AND $l \in \{1, \ldots, k-1\}$. SUPPOSE THERE EXISTS A SUBSET OF DISTINCT ELEMENTS $\{i_1, \ldots, i_l\} \subset \{1, \ldots, k\}$ SUCH THAT FOR ALL $j = \{1, \ldots, l\}$: $\hat{n}_{i_j}(x_1, \ldots, x_k) = 0$, AND IN ADDITION $(x_1, \ldots, x_k \setminus x_{i_1}, \ldots, x_{i_l}) \in R(\mathbb{T}^{k-l})$. THEN THE FOLLOWING PROPERTIES HOLD:

1. FOR ALL $i \in \{1, \ldots, k\} \setminus \{i_1, \ldots, i_l\}$:

   $\hat{n}_i(x_1, \ldots, x_k) = \hat{n}_i(x_1, \ldots, x_k \setminus x_{i_1}, \ldots, x_{i_l})$;
2. FOR ALL $y \in \mathbb{T}$: $s_{(x_1,\ldots,x_k)}(y) = s_{(x_1,\ldots,x_k \setminus x_{i_1},\ldots,x_{i_l})}(y)$.

FOR $(x_1, \ldots, x_k) \in \mathbb{T}^k$:

$$S_{(x_1,\ldots,x_k)}(y) :=$$

$$\left| \begin{pmatrix} -1 & a(x_1,x_2) & . & . & . & a(x_1,x_k) & r(x_1) \\ a(x_2,x_1) & -1 & a(x_2,x_3) & . & . & a(x_2,x_k) & r(x_2) \\ . & . & . & . & . & . & . \\ . & . & . & . & . & . & . \\ . & . & . & . & . & . & . \\ a(x_k,x_1) & . & . & . & a(x_k,x_{k-1}) & -1 & r(x_k) \\ a(y,x_1) & . & . & . & . & a(y,x_k) & r(y) \end{pmatrix} \right|$$

- FOR EACH $i \in \{1, \ldots, k\}$: $S_{(x_1,\ldots,x_k)}(x_i) = 0$
- $$\hat{n}_i(x_1, \ldots, x_k) = -\frac{S_{(x_1,\ldots,x_k \setminus x_i)}(x_i)}{|(A(x_1, \ldots, x_k)|}$$
- $$s_{(x_1,\ldots,x_k)}(y) = \frac{S_{(x_1,\ldots,x_k)}(y)}{|A(\tau_1, \ldots, \tau_k)|}$$
- $LV_k(x_1, \ldots, x_k)$ **ALLOWS FOR A UNIQUE INTERIOR REST POINT IF AND ONLY IF**

FOR ALL $i \in \{1, \ldots, k\}$: $\dfrac{|A(x_1, \ldots, x_k \setminus x_i)|}{|A(x_1, \ldots, x_k)|} s_{(x_1,\ldots,x_k \setminus x_i)}(x_i) < 0$

THESE INEQUALITIES ARE NECESSARY CONDITIONS FOR THE EXISTENCE OF C-ATTRACTORS.

IMPLICATION FOR PHENOTYPIC TRAIT EVOLUTION:

FOR INVASION OF $\langle x_1, \ldots, x_k \rangle$ BY A MUTANT POPULATION WITH PHENOTYPIC TRAIT VALUE $y = x_{k+1}$ TO LEAD TO COEXISTENCE ON $\langle x_1, \ldots, x_k, x_{k+1} \rangle$, THE FOLLOWING CONDITIONS ARE NECESSARY:

1. $\mathrm{SIGN}\,(|A(x_1, \ldots, x_k)|) = -\mathrm{SIGN}\,(|A(x_1, \ldots, x_{k+1})|)$
2. FOR ALL $i = 1, \ldots, k$: $\frac{|A(x_1,\ldots,x_{k+1} \setminus x_i)|}{|A(x_1,\ldots,x_{k+1})|} s_{(x_1,\ldots,x_{k+1} \setminus x_i)}(x_i) < 0.$

   THEREFORE:

- IF $s_{(x_1,\ldots,x_{k+1} \setminus x_i)}(x_i) > 0$, THEN

  $\mathrm{SIGN}\,(|A(x_1, \ldots, x_{k+1} \setminus x_i)|) = -\mathrm{SIGN}\,(|A(x_1, \ldots, x_{k+1})|)$;
- IF $s_{(x_1,\ldots,x_{k+1} \setminus x_i)}(x_i) < 0$, THEN

  $\mathrm{SIGN}\,(|A(x_1, \ldots, x_{k+1} \setminus x_i)|) = \mathrm{SIGN}\,(|A(x_1, \ldots, x_{k+1})|)$.

$A(x_1,\dots,x_k)_{(i,j)}$:

MATRX OBTAINED FROM THE INTERACTION MATRIX $A(x_1,\dots,x_k)$ BY DELETING ITS i-TH ROW AND j-TH COLUMN.

$k \geq 1$, $1 \leq l \leq k-1$, $j_1,\dots,j_l$ l DIFFERENT ELEMENTS OF $\{1,\dots,k\}$.

- For all $i \in \{1,\dots,k\} \setminus \{j_1,\dots,j_l\}$:

$$|A(x_1,\dots,x_k \setminus x_{j_1},\dots,x_{j_l})| S_{(x_1,\dots,x_k \setminus x_i)}(x_i) - |A(x_1,\dots,x_k)| S_{(x_1,\dots,x_k \setminus x_{j_1},\dots,x_{j_l},x_i)}(x_i) =$$

$$\sum_{\alpha=1}^{l} (-1)^{j_\alpha - i} S_{(x_1,\dots,x_k \setminus x_{j_1},\dots,x_{j_l})}(x_{j_\alpha}) |A(x_1,\dots,x_k)_{(x_{j_\alpha},i)})|$$

IF FOR ALL $\alpha = 1,\dots,l$: $S_{(x_1,\dots,x_k \setminus x_{j_1},\dots,x_{j_l})}(x_{j_\alpha}) = 0$, AND BOTH $|A(x_1,\dots,x_k)| \neq 0$ AND $|A(x_1,\dots,x_k \setminus x_{j_1},\dots,x_{j_l})| \neq 0$, THEN

$$\frac{S_{(x_1,\dots,x_k,\setminus x_i)}(x_i)}{|A(x_1,\dots,x_k)|} = \frac{S_{(x_1,\dots,x_k \setminus x_{j_1},\dots,x_{j_l},x_i)}(x_i)}{|A(x_1,\dots,x_k \setminus x_{j_1},\dots,x_{j_l})|}$$

-
$$|A(x_1,\ldots,x_k \setminus x_{j_1},\ldots,x_{j_l})|S_{(x_1,\ldots,x_k)}(x_{k+1})-$$
$$|A(x_1,\ldots,x_k)|S_{(x_1,\ldots,x_k \setminus x_{j_1},\ldots,x_{j_l})}(x_{k+1}) =$$
$$\sum_{\alpha=1}^{l}(-1)^{j_\alpha-(k+1)}S_{(x_1,\ldots,x_k \setminus x_{j_1},\ldots,x_{j_l})}(x_{j_\alpha})|A(x_1,\ldots,x_{k+1})_{(j_\alpha,k+1)}|$$

IF FOR ALL $\alpha = 1,\ldots,l$: $S_{(x_1,\ldots,x_k \setminus x_{j_1},\ldots,x_{j_l})}(x_{j_\alpha}) = 0$, AND BOTH $|A(x_1,\ldots,x_k)| \neq 0$ AND $|A(x_1,\ldots,x_k \setminus x_{j_1},\ldots,x_{j_l})| \neq 0$, THEN

$$\frac{S_{(x_1,\ldots,x_k)}(x_{k+1})}{|A(x_1,\ldots,x_k)|} = \frac{S_{(x_1,\ldots,x_k \setminus x_{j_1},\ldots,x_{j_l})}(x_{k+1})}{|A(x_1,\ldots,x_k \setminus x_{j_1},\ldots,x_{j_l})|}$$

ON $\langle x_1, \ldots, x_k \rangle$ THERE ARE

k LOCAL FITNESS GRADIENTS:

$$D_i\langle x_1, \ldots, x_k \rangle := \frac{d}{dy} s_{\langle x_1,\ldots,x_k \rangle}(y)\Big|_{y=x_i}, \; i = 1, \ldots, k.$$

i-ISOCLINE: $\{(x_1, \ldots, x_k) \in \mathbb{T}^k : D_i\langle x_1, \ldots, x_k \rangle = 0\}$

"INVASION IMPLIES FIXATION":

LET A C-ATTRACTOR $\langle x_1, \ldots, x_k \rangle$ BE GIVEN, AND LET, FOR A CERTAIN $i \in \{1, \ldots, k\}$: $D_i\langle x_1, \ldots, x_k \rangle > 0$ ($D_i\langle x_1, \ldots, x_k \rangle < 0$). THEN A MUTANT POPULATION WITH TRAIT VALUE y SUCH THAT $y - x_i > 0$ ($y - x_i < 0$) AND SUFFICIENTLY SMALL, CAN INVADE THE C-ATTRACTOR. THE INVASION WILL CAUSE THE REPLACEMENT OF POPULATION i BY THE MUTANT POPULATION. I.E., THE INVADED COMMUNITY WILL EVENTUALLY RESIDE ON $\langle x_1, \ldots, x_{i-1}, y, x_{i+1}, \ldots, x_k \rangle$.

FACTORIZATION:

$$s_{\langle x_1,\ldots,x_k\rangle}(y) = \prod_{i=1}^{k}(x_i - y) z_{\langle x_1,\ldots,x_k\rangle}(y)$$

THEREFORE: $z_{\langle x_1,\ldots,x_k\rangle}(x_i) = 0 \Rightarrow D_i(x_1,\ldots,x_k) = 0$

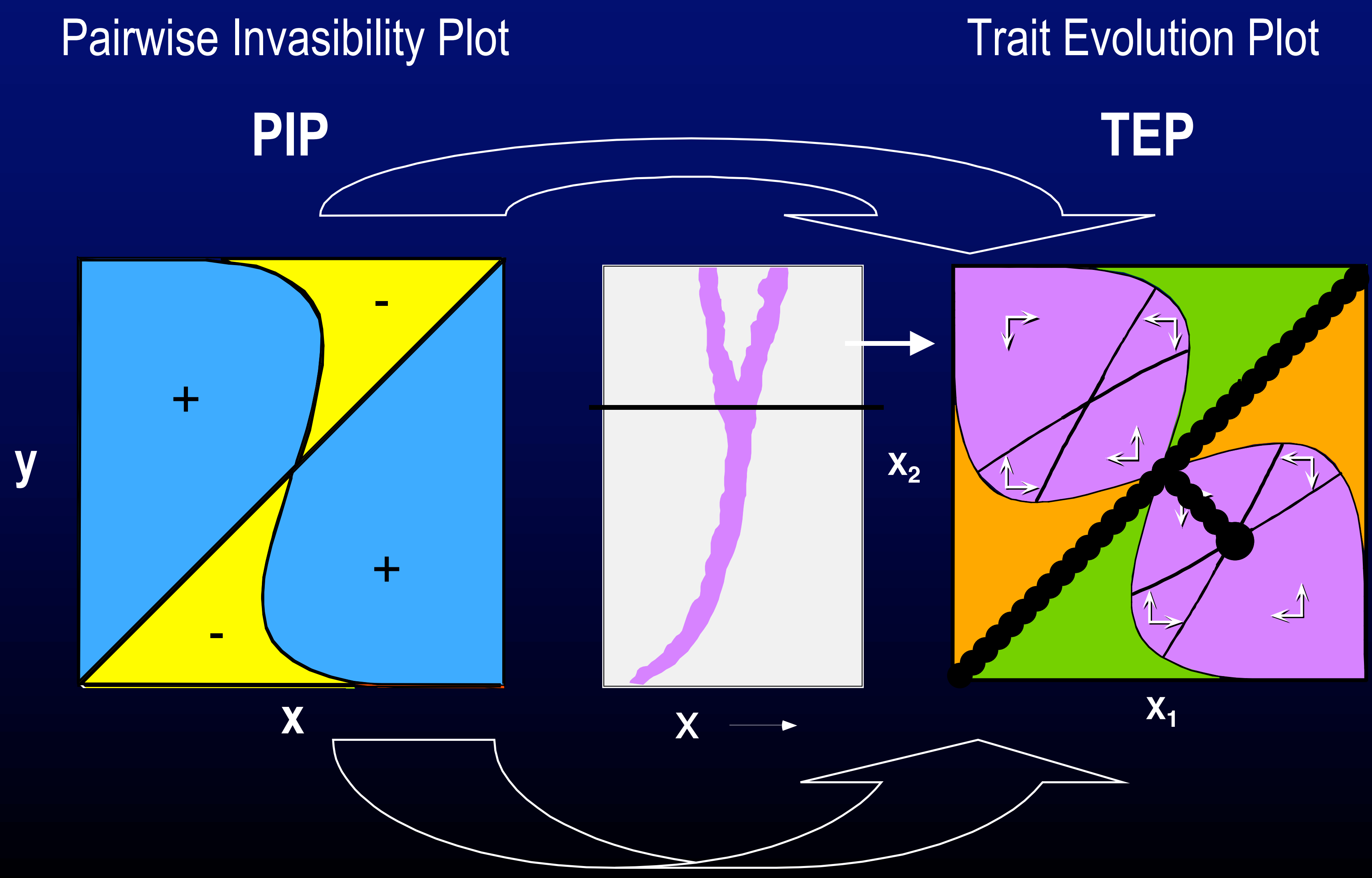
GEOMETRICALLY:

THE (EMBEDDED) i-TH ISOCLINE $D_i(x_1,\ldots,x_k) = 0$ **IS OBTAINED AS THE INTERSECTION OF THE SET** $\{(x_1,\ldots,x_k,x_{k+1}) \in \mathbb{T}^{k+1} : z_{\langle x_1,\ldots,x_k\rangle}(x_{k+1}) = 0\}$ **WITH THE DIAGONAL HYPERPLANE** $x_{k+1} = x_i$ **IN** $\mathbb{T}^{k+1}$**.**

ALSO:

$$s_{(x_1,\ldots,x_k)}(y) = \frac{\left|\begin{pmatrix} 0 & s_{(x_1)}(x_2) & . & . & s_{(x_1)}(x_k) & s_{(x_1)}(y) \\ s_{(x_2)}(x_1) & 0 & . & . & s_{(x_2)}(x_k) & s_{(x_2)}(y) \\ . & . & . & . & . & . \\ . & . & . & . & . & . \\ s_{(x_k)}(x_1) & s_{(x_k)}(x_2) & . & . & 0 & s_{(x_k)}(y) \\ r(x_1) & r(x_2) & . & . & r(x_k) & r(y) \end{pmatrix}\right|}{\left|\begin{pmatrix} 0 & s_{(x_1)}(x_2) & . & . & s_{(x_1)}(x_k) & 1 \\ s_{(x_2)}(x_1) & 0 & . & . & s_{(x_2)}(x_k) & 1 \\ . & . & . & . & . & . \\ . & . & . & . & . & . \\ s_{(x_k)}(x_1) & s_{(x_k)}(x_2) & . & . & 0 & 1 \\ r(x_1) & r(x_2) & . & . & r(x_k) & 1 \end{pmatrix}\right|}$$

A bit more adaptive dynamics theory for later reference



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