Stochastic Population Dynamics:
Persistence, Extinction, and Quasi-stationarity

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Focus and Structure of Tutorial

Mathematically, focus on discrete-time stochastic models.

Go to MS 34, Monday 8:30–10:00am, for continuous-time models

Dang Nguyen Hai (8:30am) on Stochastic Differential Equations

Alex Hening (8:55am) and Edouard Strickler (9:20am) on Piecewise Deterministic Markov Processes

Mads Hansen (9:45am) on quasi-stationarity for continuous-time Markov chains

Today: Three parts (~ 35 minutes each $+5$ minute breaks)

I. Environmental Stochasticity for single species

II. Environmental stochasticity for interacting species

III. Demographic stochasticity and quasi-stationarity


KISS
ROCK AND ROLL OVER

COMMENTARII
ACADEMIAE
SCIENTIARVM
IMPERIALIS
PETROPOLITANAE.

TOMVS V.

AD ANNOS cIↄ Iↄcc xxx. et cIↄ Iↄccxxxi.

PETROPOLI,

TYPIS ACADEMIAE.

SPECIMEN

THEORIAE NOVAE

DE

MENSVRA SORTIS.

AVCTORE

Daniele Bernoulli.

1.

"*these terms should then be multiplied together. Then of this product a root must be extracted the degree of which is given by the number of all possible cases*" Stearns [2000]

If $\mathbb{P}[f(0) = f_i] = \frac{1}{k}$, then

$$\exp(r) = \sqrt[k]{f_1 f_2 \ldots f_k}$$

Geometric mean

ON POPULATION GROWTH IN A RANDOMLY VARYING ENVIRONMENT

BY R. C. LEWONTIN AND D. COHEN*

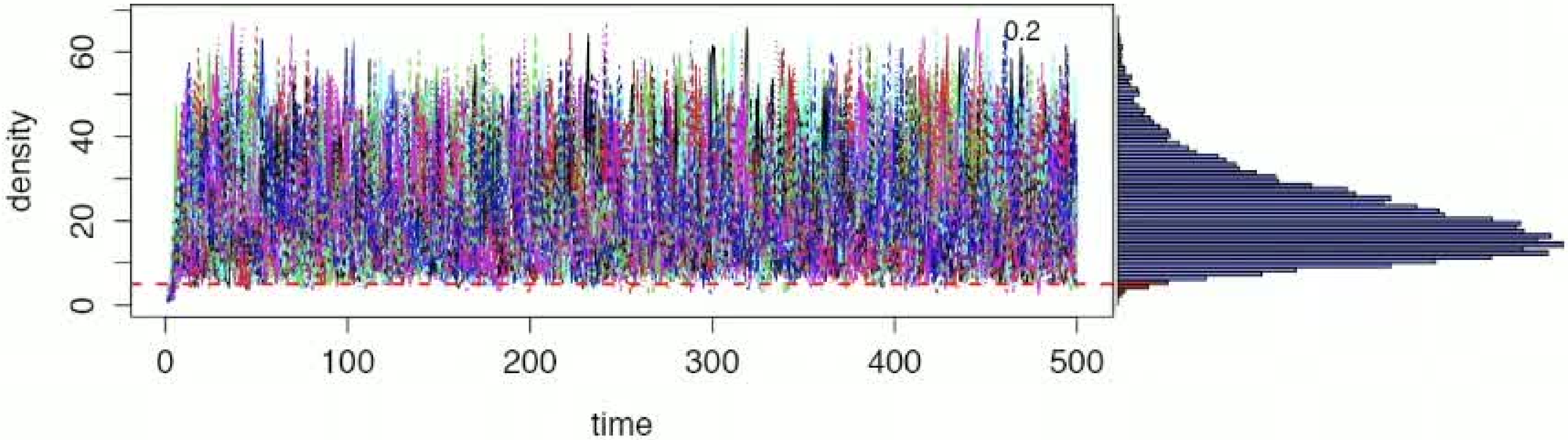
DEPARTMENT OF BIOLOGY, UNIVERSITY OF CHICAGO; AND DEPARTMENT OF BOTANY, HEBREW UNIVERSITY, JERUSALEM

Communicated February 10, 1969

Abstract.—If a population is growing in a randomly varying environment, such that the finite rate of increase per generation is a random variable with no serial autocorrelation, the logarithm of population size at any time t is normally distributed. Even though the expectation of population size may grow infinitely large with time, the probability of extinction may approach unity, owing to the difference between the geometric and arithmetic mean growth rates.

"Anyone who believes exponential growth can go on forever in a finite world is either a madman or an economist" – Kenneth Boulding, economist and President Kennedy's Environmental Advisor

$$X(t+1) = f(X(t), \xi(t))X(t) \quad \xi(1), \xi(2), \ldots \text{ i.i.d.} \qquad (\bigstar)$$

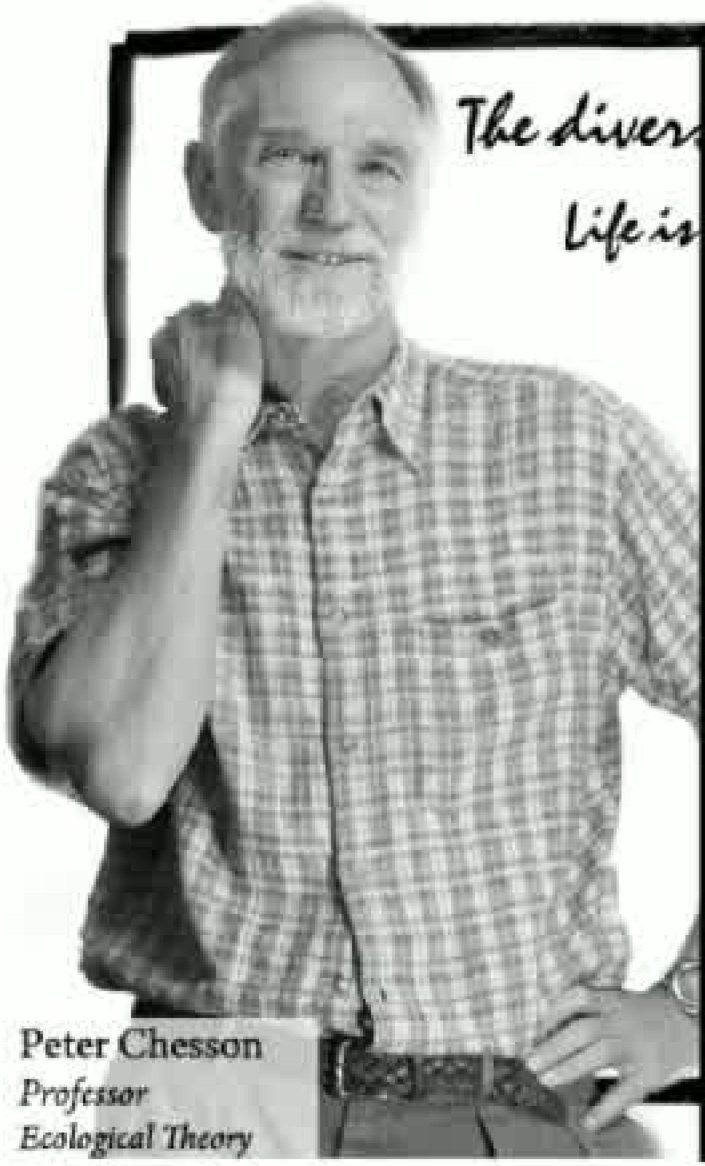


Stochastic persistence in probability [Chesson, 1982, Ellner, 1984]: For all $\varepsilon > 0$, there is a $\delta > 0$ such that

$$\limsup_{t \to \infty} \mathbb{P}[X(t) \le \delta | X(0) = x] \le \varepsilon$$

whenever $X_0 = x > 0$.

arbitrarily unlikely to be below arbitrarily small densities far into the future



"This criterion requires that the probability of observing a population below any given density, should converge to zero with density, uniformly in time. Consequently it places restrictions on the expected frequency of fluctuations to low population levels. Given that fluctuations in the environment will continually perturb population densities, it is to be expected that any nominated population density, no matter how small, will eventually be seen. Indeed this is the usual case in stochastic population models and is not an unreasonable postulate about the real world. Thus a reasonable persistence criterion cannot hope to do better than place restrictions on the frequencies with which such events occur."

Density-dependent models

$$X(t+1) = f(X(t), \xi(t))X(t) \quad \xi(1), \xi(2), \ldots \text{ i.i.d.} \qquad (\bigstar)$$

When do we get persistence? If $X(0) \approx 0$ but positive, then

$$X(t) \approx \prod_{s=0}^{t-1} f(0, \xi(s))X(0) \Rightarrow r = \mathbb{E}[\log f(0, \xi(1))]$$

Theorem [Ellner, 1984, Gyllenberg et al., 1994, Benaïm and Schreiber, 2019] If $r > 0$, then $(\bigstar)$ is stochastically persistent almost surely and in probability. If $r < 0$, then for all $\varepsilon > 0$ there is a $\delta > 0$ s.t.

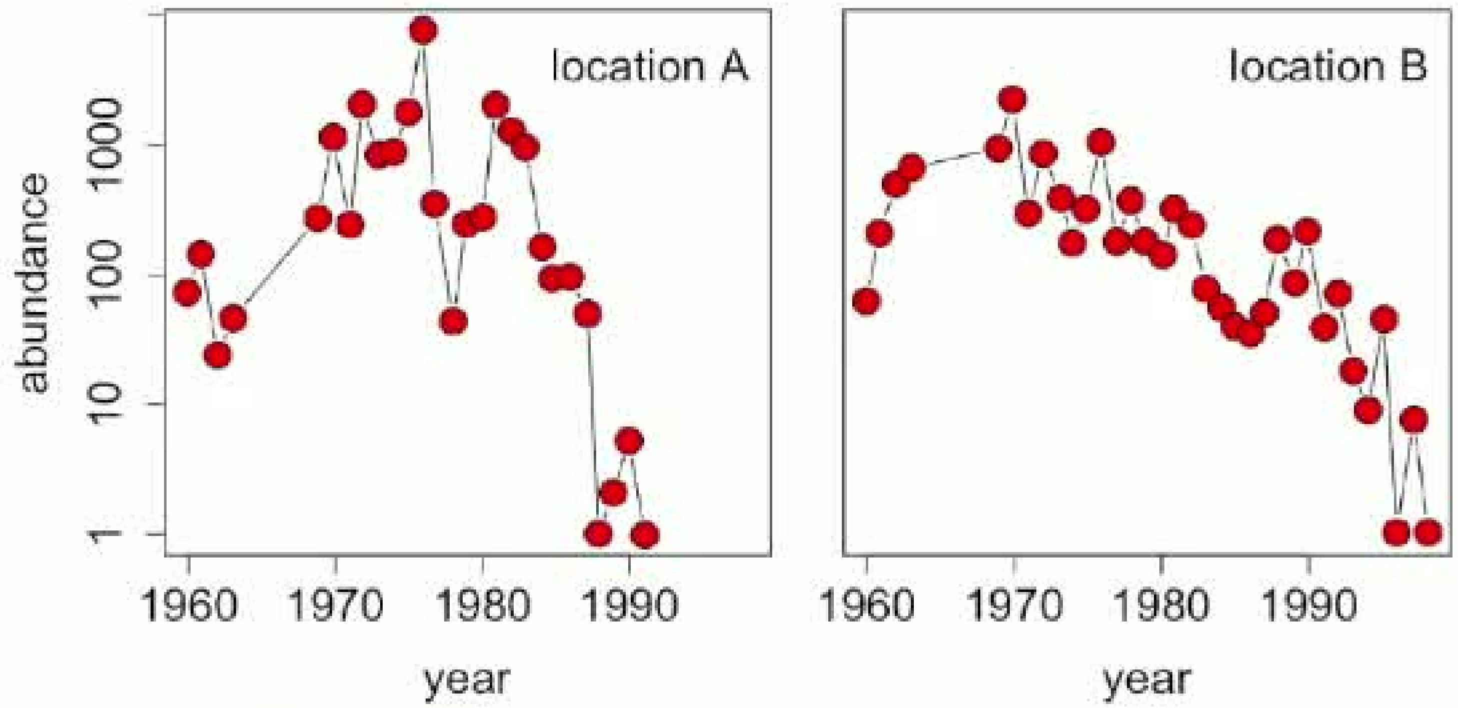
$$\mathbb{P}[\lim_{t\to\infty} \frac{1}{t} \log X(t) = r | X(0) = x] \geq 1 - \varepsilon \text{ for } x \in (0, \delta)$$

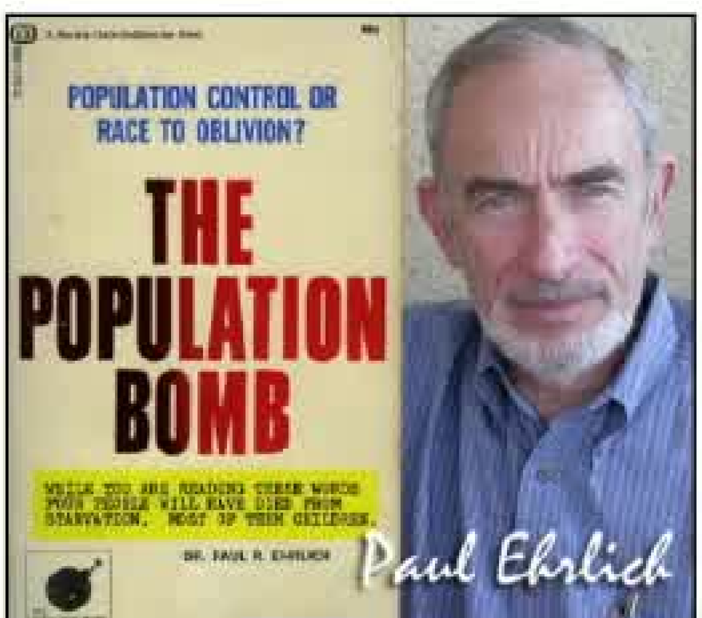
If $x = 0$ is accessible (see Benaïm and Schreiber [2019]) & $r < 0$, then $\lim_{t\to\infty} \frac{1}{t} \log X(t) = -r$ with probability one for $X(0) > 0$.

Climate induced extinction?

Bay checkerspot

2 checkerspot populations went extinct in 1990s





Paul Ehrlich

Climate induced extinction?

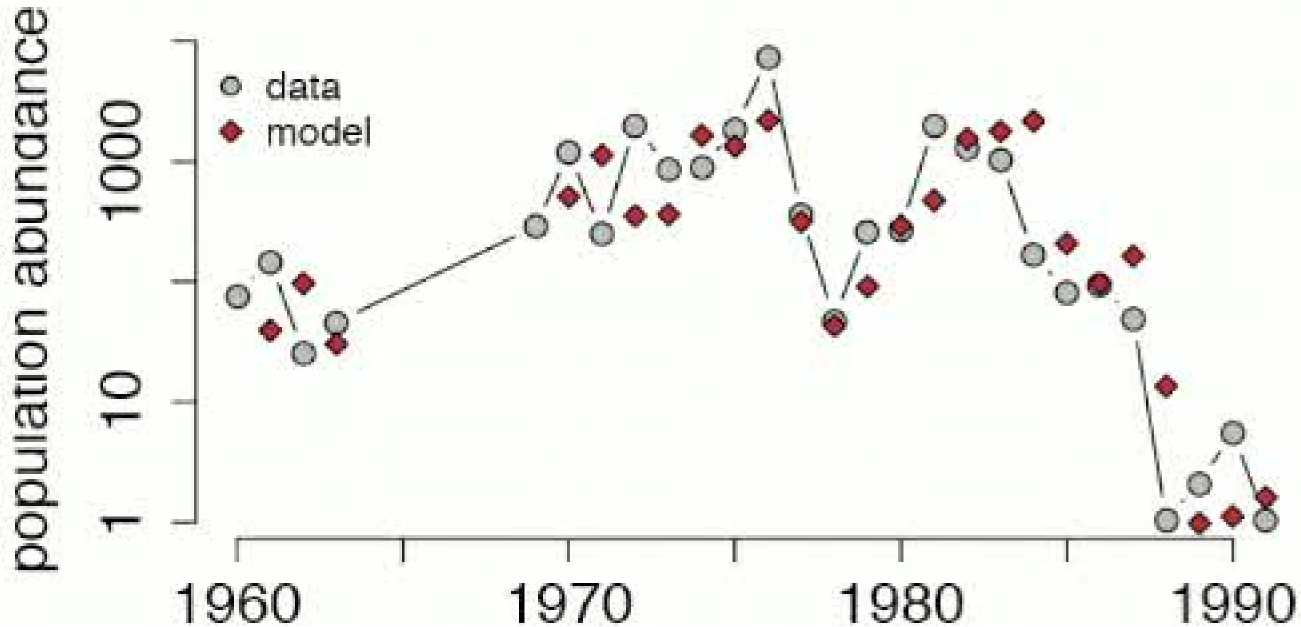
Bay checkerspot

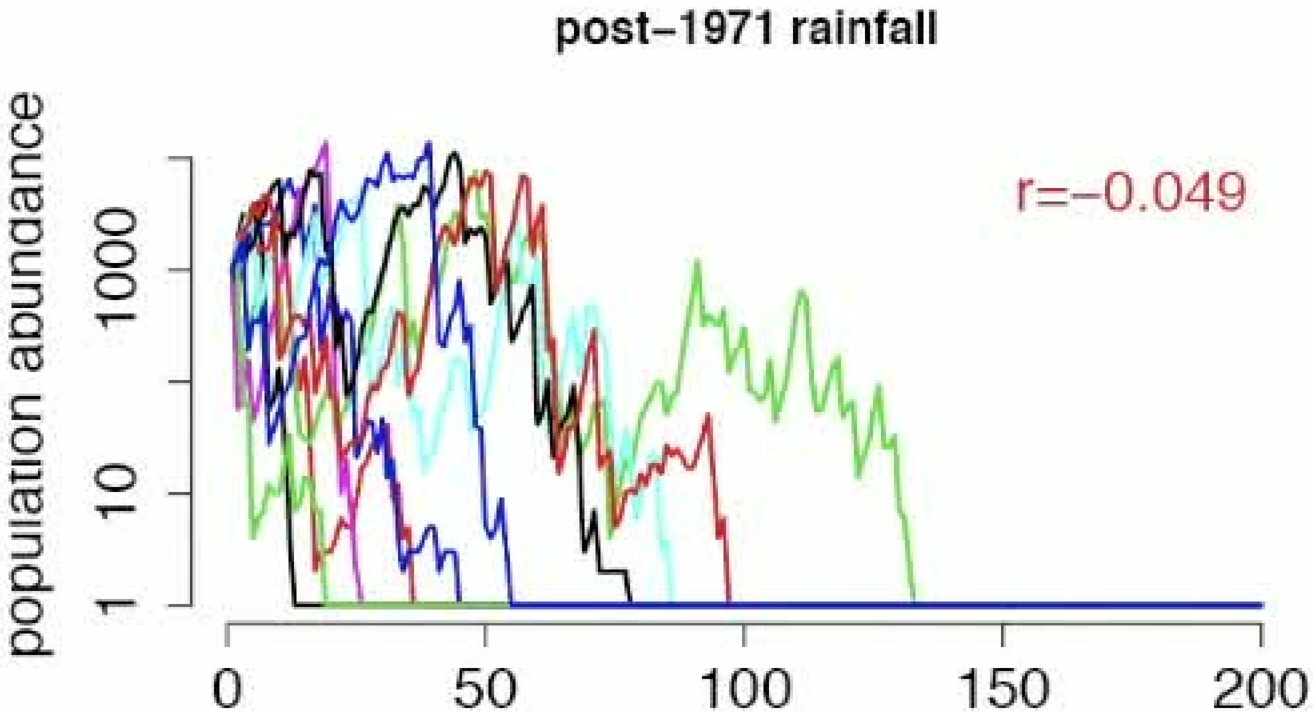
2 checkerspot populations went extinct in 1990s

A simplified version of McLaughlin et al. [2002]:

$$X(t+1) = X(t)\exp(a_0 + a_1 X(t) + a_2 \xi(t)^{\theta_2})$$

w/ $\xi(t) =$ precipitation. Here $r = \mathbb{E}[a_0 + a_1 \xi(t)^{\theta_2}]$





Two approaches to showing uniqueness of μ_+:

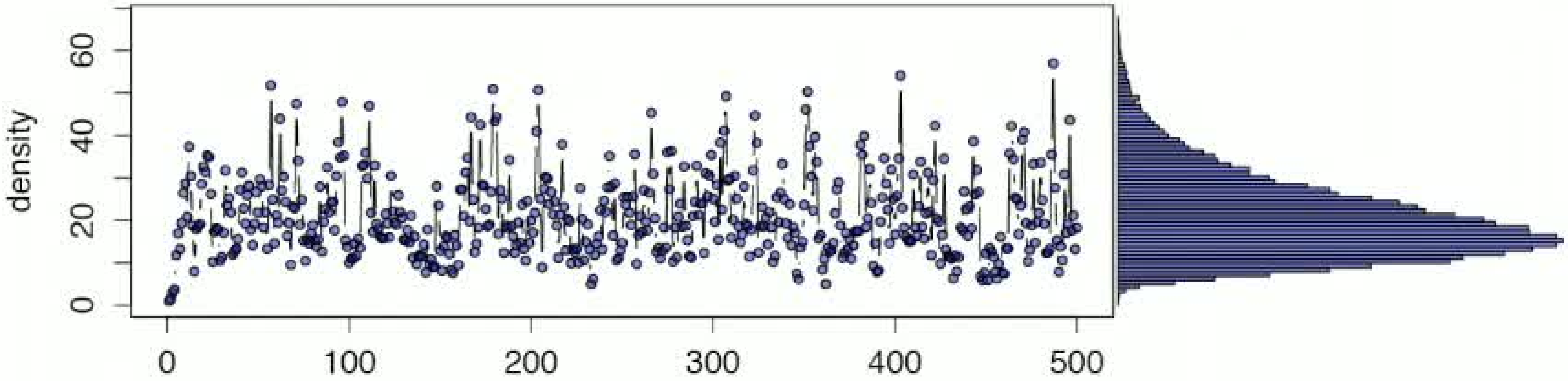
Monotonicity [Ellner, 1984, Chueshov, 2002]: $x \mapsto xf(x,\xi)$ increasing

Irreducibility [Meyn and Tweedie, 2009, Schreiber et al., 2011]: $\mathbb{P}[X(t) \in A | X(0) = x] \geq \nu(A)$ for all $x > 0$, some $t \geq 1$, and some probability measure ν on $(0, \infty)$

Both of approaches extend to higher dimensions.

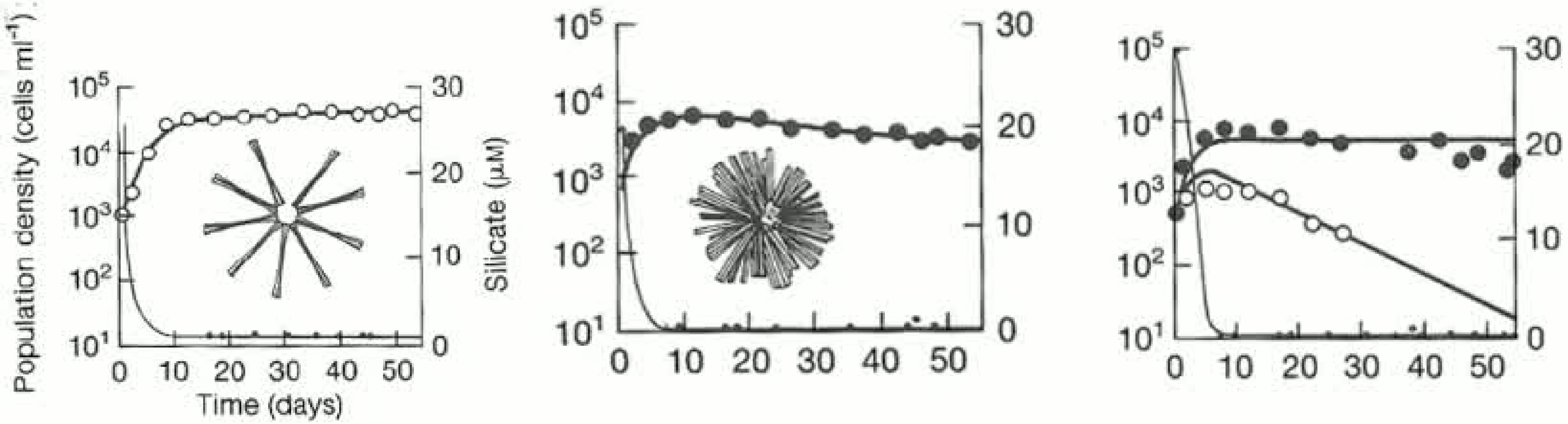
For PDMPs, there exist Lie bracket conditions on the vector fields

See talks by Alex Hening (8:55am) and Eduoard Stricker (9:20am) in Monday session MS34



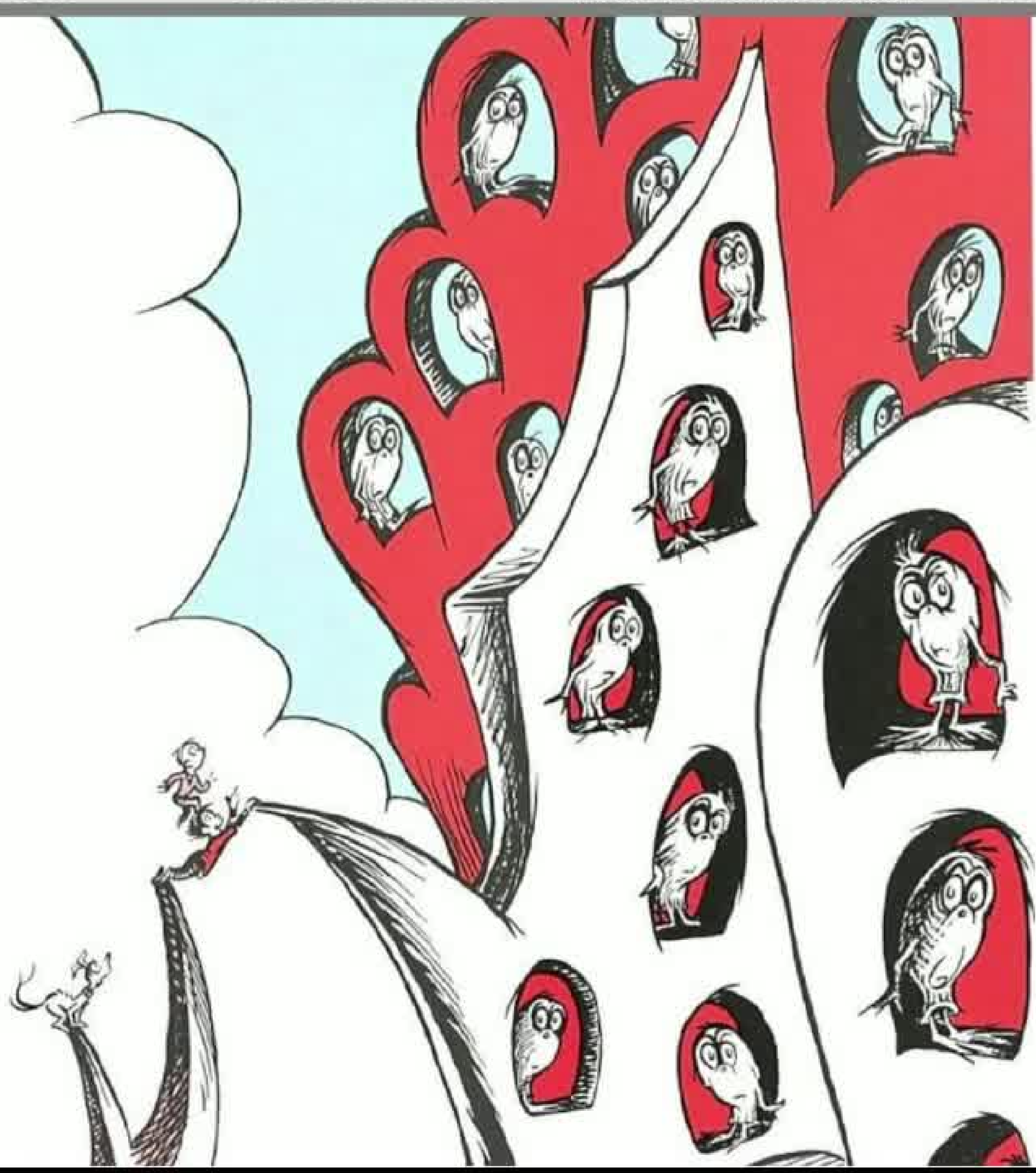



The R^* rule [Volterra, 1926, Tilman, 1977]: The competitor that suppresses a single limiting resource to the lowest equilibrium value excludes all other competitors.



Competitive exclusion principle [McGehee and Armstrong, 1977]: At most k species can coexist at a stable equilibrium on k limiting resources.

Paradox of the plankton [Hutchinson, 1961]: "The diversity … was explicable primarily by a permanent failure to achieve equilibrium as the relevant external factors changed."

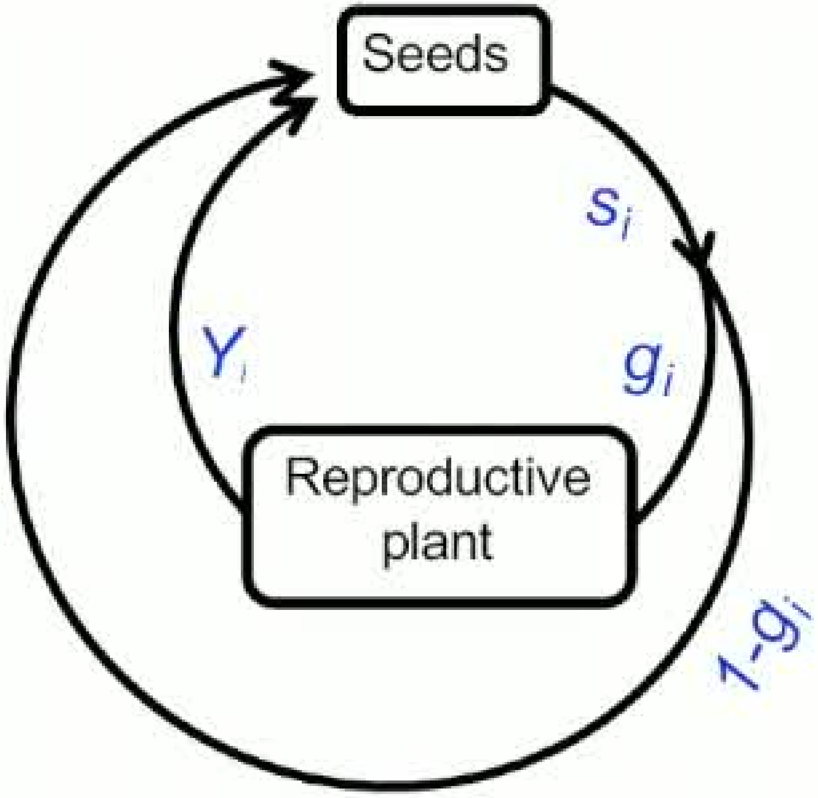


"And NUH is the letter I use to spell Nutches, Who live in small caves, known as Niches, for hutches. These Nutches have troubles, the biggest of which is the fact there are many more Nutches than Niches. Each Nutch in a Nich knows that some other Nutch Would like to move into his Nich very much. So each Nutch in a Nich has to watch that small Nich or Nutches who haven't got Niches will snitch."

Dr. Seuss

On Beyond the Zebra

Annual plant model



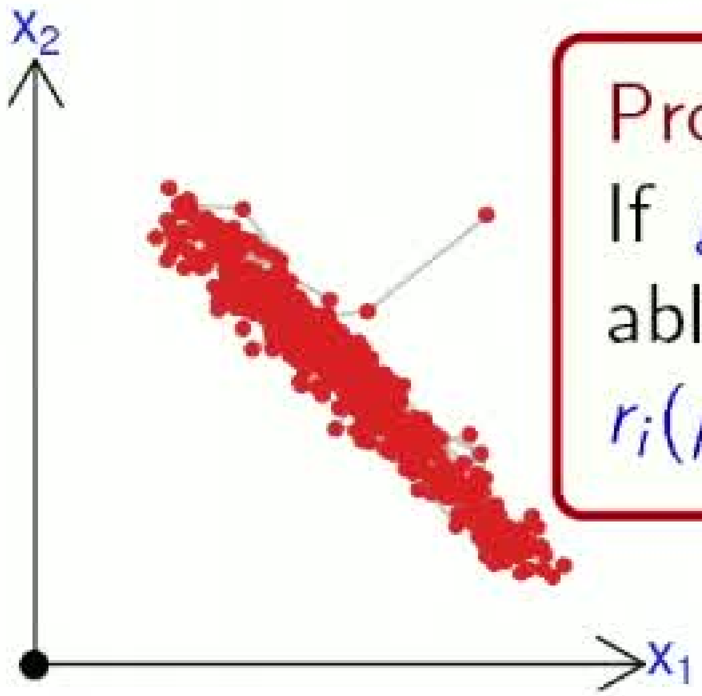
$X_i(t)$ seed density of species i

$s_1 = s_2$ seed survival

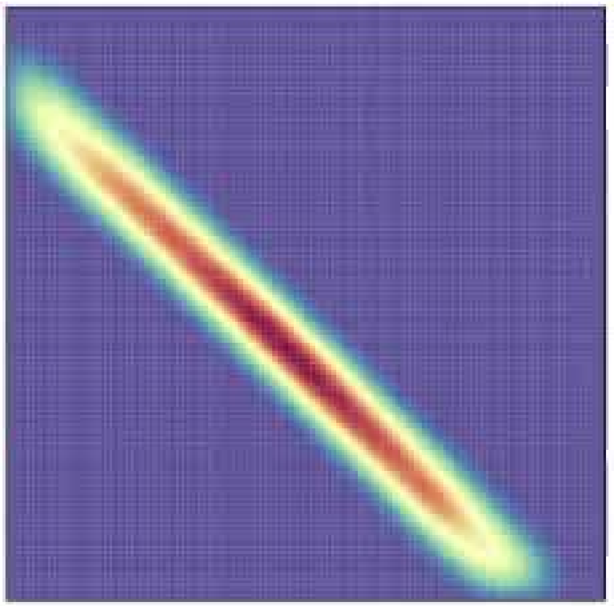
$g_i(t)$ germination probability of species i

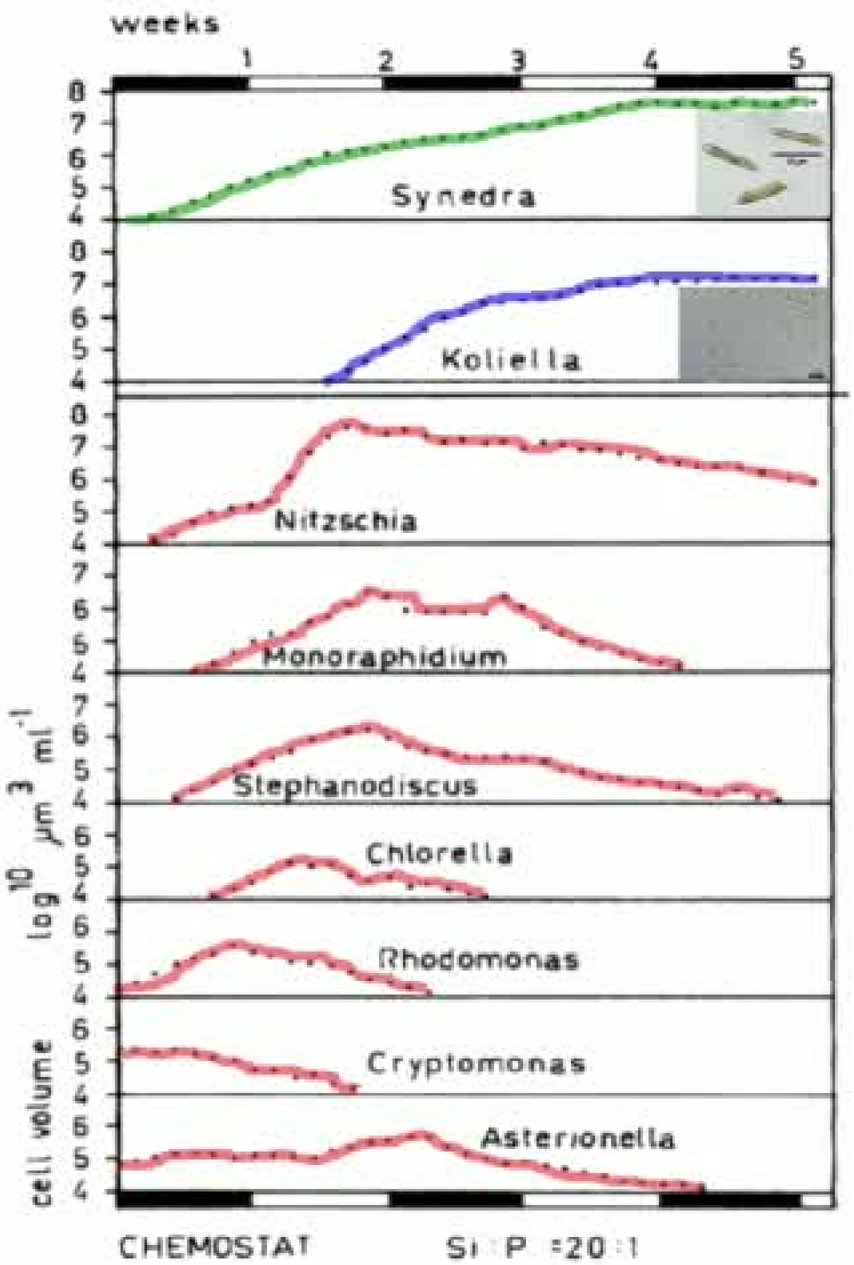
$Y_1 = Y_2$ yield of a plant

$$X_i(t+1) = X_i(t)\left(\frac{Y_i g_i(t) s_i}{1+\sum_{j=1}^{2} g_j(t) s_j X_j(t)} + (1-g_i(t))s_i\right)$$

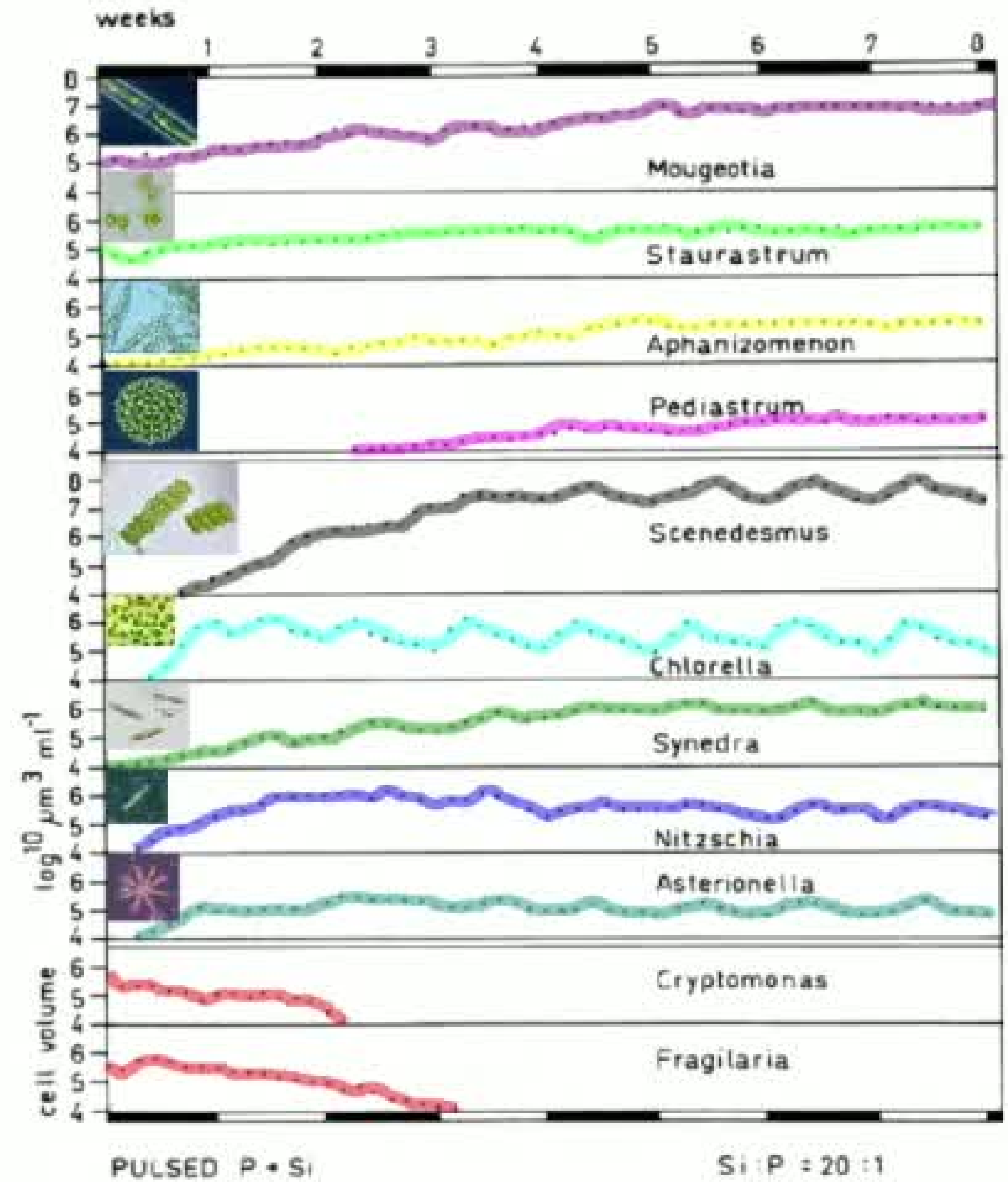


Proposition [Chesson, 1988]:
If $g_1(t)$,$g_2(t)$ are exchangeable and $\mathrm{Var}[g_1(t)] > 0$, then $r_i(\mu_j) > 0$ for $j \neq i$.





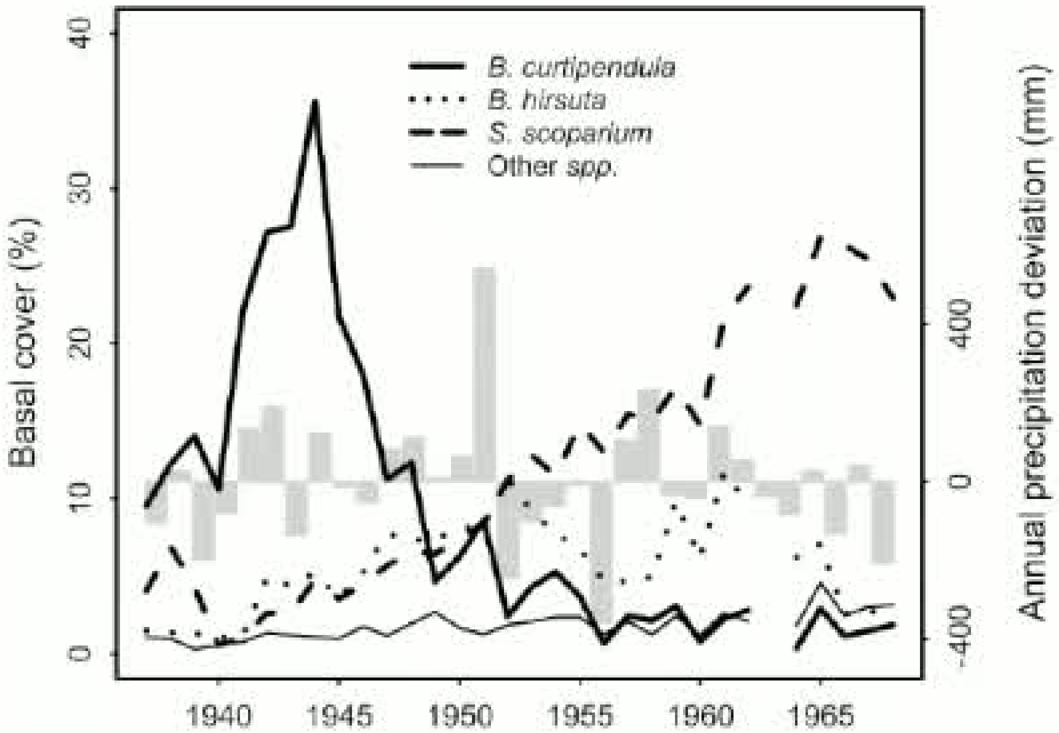
Constant inflow of Si and P



Fluctuating inflow of Si and P

Sommer [1984]

Storage in Kansas prairies [Adler et al., 2006]



Fit a stochastic model using a hierarchal Bayesian approach

Computed r_i for stochastic and deterministic environments

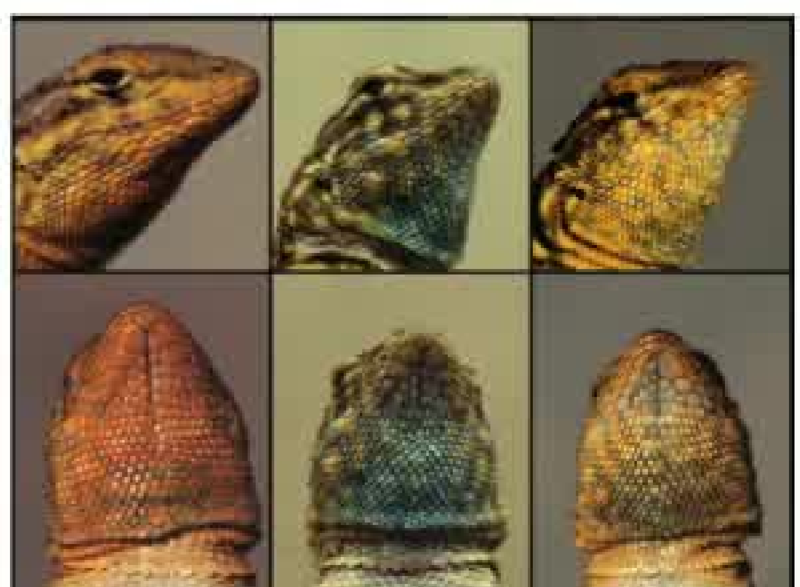
The childhood game

Cryptic coral reef communities

Buss & Jackson Am. Nat. 1979

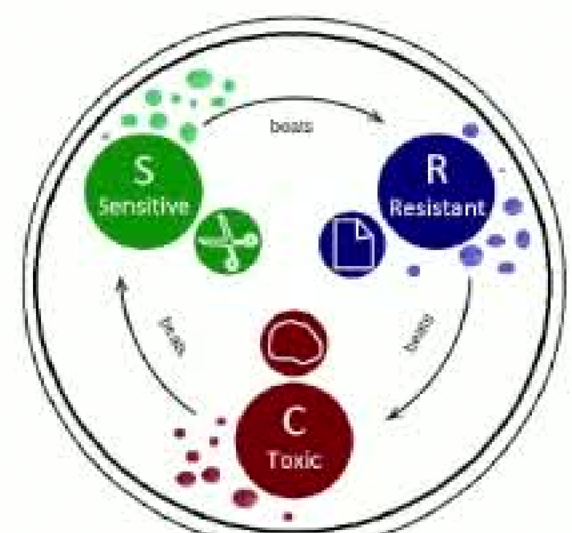
Side-blotched lizards

Sinervo & Lively Nature 1996



Chemical warfare in *E. coli*

Kerr et al. Nature 2003



Lest **biologists** suspect your **model** untrue, Keep probability in view.

> *Populations are far from the continuous matter, or flows, or fields of classical mathematical physics. They are essentially discrete and built up by individuals, who may show great variation in behavior.* Jagers [2010]

> *Demographic stochasticity describes the random fluctuations in the population size that occur because the birth and death of each individual is a discrete and probabilistic event.* –Brett Melbourne (2012)

Demographic stochasticity is typically modeled with Markov chains $X(t)$ on a countable state space $\mathcal{S}$

Dynamics determined by the transition matrix
$P_{xy} = \mathbb{P}[X(t+1) = y | X(t) = x]$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Branching processes

$X(t) \in \{0, 1, 2, 3, \dots\} = \mathbf{Z}_+$ # of individuals in population

offspring distribution: p_k probability individual has k offspring

$$X(t+1) = Y_1(t+1) + Y_2(t+1) + \cdots + Y_{X(t)}(t+1) \qquad (\star)$$

where $Y_i(t+1)$ are independent with $\mathbb{P}[Y_i(t) = k] = p_k$

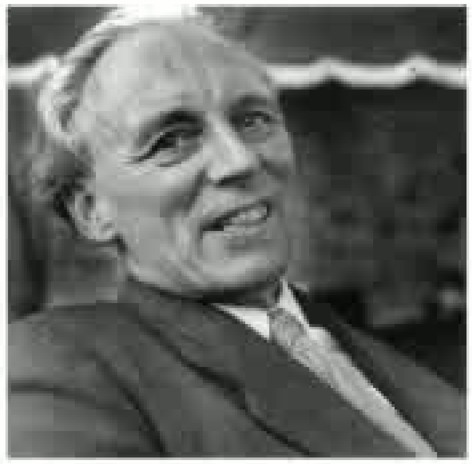
Limit Theorem Athreya and Ney [2004] Assume mean number of offspring $R_0 = \sum_{k\geq 0} kp_k < +\infty$ and $p_0 > 0$. If $R_0 \leq 1$, then

$$\mathbb{P}[X(t) = 0 \text{ for some } t \geq 1 | X(0) = 1] = 1$$

If $R_0 > 1$, then

$$s^* = \mathbb{P}[X(t) = 0 \text{ for some } t \geq 1 | X(0) = 1] < 1$$

and is the minimal solution to $s = \sum_k p_k s^k$ for $s \in [0, 1]$.



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Any population allowing individual variation in reproduction, ultimately dies out–unless it grows beyond all limits, an impossibility in a bounded world.

Jagers [2010]

Example: Host-Parasitoid Dynamics

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Parasitoid: An organism that, during its development, lives in or on the body of a single host individual, eventually killing that individual.

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Example: Host-Parasitoid Dynamics

1995: Herren

SHARE

Dr. Hans Rudolf Herren

SWITZERLAND

DR. HANS RUDOLF HERREN, recipient of the 1995 World Food Prize, was only 31 years old when he took a new job in Africa and landed right in the middle of an unprecedented crisis: an insect, the cassava mealybug, was devastating the continent's staple crops, and widespread hunger was emerging as a real possibility. Within ten years, Dr. Herren had almost single-handedly developed a chemical-free biological control for the mealybug, eliminated the threat to cassava production, averted disastrous famine, and saved upward of 20 million lives.

Resampling from the Past [Aldous et al., 1988]

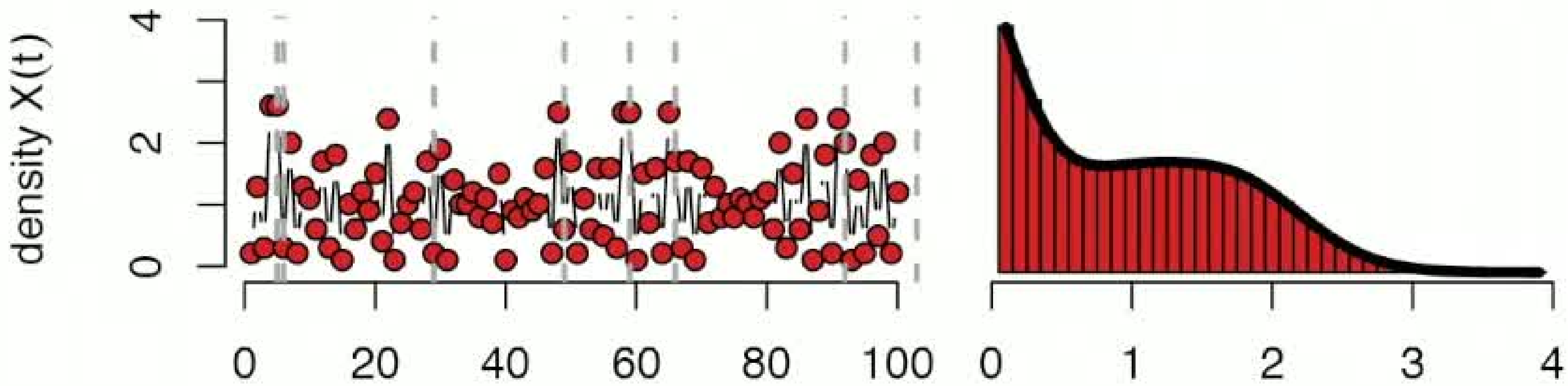
To approximate QSD, define $Y(t)$ on $\mathcal{S}_+$ by:

- Choose $\widetilde{Y}$ according to $\mathbb{P}[\widetilde{Y} = y | Y(t) = x]$
- If $\widetilde{Y} \in \mathcal{S}_+$, set $Y(t+1) = \widetilde{Y}$
- If $\widetilde{Y} \in \mathcal{E}$, then update $Y(t+1)$ according to

$$\mathbb{P}[Y(t+1) = y] = \frac{\#\{0 \leq s \leq t : Y(s) = y\}}{t+1}$$

Aldous et al. [1988] proved that

$$\lim_{t\to\infty} \frac{\#\{0 \leq s \leq t-1 : Y(s) = x\}}{t} = \pi(x) \text{ with probability one}$$



California Annuals in Serpentine Soils ($k = 2$)

λ_i maximal per-capita seed production of species i
α_{ij} competitive effect of species j on species i

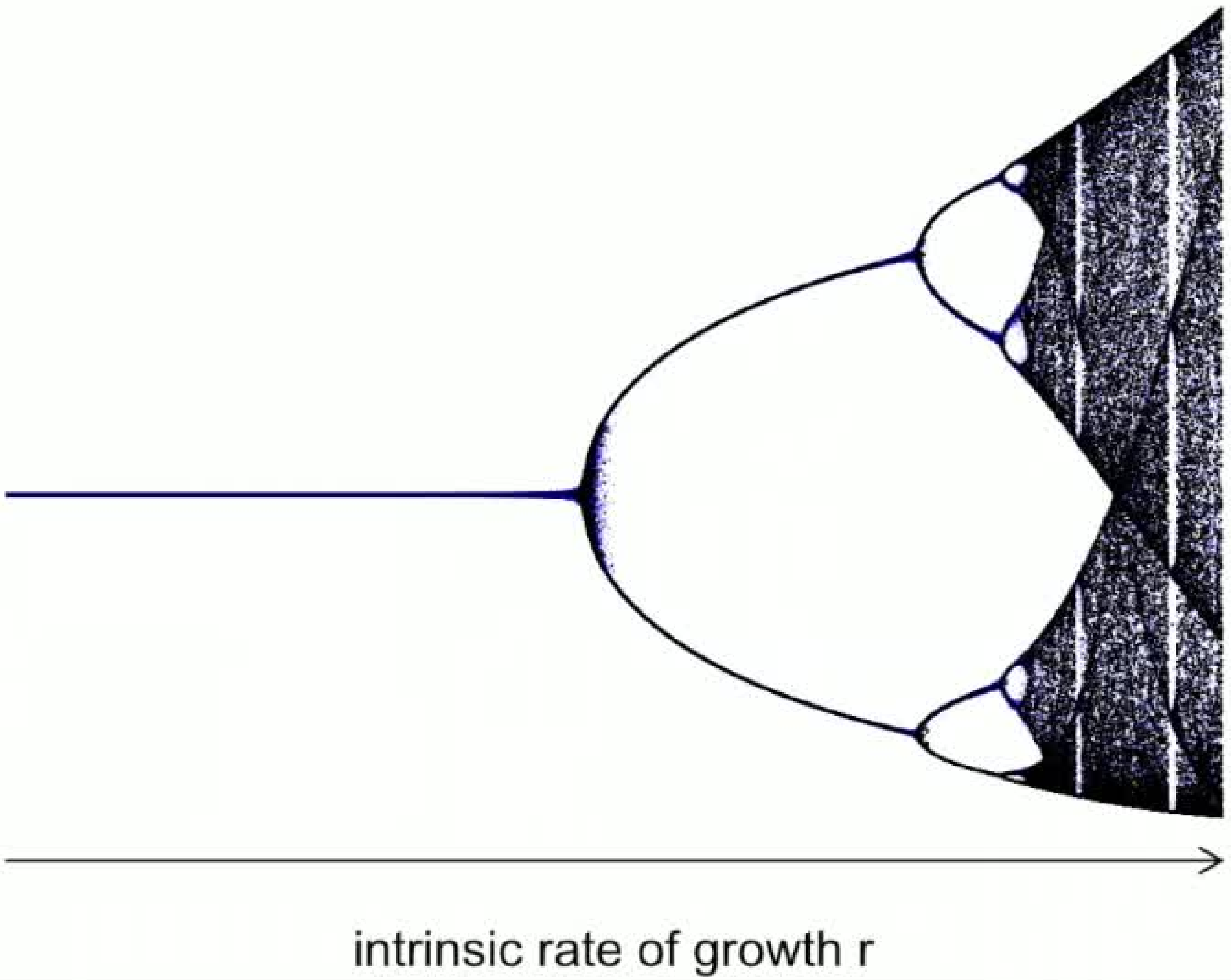
$$x_1(t+1) = x_1(t)\frac{\lambda_1}{1 + \alpha_{11}x_1(t) + \alpha_{12}x_2(t)}$$
$$x_2(t+1) = x_2(t)\frac{\lambda_2}{1 + \alpha_{22}x_2(t) + \alpha_{21}x_1(t)}$$

Schreiber et al. [2018]



Revenge of the Ricker ($k = 1$)

$x_{t+1} = x_t \exp(r(1 - x_t))$. Kozlovski [2003] $\Rightarrow$ an open and dense set of positive r values satisfying Theorem's assumptions



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Parasitoid: An organism that, during its development, lives in or on the body of a single host individual, eventually killing that individual.