Invasion Fitness near Evolutionary Singularities

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Adaptive Dynamics: evolution driven by repeated establishment of mutants

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- mathematically consistent framework for considering long-term evolution
- study evolutionary outcomes of invasion/replacement dynamics
- model evolution by accumulating diversity

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- rare mutation events:
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- rare mutants in a large, well-mixed resident population
  $\Rightarrow$ invaders influence residents nor invaders,
  $\Rightarrow$ stochasticity may slow down evolution

The invasion fitness function

$s_X(Y) \doteq$ the long-term average *PC* growthrate of a rare Y-type invader in an X-resident population at equilibrium

The invasion fitness function

Example (LV):

$$\frac{1}{n}\frac{\mathrm{d}n}{\mathrm{d}t} = r_{\boldsymbol{X}} - a(\boldsymbol{X},\boldsymbol{X})n - a(\boldsymbol{X},\boldsymbol{Y})m$$

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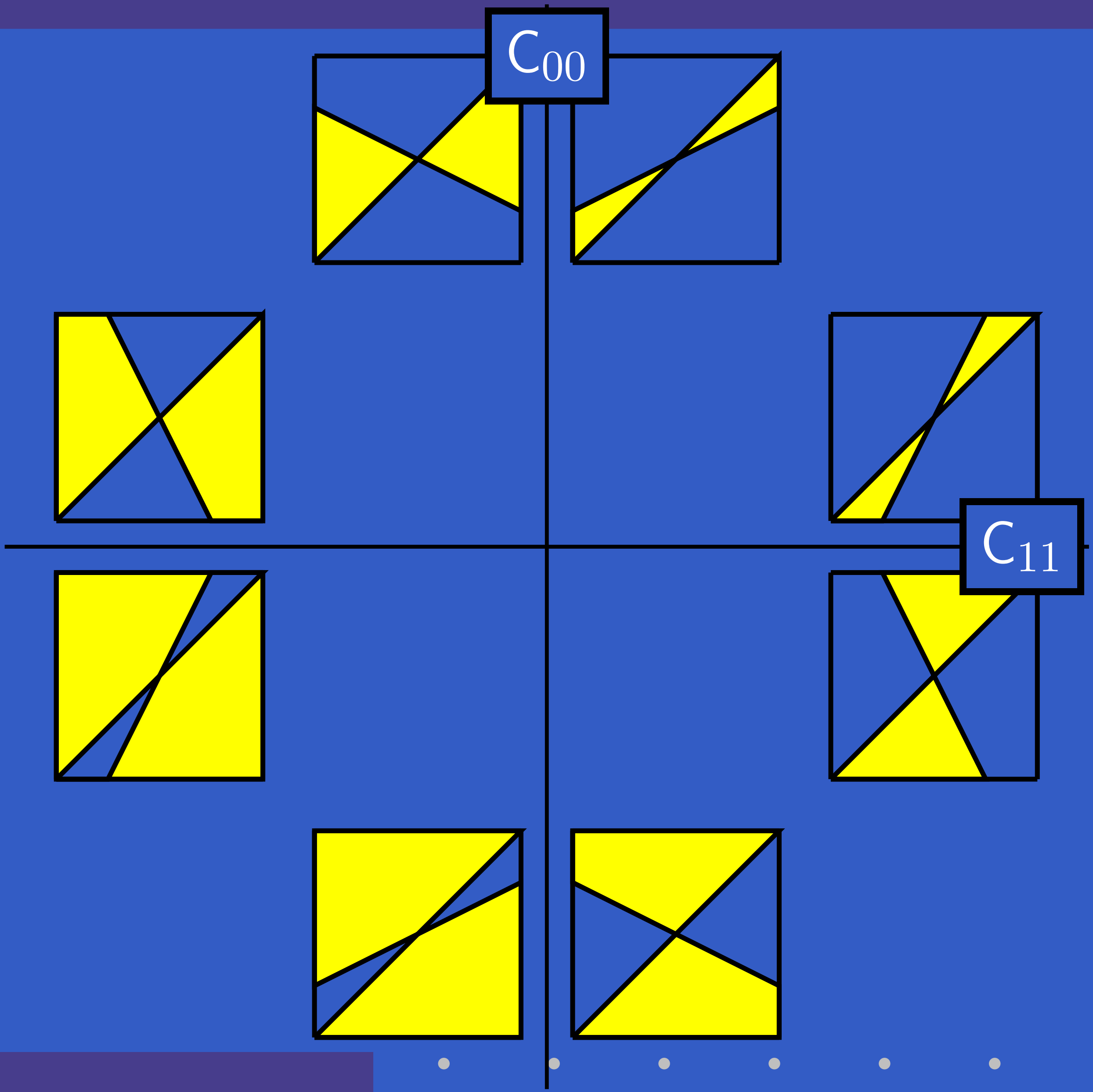
  - normal form $\Rightarrow$ classification (1dim strategies)

the 8-fold classification of 1D singularities



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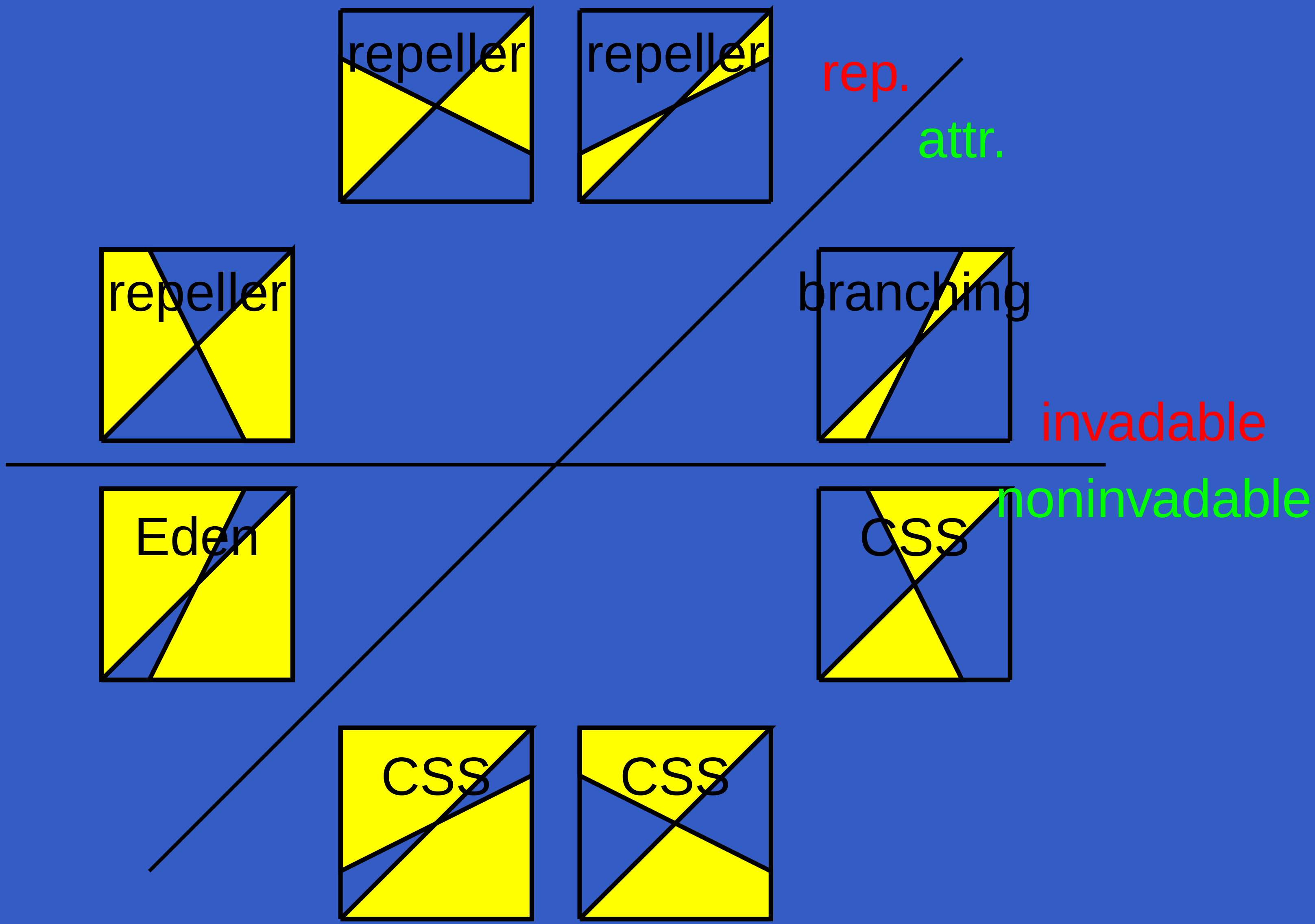

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  2-resident Lotka-Volterra system $\{\boldsymbol{X}_1, \boldsymbol{X}_2\} \equiv \mathbb{X}$
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where $\overline{\boldsymbol{U}} \equiv \frac{\boldsymbol{U}_1+\boldsymbol{U}_2}{2}$ $\qquad \boldsymbol{\Delta} \equiv \frac{\boldsymbol{U}_1-\boldsymbol{U}_2}{2}$

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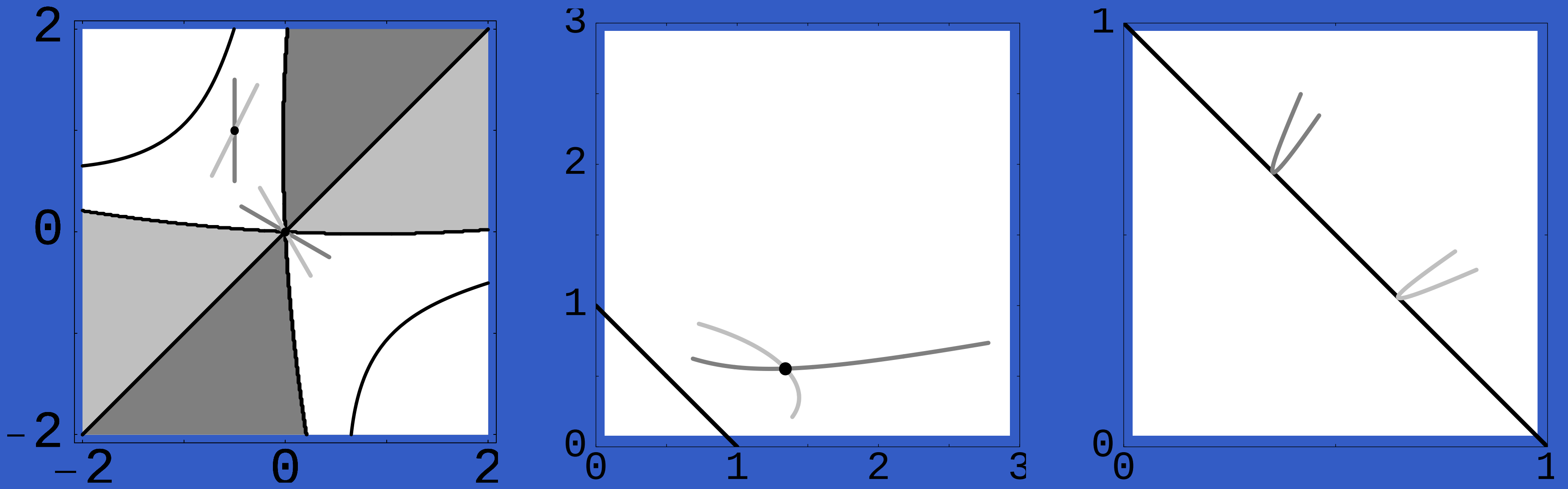

Directional blowup

- all N residents and all mutants are close to $\boldsymbol{X}^*$

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- normal form $\Rightarrow$ try proof for very general systems

Physiologically Structured Populations

birth rate vector b:

steady birth rate in all possible birth states

environmental condition $\boldsymbol{I}$:

as far as influenced by interaction. Individuals are independent for a given $\boldsymbol{I}$

next-generation matrix $\mathsf{L}(\boldsymbol{X}, \boldsymbol{I})_{lm}$:

expected number of offspring with birth state l from an $\boldsymbol{X}$-type parent born with state m

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$$\mathsf{s}_{\mathbb{X}}(\boldsymbol{Y}) = \log \lambda(\,\mathsf{L}(\boldsymbol{Y}, \boldsymbol{I}(\mathbb{X}))\,)\;/\;T_f(\boldsymbol{Y}, \boldsymbol{I}(\mathbb{X})) + o(\varepsilon^2)$$

N-species normal form

- monomorphic fitness near singularity:
  $\mathsf{s}_{\boldsymbol{X}}(\boldsymbol{Y}) = \boldsymbol{U}^\top \mathsf{C}_{11} \boldsymbol{U} + 2\boldsymbol{U}^\top \mathsf{C}_{10} \boldsymbol{V} + \boldsymbol{V}^\top \mathsf{C}_{00} \boldsymbol{V} + o(\varepsilon^2)$

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- polymorphic fitness for $\mathbb{X} \equiv \{\boldsymbol{X}_1, \boldsymbol{X}_2, \ldots, \boldsymbol{X}_N\}$:
  $\mathsf{s}_{\mathbb{X}}(\boldsymbol{Y}) = \theta + 2\left(\sum_i p_i \boldsymbol{U}_i^{\mathsf{T}}\right)\mathsf{C}_{10}\boldsymbol{V} + \boldsymbol{V}^{\mathsf{T}}\mathsf{C}_{00}\boldsymbol{V} + o(\varepsilon^2)$
  where

$$\begin{pmatrix} p_1 \\ \vdots \\ p_N \\ \theta \end{pmatrix} = \begin{pmatrix} 2\boldsymbol{U}_1^{\mathsf{T}}\mathsf{C}_{10}\boldsymbol{U}_1 & \cdots & 2\boldsymbol{U}_N^{\mathsf{T}}\mathsf{C}_{10}\boldsymbol{U}_1 & 1 \\ \vdots & \ddots & \vdots & \vdots \\ 2\boldsymbol{U}_1^{\mathsf{T}}\mathsf{C}_{10}\boldsymbol{U}_N & \cdots & 2\boldsymbol{U}_N^{\mathsf{T}}\mathsf{C}_{10}\boldsymbol{U}_N & 1 \\ 1 & \cdots & 1 & 0 \end{pmatrix}^{-1} \begin{pmatrix} -\boldsymbol{U}_1^{\mathsf{T}}\mathsf{C}_{00}\boldsymbol{U}_1 \\ \vdots \\ -\boldsymbol{U}_N^{\mathsf{T}}\mathsf{C}_{00}\boldsymbol{U}_N \\ 1 \end{pmatrix}$$

N-species normal form

- monomorphic fitness near singularity:
  $\mathsf{s}_{\boldsymbol{X}}(\boldsymbol{Y}) = \boldsymbol{U}^\mathsf{T}\mathsf{C}_{11}\boldsymbol{U} + 2\boldsymbol{U}^\mathsf{T}\mathsf{C}_{10}\boldsymbol{V} + \boldsymbol{V}^\mathsf{T}\mathsf{C}_{00}\boldsymbol{V} + o(\varepsilon^2)$
- polymorphic fitness for $\mathbb{X} \equiv \{\boldsymbol{X}_1, \boldsymbol{X}_2, \ldots, \boldsymbol{X}_N\}$:
  $\mathsf{s}_{\mathbb{X}}(\boldsymbol{Y}) = \theta + 2\left(\sum_i p_i \boldsymbol{U}_i^\mathsf{T}\right)\mathsf{C}_{10}\boldsymbol{V} + \boldsymbol{V}^\mathsf{T}\mathsf{C}_{00}\boldsymbol{V} + o(\varepsilon^2)$
  where

$$\begin{pmatrix} p_1 \\ \vdots \\ p_N \\ \theta \end{pmatrix} = \begin{pmatrix} 2\boldsymbol{U}_1^\mathsf{T}\mathsf{C}_{10}\boldsymbol{U}_1 & \cdots & 2\boldsymbol{U}_N^\mathsf{T}\mathsf{C}_{10}\boldsymbol{U}_1 & 1 \\ \vdots & \ddots & \vdots & \vdots \\ 2\boldsymbol{U}_1^\mathsf{T}\mathsf{C}_{10}\boldsymbol{U}_N & \cdots & 2\boldsymbol{U}_N^\mathsf{T}\mathsf{C}_{10}\boldsymbol{U}_N & 1 \\ 1 & \cdots & 1 & 0 \end{pmatrix}^{-1} \begin{pmatrix} -\boldsymbol{U}_1^\mathsf{T}\mathsf{C}_{00}\boldsymbol{U}_1 \\ \vdots \\ -\boldsymbol{U}_N^\mathsf{T}\mathsf{C}_{00}\boldsymbol{U}_N \\ 1 \end{pmatrix}$$

- multiple birthstates: p_i *vector*, but $(p_i)_l = (p_i)_o + o(1)$

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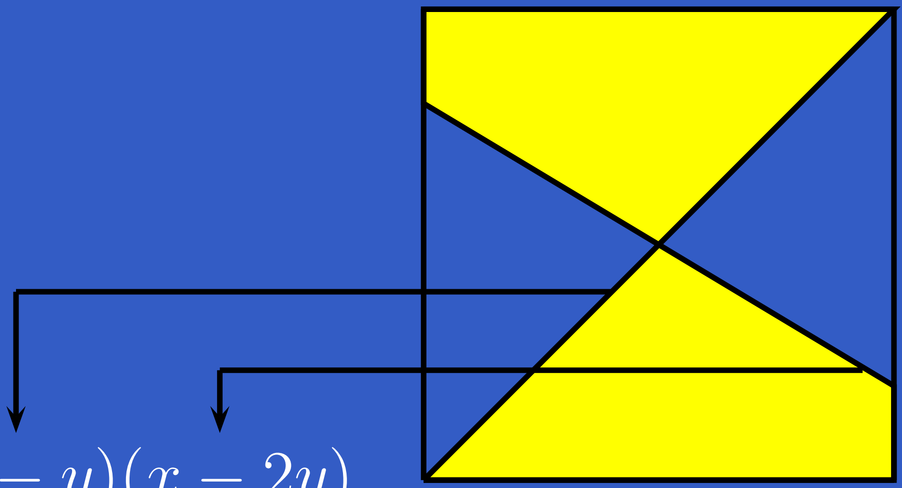
- multiple birthstates: p_i *vector*, but $(p_i)_l = (p_i)_o + o(1)$
- invertibility of E^*: m-dim strategy $\rightarrow N \leq m+1$, ...

Discussion

- use, for any model: monomorphic $\mathsf{s}_{\boldsymbol{X}}(\boldsymbol{Y})$
  $\Rightarrow$ fit a Lotka-Volterra model
  $\Rightarrow$ polymorphic invasion fitness (up to $o(\varepsilon^2)$)
- for unfolding codim-1 bifurcations, $o(\varepsilon^3)$ is needed: e.g. (scalar):



$$\mathsf{s}_x(y) = (x-y)(x-2y)$$