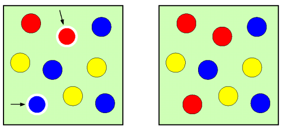
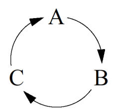
Well mixed Populations

## The Rock-Scissors-Paper Game



Consider a fixed population of N individuals in a well mixed environment ("urn model")

$$A + B \xrightarrow{k_A} A + A$$
$$B + C \xrightarrow{k_B} B + B$$
$$C + A \xrightarrow{k_C} C + C$$




Cyclic competition between three species A, B, C

T. Reichenbach, M. Mobilia and E. Frey, PRE (2006)

## Deterministic Evolution

Rate equations:

$$\boxed{\begin{aligned} \dot{a} &= a(k_A b - k_C c) \\ \dot{b} &= b(k_B c - k_A a) \\ \dot{c} &= c(k_C a - k_B b) \end{aligned}}$$

$$a + b + c = 1$$

Constant of motion:

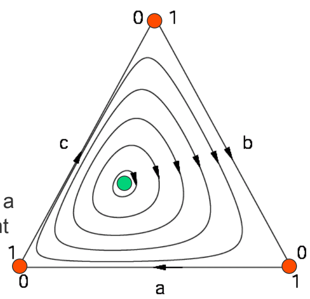
$$K = a(t)^{k_B}\, b(t)^{k_C}\, c(t)^{k_A}$$

cyclic trajectories around a neutrally stable fixed point

coexistence

absorbing fixed point

reactive (center) fixed point



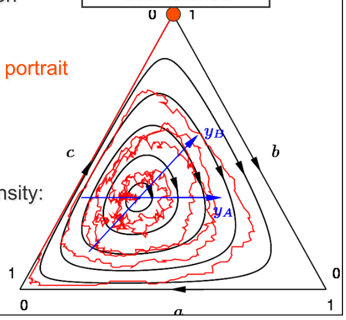
## Stochastic Evolution

- processes are probabilistic
- K not a constant of motion
- neutrally stable cycles!
- "random walk" on phase portrait

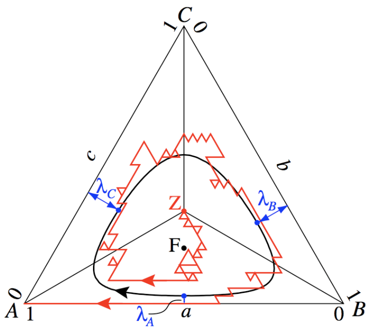
stochasticity causes loss of coexistence

Stochastic description in terms of a probability density:

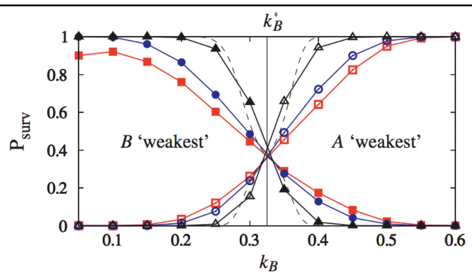
$\boxed{P(a,b,c;t) = P(\mathbf{x},t)}$




## „The Law of the Weakest"




M. Berr, T. Reichenbach, M. Schottenloher and E. Frey, PRL (2009)




Fix time scale: $k_A+k_B+k_C=1$
Fix $k_C=0.35$

As $k_B$ passes through 0.325 species A becomes the weakest species.

## E.coli

$$k_C \gg k_S > k_R$$

The resistant strain has the smallest growth rate and in this sense is the weakest.

Hence the resistant strain always survives!

In finite populations stochasticity causes loss of coexistence.

The typical extinction time T is proportional to the population size, T ~ N (neutrality).

The weakest always wins the game for large N

## May-Leonard Model (well mixed)

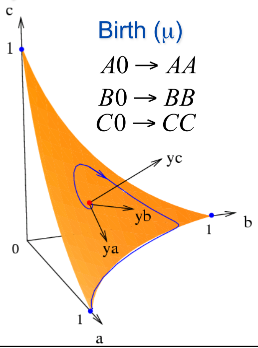
Species A,B,C and empty sites 0

Cyclic dominance ($\sigma$)

$AB \to A0$
$BC \to B0$
$CA \to C0$

Birth ($\mu$)

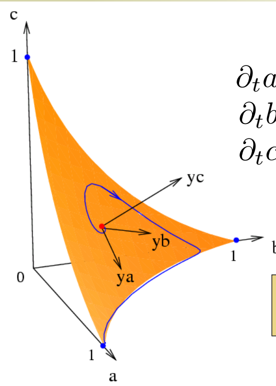
$A0 \to AA$
$B0 \to BB$
$C0 \to CC$




Without spatial structure coexistence fixed point is unstable

loss of biodiversity

## Rate equations (deterministic limit)




$$\rho = a + b + c$$

$$\begin{aligned}\partial_t a &= a[\mu(1-\rho) - \sigma c]\\ \partial_t b &= b[\mu(1-\rho) - \sigma a]\\ \partial_t c &= c[\mu(1-\rho) - \sigma b]\end{aligned}$$

$$\downarrow$$

$$\boxed{\partial_t \vec{a} = \vec{F}(\vec{a})}$$

## Jordan normal form

Reactive fixed point: $\vec{a}^*$

$\vec{x} = \vec{a} - \vec{a}^*$

$\partial_t \vec{x} = \vec{F}(\vec{x} + \vec{a}) = A\vec{x} + \vec{G}(\vec{x})$

Jacobian: $A = DF\,|_{\vec{a}*}$

Eigenvalues: $\begin{aligned}\lambda_0 &= -\mu\\ \lambda_\pm &= c_1(\mu,\sigma) \pm i\omega(\mu,\sigma)\end{aligned}$

Jordan normal form: $\vec{y} = \mathcal{S}\vec{x}$

$$J = SAS^{-1} = \begin{pmatrix} c_1 & \omega & 0\\ -\omega & c_1 & 0\\ 0 & 0 & -\mu \end{pmatrix}$$

$$\partial_t \vec{y} = J\vec{y} + S\vec{G}(S^{-1}\vec{y}) \equiv J\vec{y} + \vec{H}(\vec{y})$$

## Invariant manifold

An invariant manifold is a subspace, embedded in the phase space, which is left invariant by the nonlinear dynamics.

$$y_C = M(y_A, y_B)$$

$$\partial_t M\big(y_A(t), y_B(t)\big) = \frac{\partial M}{\partial y_A}\partial_t y_A + \frac{\partial M}{\partial y_B}\partial_t y_B = \partial_t y_C\Big|_{y_C = M}$$

$$y_C = M(y_A, y_B) = \frac{\sigma}{4\mu}\frac{3\mu + \sigma}{3\mu + 2\sigma}(y_A^2 + y_B^2)$$

## Normal form

Dynamics on the reactive manifold:

$$\partial_t y_A = \tfrac{\mu\sigma}{2(3\mu+\sigma)}\left[y_A + \sqrt{3}y_B\right] + \tfrac{\sqrt{3}}{4}\sigma\left[y_A^2 - y_B^2\right] - \tfrac{\sigma}{2}y_A y_B$$
$$-\tfrac{\sigma(3\mu+\sigma)}{8\mu(3\mu+2\sigma)}\left(y_A^2 + y_B^2\right)\left[(6\mu+\sigma)y_A - \sqrt{3}\sigma y_B\right] + o(y^3)$$

$$\partial_t y_B = \tfrac{\mu\sigma}{2(3\mu+\sigma)}\left[y_B - \sqrt{3}y_A\right] - \tfrac{\sigma}{4}\left[y_A^2 - y_B^2\right] - \tfrac{\sqrt{3}}{2}\sigma y_A y_B$$
$$-\tfrac{\sigma(3\mu+\sigma)}{8\mu(3\mu+2\sigma}\left(y_A^2 + y_B^2\right)\left[\sqrt{3}\sigma y_A + (6\mu+\sigma)y_B\right] + o(y^3)$$

Nonlinear Transformation:

$$\begin{aligned} z_A &= \quad y_A + \tfrac{3\mu+\sigma}{28\mu}[\sqrt{3}y_A^2 + 10y_A y_B - \sqrt{3}y_B^2]\,, \\ z_B &= \quad y_B + \tfrac{3\mu+\sigma}{28\mu}[5y_A^2 - 2\sqrt{3}y_A y_B - 5y_B^2]\,. \end{aligned}$$

## Normal form:

$$z = z_A + i z_B$$
$$\partial_t z = (c_1 - i\omega)z - c_2(1 + ic_3) \mid z \mid^2 z$$

$$\begin{aligned} \omega &= \frac{\sqrt{3}}{2}\frac{\mu\sigma}{3\mu+\sigma} \\ c_1 &= \frac{1}{2}\frac{\mu\sigma}{3\mu+\sigma} \\ c_2 &= \frac{\sigma(3\mu+\sigma)(48\mu+11\sigma)}{56\mu(3\mu+2\sigma)} \\ c_3 &= \frac{\sqrt{3}(18\mu+5\sigma)}{48\mu+11\sigma} \end{aligned}$$

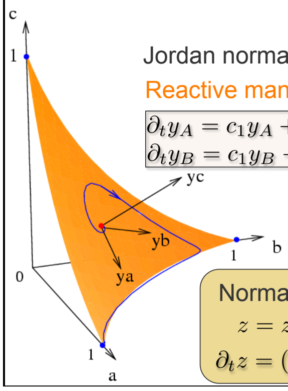
## Polar coordinates

$z_A = r\cos\phi \quad z_B = r\sin\phi$

$$\boxed{\begin{aligned} \partial_t r &= r[c_1 - c_2 r^2] \\ \partial_t \theta &= -\omega + c_2 c_3 r^2 \end{aligned}}$$

Limit cycle: $r = \sqrt{c_1/c_2}$

## Nonlinear dynamics




$$\partial_t \vec{a} = \vec{F}(\vec{a})$$

Jordan normal form: $\partial_t \vec{y} = J\vec{y} + \vec{H}(\vec{y})$

Reactive manifold: $y_C = M(y_A, y_B)$

$$\boxed{\begin{aligned}\partial_t y_A &= c_1 y_A + \omega y_B + f(y^2, y^3) + o(y^3)\\ \partial_t y_B &= c_1 y_B - \omega y_A + g(y^2, y^3) + o(y^3)\end{aligned}}$$

$$\vec{z} = \mathrm{NL}(\vec{y})$$

Normal form of nonlinear dynamics:

$$z = z_A + i z_B$$

$$\partial_t z = (c_1 - i\omega)z - c_2\big(1 + i c_3\big) \mid z \mid^2 z$$