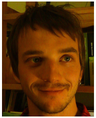
Invasion fitness, indirect feedbacks and alternative stable states in ecological community models

Jean-Francois Arnoldi,
Matthieu Barbier, Gyuri Barabas, Andrew Jackson, Guy Bunin

Lotka-Volterra Models: when Random Matrix Theory meets theoretical Ecology, Paris, December 2019



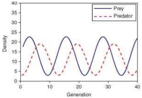
Ecological context

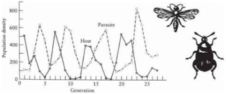
"Contemplate an entangled bank, clothed with many plants

with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth."

species interactions often studied in isolation

Predator-Prey cycles





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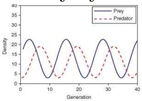
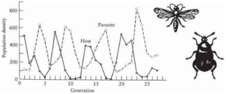
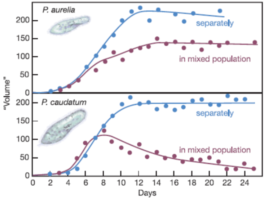




Competitive exclusion



Growth of two *paramecium* species separately and in combination.
Source: Gause, Georgyi Frantsevitch. 1934 *The Struggle for Existence.* Dover Publications, 1971 reprint of original text.

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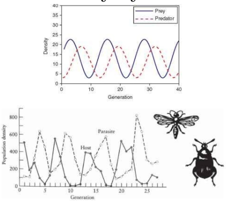

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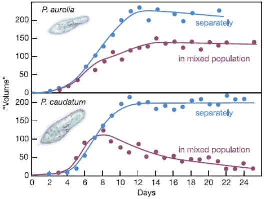

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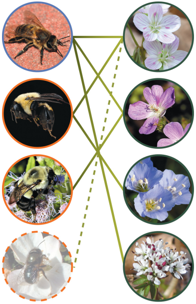
Extinction cascades in mutualistic networks



Tylianakis science 2013

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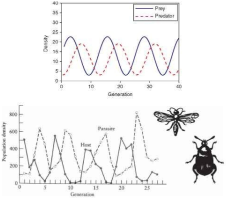

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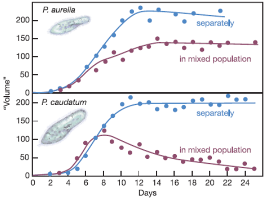

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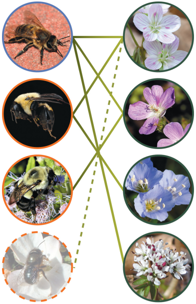

Tylianakis science 2013

- different interaction types yield qualitatively different behaviour

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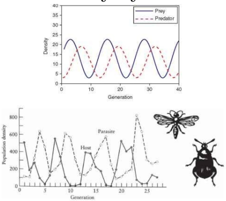

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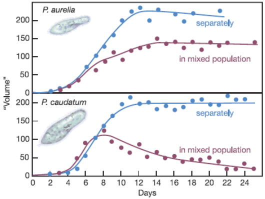

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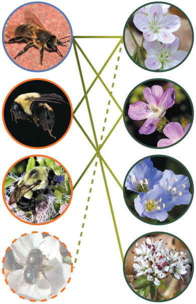
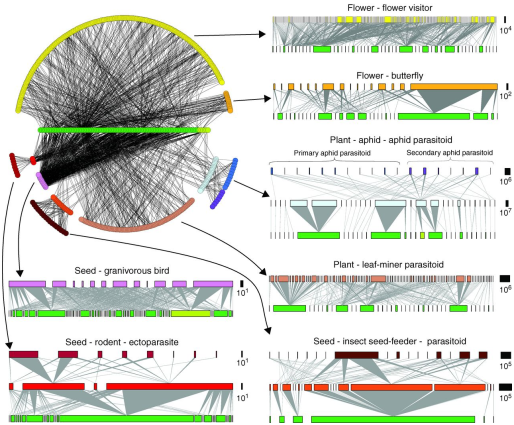


Tylianakis science 2013

- different interaction types yield qualitatively different behaviour
- Specific interaction motifs are important

yet natural communities form complex networks



Pocock et al, Science 2012.

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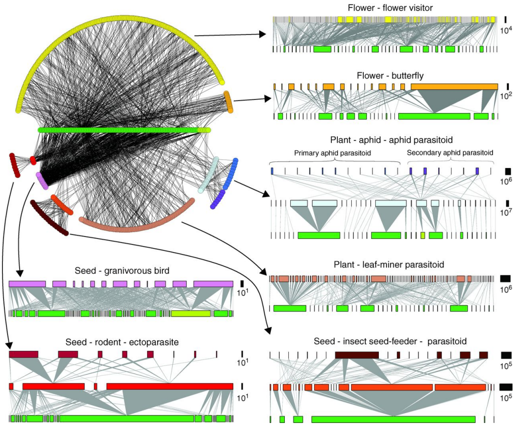

Pocock et al, Science 2012.

- uncertain knowledge in values of interaction strength
- How could there be any pattern emerging from this complexity?

A caricature of Darwin's entangled bank: random Lotka-Volterra system of ODEs

$$\frac{1}{N_i}\frac{dN_i}{dt} = \frac{r_i}{k_i}(k_i - N_i - \sum_{j\neq i}^{S} A_{ij}N_j);\; i = 1, ..., S$$

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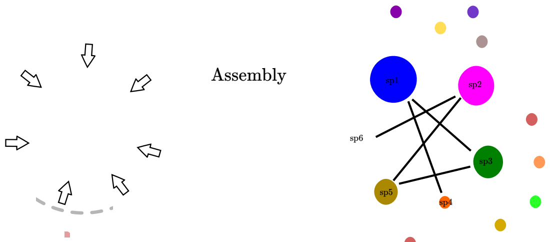


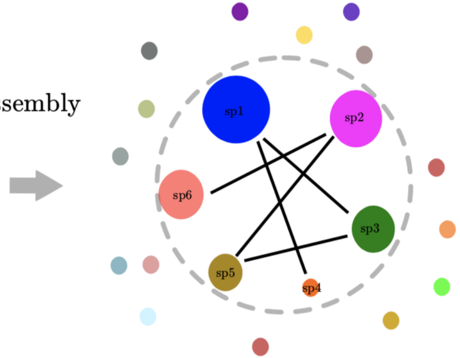
S species in regional pool

S^* survive and form an uninvadable community

$r_i > 0$ plays no role in what follows.

Random Lotka-Volterra vs Random matrices

Assembly



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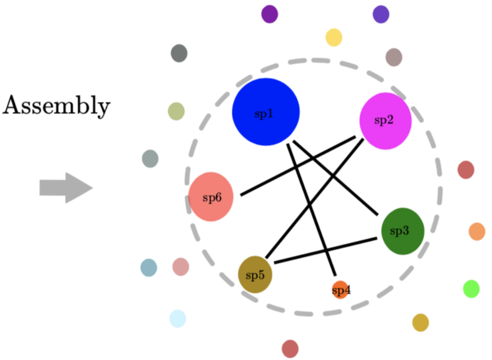

S* survive and form an uninvadable community

At equilibrium
$N^* = (N_i^*) = (\mathbb{I} + A^*)^{-1} k^*$

$$J = -\mathrm{Diag}(\frac{r^* N^*}{k^*})(\mathbb{I} + A^*)$$

with A^* is the $S^* \times S^*$ interaction matrix restricted to surviving species

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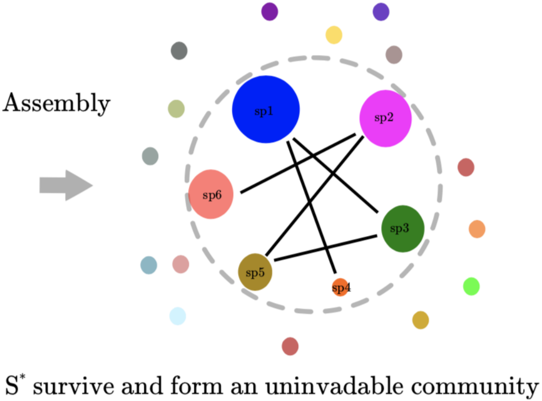

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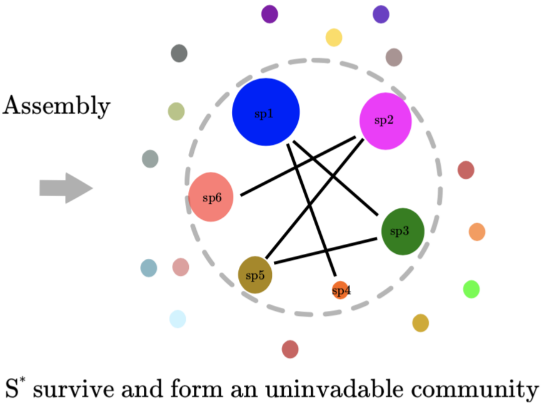

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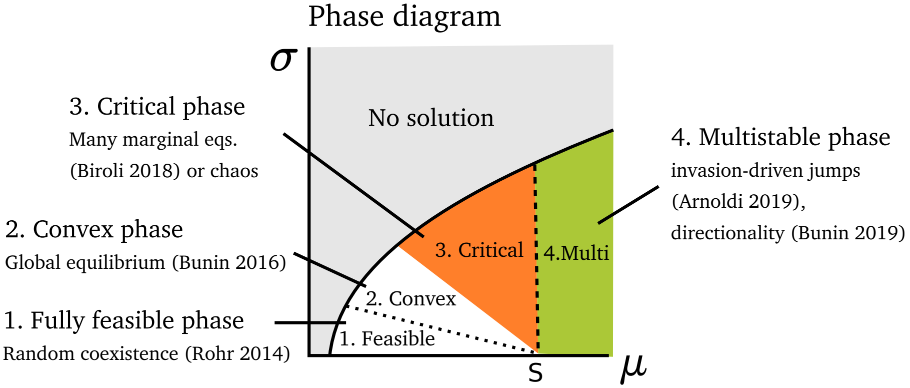
Stability is determined by the spectrum of A^* which is not exactly random if $S^* < S$

Behaviour of random L-V: the emergent phase diagram

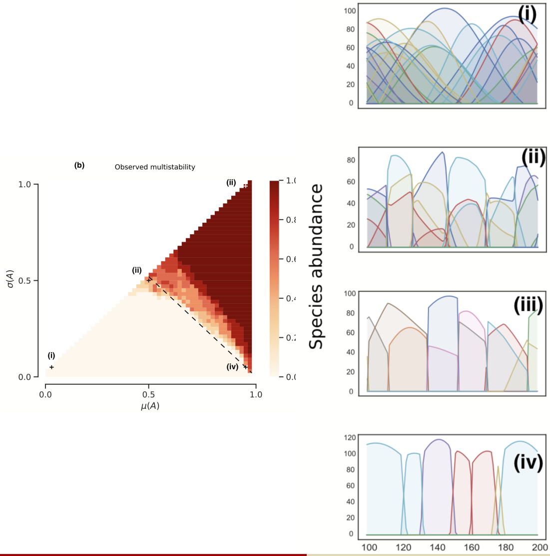
description in simulation: (Kessler and Shnerb, 2015)



interaction statistics: $\mu = S\text{mean}A_{ij}$ $\sigma = S\text{Var}A_{ij}$

In the multistable phase: abrupt transitions of community compositions along an environmental gradient

Example of competitive L-V (Liautaud et al, Ecol Lett 2019)



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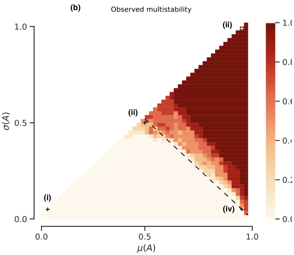

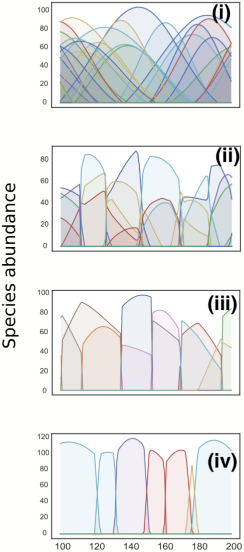

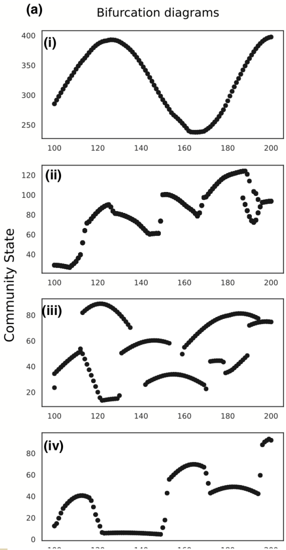

Transitions are triggered by invasions

Resident community equilibrium N_i^*. Species 0 invades from rarity if invasion fitness

$$\frac{1}{N_0}\frac{dN_0}{dt}|_{N^*} = W_0(N_0 = 0)$$

is positive.

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$$W_0(N_0) = 0 \Leftrightarrow \underbrace{W_0(0)}_{\text{fitness}\, w_0} + \underbrace{\frac{dW_0}{dN_0}}_{\text{feedback}\, -1/v_0} \times N_0 = 0$$

Thus when

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Unless extinctions occurred: either because w_0 is large or because v_0 is large (or both). If $v_0 \leq 0$: coexistence state is unstable, and we have an abrupt transition

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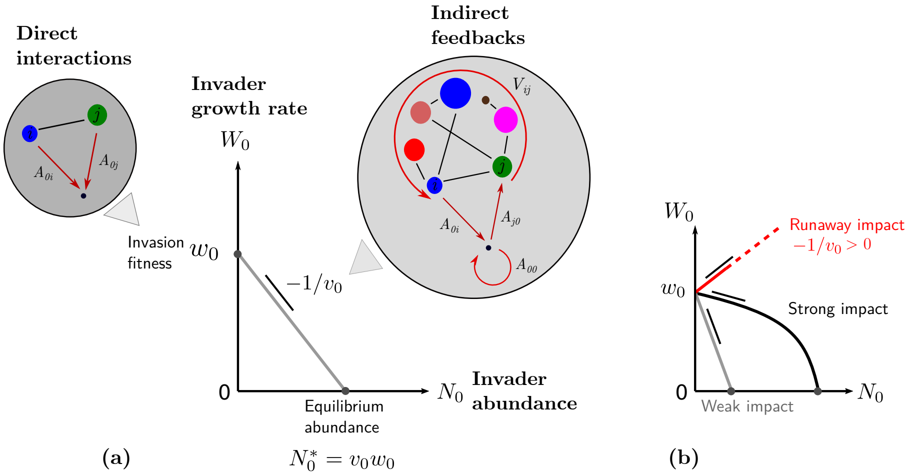
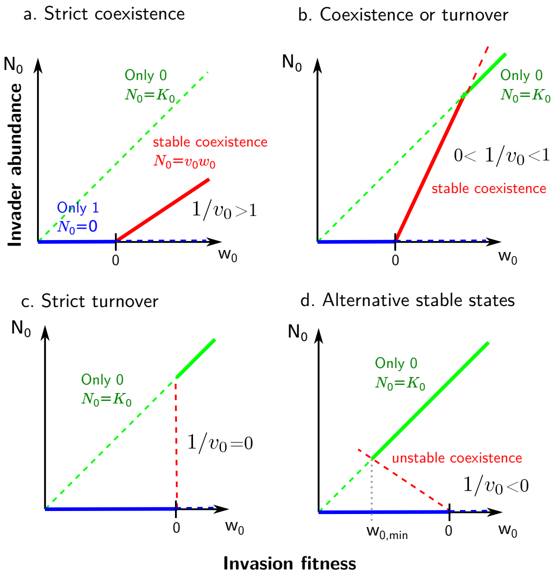


A tale of two species



Invasion fitness:

$$w_0 = k_0 - A_{01} k_1$$

equilibrium

$$N_0 = \frac{w_0}{1 - A_{01} A_{10}}$$

Thus

$$1/v_0 = 1 - A_{01} A_{10}$$

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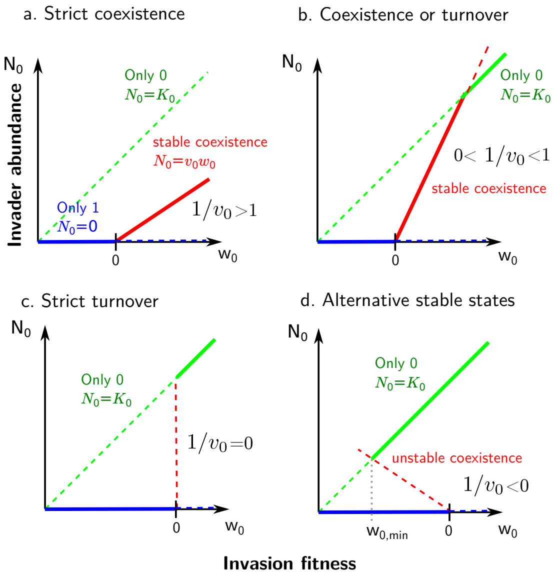

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sign of v_0 determines if the species can coexist.

General case: feedback and stability

Small increase in abundance of the invader

$$0 \to N_0$$

is a perturbation $-A_{i0}N_0$ of resident species,

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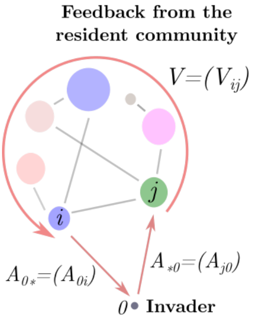

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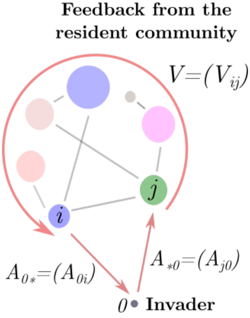

in the case of coexistence, the invasion ends when $W_0(N_0) = 0$ which gives

$$N_0 = v_0 w_0 \text{ where } 1/v_0 = 1 - \sum_{i,j} A_{0i}V_{ij}A_{j0}$$

The fitness-feedback map

$w_0 = 0$ is a bifurcation point, $1/v_0 = 0$ is the boundary between continuous and discontinuous invasions.

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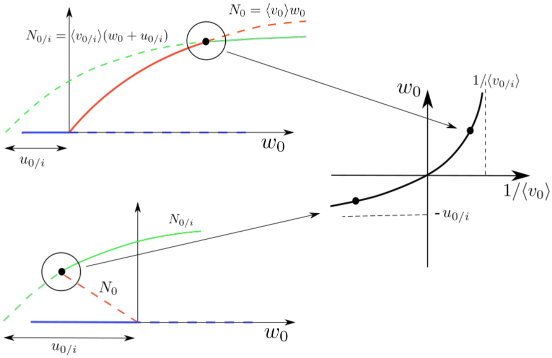

for L-V the branches are straight lines, and $\langle v_0 \rangle \equiv v_0$

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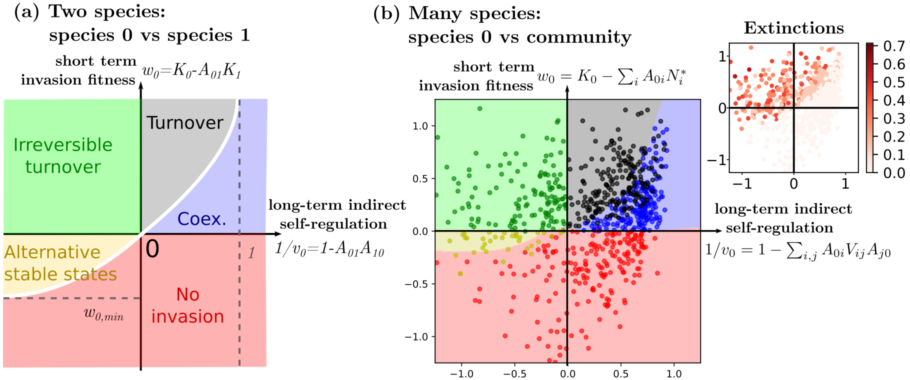

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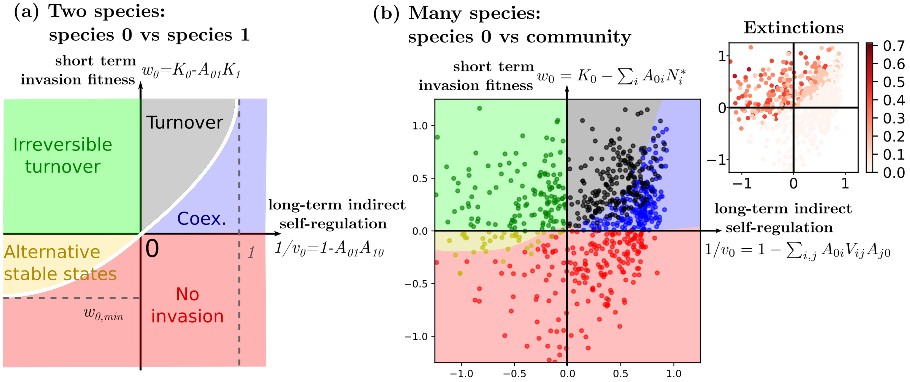
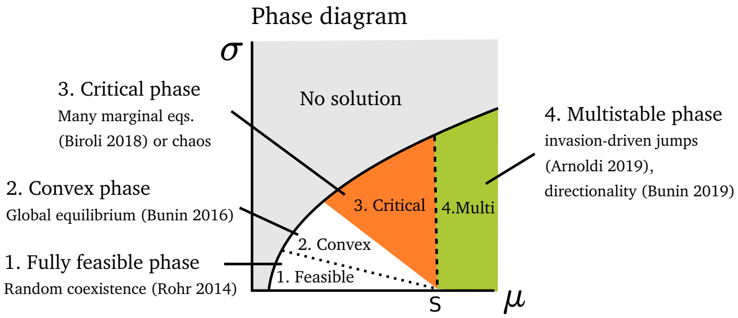


fitness and feedbacks are the two axis that determine the impacts of invasions

Arnoldi, Barbier et al, BioRxiv 2019

Back to the phase diagram (Heuristics)



what happens to $1/v_0$ in large random L-V systems?

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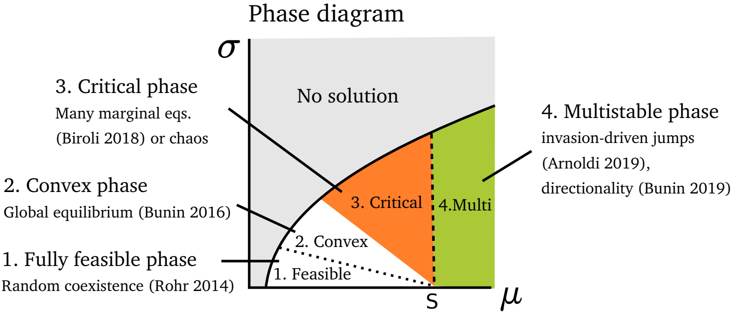

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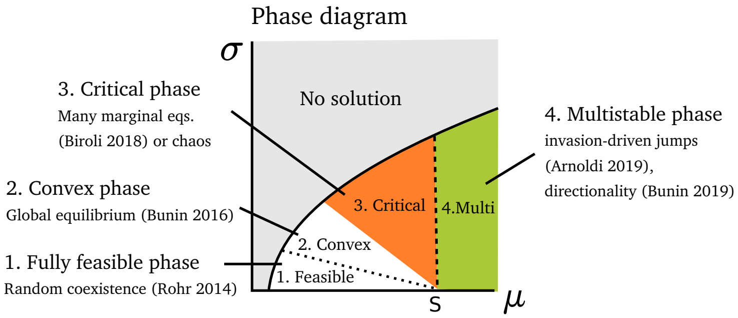

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$$\mathrm{Var}(V_{ii}) \sim \sigma^2/S^* \; V_{ij} \sim \sigma\sqrt{1/S^*}$$

Feedback is self-averaging in the standard scaling with S

Since invaders and resident are drawn from the same distribution,

$$1/v_0 = 1 - \sum_{i,j} A_{0i} V_{ij} A_{i0} \to 1 - \gamma\phi\sigma^2 \langle V_{ii} \rangle \text{ and } v_0 \equiv \langle V_{ii} \rangle$$

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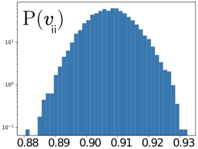

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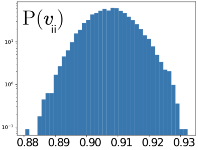

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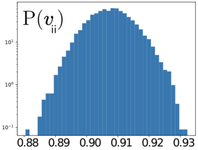

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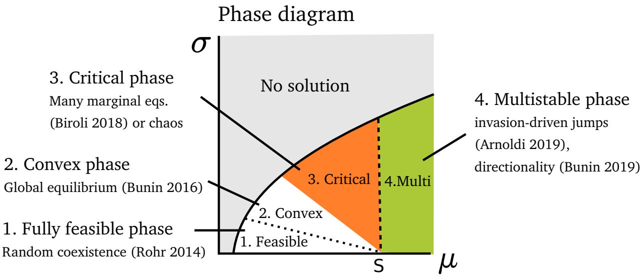
- Sensitivity matrix V can become unstable before v stops being self-averaging: transition to the critical phase (cf. Guy and Guilio's talks)

Generic alternative stable states require occurrence of strong pair-wise competition



High diversity phase where invasions cause abrupt transitions:

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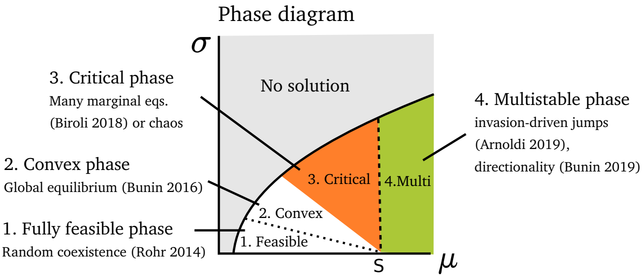
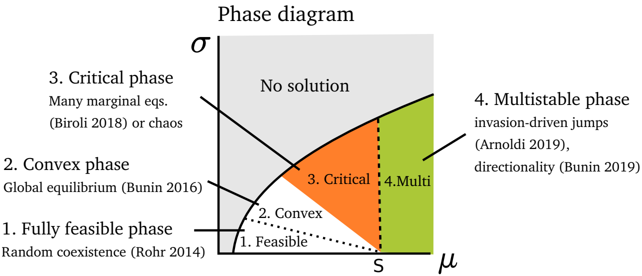


High diversity phase where invasions cause abrupt transitions:

- σ cannot grow with S without leading to unrealistic divergences.

Generic alternative stable states require occurrence of strong pair-wise competition

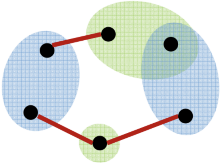


High diversity phase where invasions cause abrupt transitions:

- σ cannot grow with S without leading to unrealistic divergences.
- only possibility is $\mu \sim S$ with $\mu = S$ and $\sigma = 0$ corresponding to the Hubbell point (neutral dynamics).

The behaviour of the multistable phase (Bunin 2019)

$\mu \sim S$ leads to cliques of nonexcluding species (Fried et al, 2017)



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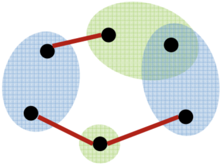
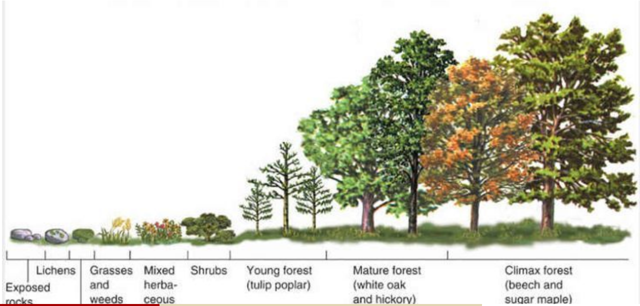


As Guy Bunin will show, the alternative states are ordered (maturity) so that transitions between them are directional



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- Reveals the inherent relationship between stability and assembly
- Alternative stable states occur when (indirect) interactions generate positive feedback loops
- Alternative stable states in random Lotka-Volterra systems require strong competitive pair-wise interactions. Different scaling with S than the usual one used in random matrix theory.

Open questions

- How to properly determine the chaos/alternative-states phase transition? Here only heuritical argument presented. There could be many unforseen subtleties

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- can we understand the chaotic phase through the invasion dynamics (onset of positive feedbacks that require perturbations of all species to manifest, not just via the invader)
- Alternative stable states require strong interactions (pair-wise competitive exclusion) to generically manifest. Is this the case in natural systems that present abrupt transitions?