To persist or not to persist?
On the mathematics of species coexistence

Sebastian Schreiber
Department of Evolution and Ecology
and Center for Population Biology
University of California, Davis
What are the minimal conditions to ensure the long-term persistence of an ecological community? Models have been useful...
What are the **minimal conditions** to ensure the long-term persistence of an ecological community?
What are the minimal conditions to ensure the long-term persistence of an ecological community?

Models have been useful...
\[
\frac{dN_1}{dt} = r_1 N_1 (1 - \alpha_{11} N_1 - \alpha_{12} N_2)
\]
\[
\frac{dN_2}{dt} = r_2 N_2 (1 - \alpha_{22} N_2 - \alpha_{21} N_1)
\]
\[
\frac{dN}{dt} = r N (1 - N/K) - \frac{aNP}{1 + bN}
\]
\[
\frac{dP}{dt} = \frac{cNP}{1 + bN} - dP
\]
\[ X_{t+1}^i = A_i(\xi_{t+1}, X_t)X_t^i \]
What are the minimal conditions to ensure the long-term persistence of an ecological community?
What are the **minimal conditions** to ensure the long-term persistence of an ecological community?

\[
\frac{dx^i}{dt} = r_i(x) x^i \text{ where } x = (x^1, \ldots, x^n)
\]

The presence or the absence of a species is sometimes the point of interest regardless of some variation in their numbers. – Richard Lewontin on The Meaning of Stability
What are the **minimal conditions** to ensure the long-term persistence of an ecological community?

\[
\frac{dx^i}{dt} = r_i(x) \cdot x^i \quad \text{where } x = (x^1, \ldots, x^n)
\]

\[
\frac{dX^i}{dt} = A_i(X) \cdot X^i \quad \text{where } X^i = (X^{i1}, \ldots, X^{ik_i})^T
\]
What are the minimal conditions to ensure the long-term persistence of an ecological community?

\[
\frac{dx^i}{dt} = r_i(x)x^i \quad \text{where } x = (x^1, \ldots, x^n)
\]

\[
\frac{dX^i}{dt} = A_i(X)X^i \quad \text{where } X^i = (X^{i1}, \ldots, X^{ik_i})^T
\]

\[
X^i_{t+1} = A_i(X_t)X^i_t \quad \text{where } X = (X^1, \ldots, X^n)
\]
What are the **minimal conditions** to ensure the long-term persistence of an ecological community?

per-capita growth  
\[
\frac{dx^i}{dt} = r_i(x)x^i \quad \text{where } x = (x^1, \ldots, x^n)
\]

density of species \(i\)

matrices  
\[
\frac{dX^i}{dt} = A_i(X)X^i \quad \text{where } X^i = (X^{i1}, \ldots, X^{ik_i})^T
\]

stationary sequence of random variables  
\[
X^i_{t+1} = A_i(\xi_{t+1}, X_t)X^i_t \quad \text{where } X = (X^1, \ldots, X^n)
\]
What are the **minimal conditions** to ensure the long-term persistence of an ecological community?

\[
\frac{dx^i}{dt} = r_i(x)x^i
\]

where \( x = (x^1, \ldots, x^n) \)

\[
\frac{dX^i}{dt} = A_i(X)X^i
\]

where \( X^i = (X^{i1}, \ldots, X^{ik_i})^T \)

stationary sequence of random variables

\[
X^i_{t+1} = A_i(\xi_{t+1}, X_t)X_t^i
\]

where \( X = (X^1, \ldots, X^n) \)

“The presence or the absence of a species is sometimes the point of interest regardless of some variation in their numbers.” — Richard Lewontin on *The Meaning of Stability*
How do species interactions and population structure impact species coexistence?
  – keystone predation
  – spatial heterogeneity

How does demographic and environmental stochasticity impact species coexistence?
  – metastability
  – storage effect
How do species interactions and population structure impact species coexistence?
  – keystone predation
  – spatial heterogeneity

How does demographic and environmental stochasticity impact species coexistence?
  – metastability
  – storage effect
Consider \( n \) species modeled by

\[
\frac{dx^i}{dt} = x^i r_i(x) \quad i = 1, \ldots, n
\]

per-capita growth of species \( i \)
Consider \( n \) species modeled by

\[
\frac{dx_i}{dt} = x_i^i r_i(x) \quad i = 1, \ldots, n \quad x_t = (x_t^1, \ldots, x_t^n)
\]

per-capita growth of species \( i \) solution with initial condition \( x_0 \)
Consider $n$ species modeled by

$$\frac{dx^i}{dt} = x^i r_i(x) \quad i = 1, \ldots, n \quad x_t = (x_t^1, \ldots, x_t^n)$$

per-capita growth of species $i$

solution with initial condition $x_0$

Assume to be dissipative: there is $M > 0$ such that for any $x_0, i$

$$x_t^i \leq M \text{ whenever } t \text{ sufficiently large}$$
Consider $n$ species modeled by

$$\frac{dx^i}{dt} = x^i r_i(x) \quad i = 1, \ldots, n \quad x_t = (x_t^1, \ldots, x_t^n)$$

per-capita growth of species $i$ \hspace{1cm} solution with initial condition $x_0$

Assume to be **dissipative**: there is $M > 0$ such that for any $x_0$, $i$

$$x_t^i \leq M \text{ whenever } t \text{ sufficiently large}$$

**cooperative**, permanent or uniformly persistent: there is $m > 0$ such that whenever $\prod_i x_0^i > 0$,

$$x_t^i \geq m \text{ for all } i \text{ and } t \text{ sufficiently large}$$

Schuster, Sigmund, Wolff (1979) JDE
Consider \( n \) species modeled by

\[
\frac{dx^i}{dt} = x^i r_i(x) \quad i = 1, \ldots, n \\
x_t = (x^1_t, \ldots, x^n_t)
\]

per-capita growth of species \( i \) \hspace{1cm} \text{solution with initial condition } x_0

Assume to be dissipative: there is \( M > 0 \) such that for any \( x_0, i \)

\[
x^i_t \leq M \text{ whenever } t \text{ sufficiently large}
\]

cooperative, permanent or uniformly persistent: there is \( m > 0 \) such that whenever \( \prod_i x^i_0 > 0 \),

\[
x^i_t \geq m \text{ for all } i \text{ and } t \text{ sufficiently large}
\]

Schuster, Sigmund, Wolff (1979) JDE; Butler & Waltman (1986) JDE
Consider $n$ species modeled by

$$\frac{dx^i}{dt} = x^i r_i(x) \quad i = 1, \ldots, n \quad x_t = (x^1_t, \ldots, x^n_t)$$

per-capita growth of species $i$ \hspace{1cm} solution with initial condition $x_0$

Assume to be dissipative: there is $M > 0$ such that for any $x_0$, $i$

$$x^i_t \leq M \text{ whenever } t \text{ sufficiently large}$$

cooperative, permanent or uniformly persistent: there is $m > 0$ such that whenever \(\prod_i x^i_0 > 0\),

$$x^i_t \geq m \text{ for all } i \text{ and } t \text{ sufficiently large}$$

Robustly permanent if robust to perturbations of $r_i$.

Schuster, Sigmund, Wolff (1979) JDE; Butler & Waltman (1986) JDE
Consider $n$ species modeled by

$$\frac{dx^i}{dt} = x^i r_i(x) \quad i = 1, \ldots, n \quad x_t = (x_t^1, \ldots, x_t^n)$$

per-capita growth of species $i$  

solution with initial condition $x_0$

Assume to be **dissipative**: there is $M > 0$ such that for any $x_0$, $i$

$$x^i_t \leq M$$

whenever $t$ sufficiently large

**cooperative, permanent or uniformly persistent**: there is $m > 0$

such that whenever $\prod_i x^i_0 > 0$,

$$x^i_t \geq m$$

for all $i$ and $t$ sufficiently large

**Robustly permanent** if robust to perturbations of $r_i$.

persist despite large pulsed perturbations

and small, long-term perturbations

Schuster, Sigmund, Wolff (1979) JDE; Butler & Waltman (1986) JDE
Suppose $x_0^i = 0$

$$\frac{dz^i}{dt} = r_i(x_t)z^i$$
Suppose $x_0^i = 0$

$$\frac{dz^i}{dt} = r_i(x_t)z^i \Rightarrow \log z^i_t = \log z^i_0 + \int_0^t r_i(x_s) \, ds$$
Suppose $x^i_0 = 0$

\[
\frac{dz^i}{dt} = r_i(x_t)z^i \Rightarrow \log z^i_t = \log z^i_0 + \int_0^t r_i(x_s) \, ds
\]

Define the invasion rate when rare (IRWR) for species $i$ at $x_0$

\[
\bar{r}_i(x_0) := \limsup_{t \to \infty} \frac{1}{t} \int_0^t r_i(x_s) \, ds
\]
Suppose $x_0^i = 0$

$$\frac{dz^i}{dt} = r_i(x_t)z^i \Rightarrow \log z_t^i = \log z_0^i + \int_0^t r_i(x_s) \, ds$$

Define the inversion rate when rare (IRWR) for species $i$ at $x_0$

$$\bar{r}_i(x_0) := \limsup_{t \to \infty} \frac{1}{t} \int_0^t r_i(x_s) \, ds$$

$\bar{r}(x_0) > 0 \Rightarrow$ species $i$ increases when introduced at low densities.
Suppose $x_0^i = 0$

\[
\frac{dz^i}{dt} = r_i(x_t)z^i \Rightarrow \log z_t^i = \log z_0^i + \int_0^t r_i(x_s) \, ds
\]

Define the invasion rate when rare (IRWR) for species $i$ at $x_0$

\[
\bar{r}_i(x_0) := \limsup_{t \to \infty} \frac{1}{t} \int_0^t r_i(x_s) \, ds
\]

$\bar{r}(x_0) > 0 \Rightarrow$ species $i$ increases when introduced at low densities.

**Theorem** If there exist positive weights $p_1, \ldots, p_n$ such that

\[
\sum_{i=1}^n p_i \bar{r}_i(x_0) > 0
\]

for all $x_0$ with $\prod_i x_0^i = 0$, then the system is permanent. If the inequality is reversed, the extinction set is an attractor. Hofbauer (1981) Mh. Math
Suppose $x_0^i = 0$

$$\frac{dz^i}{dt} = r_i(x_t)z^i \Rightarrow \log z^i_t = \log z^i_0 + \int_0^t r_i(x_s) \, ds$$

Define the invasion rate when rare (IRWR) for species $i$ at $x_0$

$$\bar{r}_i(x_0) := \limsup_{t \to \infty} \frac{1}{t} \int_0^t r_i(x_s) \, ds$$

$$\bar{r}(x_0) > 0 \Rightarrow \text{species } i \text{ increases when introduced at low densities.}$$

**Theorem** If there exist positive weights $p_1, \ldots, p_n$ such that

$$\sum_{i=1}^n p_i \bar{r}_i(x_0) > 0$$

for all recurrent $x_0$ with $\prod_i x_0^i = 0$, then the system is **robustly** permanent. If the inequality is reversed, the extinction set is an attractor. Schreiber (2000) JDE; Garay & Hofbauer (2003) SIAM Math.Anal.
Suppose $x_0 = 0$.

Define the invasion rate when rare (IRWR) for species $i$ at $x_0$ as

$$
\overline{r}_i(x_0) := \limsup_{t \to \infty} \frac{1}{t} \int_0^t r_i(x_s) \, ds
$$

for all recurrent $x_0$ with $\prod_i x_i < 0$, then the system is robustly permanent. If the inequality is reversed, the extinction set is an attractor. Schreiber (2000) JDE; Garay & Hofbauer (2003) SIAM Math. Anal.

If the community on average increases when rare, then it persists robustly.

If there exist positive weights $p_1, \ldots, p_n$ such that $\sum_{i=1}^n p_i \overline{r}_i(x_0) > 0$, then the system is robustly permanent. If the inequality is reversed, the extinction set is an attractor.


If the community on average increases when rare, then it persists robustly.
Cryptic coral reef communities

Buss & Jackson Am. Nat. 1979
Cryptic coral reef communities

Buss & Jackson Am. Nat. 1979
Side-blotched lizards

Sinervo & Lively Nature 1996
Side-blotched lizards
Sinervo & Lively Nature 1996

Strains of E.coli
Kerr et al. Nature 2002
\[
\frac{dx^1}{dt} = x^1 \rho (1 - x^1 - (1 + c)x^2 - (1 - b)x^3)
\]
\[
\frac{dx^2}{dt} = x^2 \rho (1 - (1 - b)x^1 - x^2 - (1 + c)x^3)
\]
\[
\frac{dx^3}{dt} = x^3 \rho (1 - (1 + c)x^1 - (1 - b)x^2 - x^3)
\]
\[
\begin{align*}
\frac{dx^1}{dt} &= x^1 \rho (1 - x^1 - (1 + c)x^2 - (1 - b)x^3) \\
\frac{dx^2}{dt} &= x^2 \rho (1 - (1 - b)x^1 - x^2 - (1 + c)x^3) \\
\frac{dx^3}{dt} &= x^3 \rho (1 - (1 + c)x^1 - (1 - b)x^2 - x^3)
\end{align*}
\]
\[
\begin{align*}
\frac{dx_1}{dt} &= x_1 \rho (1 - x_1) - (1 + c)x_2 - (1 - b)x_3 \\
\frac{dx_2}{dt} &= x_2 \rho (1 - (1 - b)x_1 - x_2) - (1 + c)x_3 \\
\frac{dx_3}{dt} &= x_3 \rho (1 - (1 + c)x_1 - (1 - b)x_2 - x_3)
\end{align*}
\]
\[
\begin{align*}
\frac{dx_1}{dt} &= x_1 \rho (1 - x_1 - (1 + c)x_2 - (1 - b)x_3) \\
\frac{dx_2}{dt} &= x_2 \rho (1 - (1 - b)x_1 - x_2 - (1 + c)x_3) \\
\frac{dx_3}{dt} &= x_3 \rho (1 - (1 + c)x_1 - (1 - b)x_2 - x_3)
\end{align*}
\]
Recurrent points $\hat{x}$: $(0,0,0), (1,0,0), (0,1,0), (0,0,1)$.
Recurrent points $\hat{x}$: $(0, 0, 0)$, $(1, 0, 0)$, $(0, 1, 0)$, $(0, 0, 1)$.

want $\sum_i p_i r_i(\hat{x}) > 0$
\[
\begin{align*}
\frac{dx^1}{dt} &= x^1 \rho (1 - x^1 - (1 + c)x^2 - (1 - b)x^3) \\
\frac{dx^2}{dt} &= x^2 \rho (1 - (1 - b)x^1 - x^2 - (1 + c)x^3) \\
\frac{dx^3}{dt} &= x^3 \rho (1 - (1 + c)x^1 - (1 - b)x^2 - x^3)
\end{align*}
\]

Recurrent points \( \hat{x} \): \((0, 0, 0), (1, 0, 0), (0, 1, 0), (0, 0, 1) \).

Want \( \sum_i p_i r_i (1, 0, 0) > 0 \)
\[
\frac{dx_1}{dt} = x_1 \rho(1 - x_1 - (1 + c)x_2 - (1 - b)x_3)
\]
\[
\frac{dx_2}{dt} = x_2 \rho(1 - (1 - b)x_1 - x_2 - (1 + c)x_3)
\]
\[
\frac{dx_3}{dt} = x_3 \rho(1 - (1 + c)x_1 - (1 - b)x_2 - x_3)
\]

Recurrent points \( \hat{x} \): \((0, 0, 0), (1, 0, 0), (0, 1, 0), (0, 0, 1) \).

want \( p_1 \cdot 0 + p_2 b + p_3(-c) > 0 \)
\[
\begin{align*}
\frac{dx_1}{dt} &= x_1 \rho (1 - x_1 - (1 + c)x_2 - (1 - b)x_3) \\
\frac{dx_2}{dt} &= x_2 \rho (1 - (1 - b)x_1 - x_2 - (1 + c)x_3) \\
\frac{dx_3}{dt} &= x_3 \rho (1 - (1 + c)x_1 - (1 - b)x_2 - x_3)
\end{align*}
\]

Recurrent points \( \hat{x} \): \((0, 0, 0), (1, 0, 0), (0, 1, 0), (0, 0, 1) \).

want \( \frac{1}{3}(b - c) > 0 \)
Recurrent points \( \hat{x} \): \((0,0,0), (1,0,0), (0,1,0), (0,0,1) \).

\[
\begin{align*}
\frac{dx_1}{dt} &= x_1 \rho (1 - x_1) - x_1 (1 + c)x_2 - (1 - b)x_3 \\
\frac{dx_2}{dt} &= x_2 \rho (1 - (1 - b)x_1 - x_2) - (1 + c)x_3 \\
\frac{dx_3}{dt} &= x_3 \rho (1 - (1 + c)x_1 - (1 - b)x_2 - x_3)
\end{align*}
\]

want \( \frac{1}{3} (b - c) > 0 \)

robustly permanent if \( b > c \)
Recall the system of differential equations:

\[
\begin{align*}
\frac{dx_1}{dt} &= x_1 \rho(1 - x_1 - (1 + c)x_2 - (1 - b)x_3) \\
\frac{dx_2}{dt} &= x_2 \rho(1 - (1 - b)x_1 - x_2 - (1 + c)x_3) \\
\frac{dx_3}{dt} &= x_3 \rho(1 - (1 + c)x_1 - (1 - b)x_2 - x_3)
\end{align*}
\]

Recurrent points \( \hat{x} \): \((0, 0, 0), (1, 0, 0), (0, 1, 0), (0, 0, 1) \).

We want \( \frac{1}{3}(b - c) > 0 \)

robustly permanent if \( b > c \) and boundary is an attractor if \( c > b \)
Competitive Exclusion Principle

\[ x^i \] frequency of species \( i \) in landscape

\[ \frac{dx^i}{dt} \]
Competitive Exclusion Principle

\( x^i \) frequency of species \( i \) in landscape

\[ \frac{dx^i}{dt} = x^i b_i (1 - \sum x^j) \]

free space
Competitive Exclusion Principle

\( x^i \) frequency of species \( i \) in landscape

\[
\frac{dx^i}{dt} = x^i b_i (1 - \sum x^j) - d_i x^i
\]

free space
Competitive Exclusion Principle

\( x^i \) frequency of species \( i \) in landscape

\[
\frac{dx^i}{dt} = x^i b_i \left( 1 - \sum x^j \right) - d_i x^i
\]

free space

If \( b_1/d_1 > b_i/d_i > 1 \) for \( i \geq 2 \),
Competitive Exclusion Principle

\( x^i \) frequency of species \( i \) in landscape

\[
\frac{dx^i}{dt} = x^i b_i \left( 1 - \sum x^j \right) - d_i x^i
\]

free space

If \( b_1/d_1 > b_i/d_i > 1 \) for \( i \geq 2 \), then

\[
\lim_{t \to \infty} (x_1^t, \ldots, x_n^t) = (1 - d_1/b_1, 0, 0, \ldots, 0)
\]

whenever \( x_0^1 > 0 \).
Competitive Exclusion Principle

\[ x^i \] frequency of species \( i \) in landscape

\[
\frac{dx^i}{dt} = x^i b_i \left( 1 - \sum x^j \right) - d_i x^i
\]

free space

If \( b_1/d_1 > b_i/d_i > 1 \) for \( i \geq 2 \), then

\[
\lim_{t \to \infty} (x_1, \ldots, x^n) = (1 - d_1/b_1, 0, 0, \ldots, 0)
\]

whenever \( x_0^1 > 0 \).

The species that suppresses free space to the lowest frequency excludes all others.

Volterra (1928) Journal du Conseil
Ubiquity of competition

Many species engage in competitive interactions: increasing the abundance of one has a negative effect on the other†

Ubiquity of competition

Many species engage in competitive interactions: increasing the abundance of one has a negative effect on the other†

How it is possible for so many species to coexist?

Mechanisms?

“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 Zebra (1955)
“Every neighboring state is an enemy and the enemy’s enemy is a friend”
Paine 1966 American Naturalist

Tatoosh Island, WA
Removal of top predator reduced diversity from 15 to 8
Removal of top predator reduced diversity from 15 to 8.
What do the models say?

\[
\frac{dx_i}{dt} = b_i x_i (1 - \sum_j x_j) - d_i x_i
\]

frequency of prey \(i\)
What do the models say?

\[
\frac{dx_i}{dt} = b_i x_i (1 - \sum_j x^j) - d_i x_i - \alpha_i y x^i
\]

frequency of prey \(i\)

\[
\frac{dy}{dt} = \sum \theta_i \alpha_i x^i y - \delta y
\]

predator consumption

predator assimilation


Robust permanence not possible if \(n \geq 3\) as no unique internal equilibrium.

However, replacing \(\alpha_i \mapsto \alpha_p(x)\) where \(p(x) = 0\) iff \(x_i = 0\) then coexistence is possible for \(n \geq 3\) provided \(\alpha \gg 0\).

Schreiber, unpublished notes.
What do the models say?

\[ \frac{dx_i}{dt} = b_i x^i (1 - \sum_j x^j) - d_i x^i - \alpha_i y x^i \]

Predator consumption

\[ \frac{dy}{dt} = \sum \theta_i \alpha_i x^i y - \delta y \]

Predator assimilation

What do the models say?

\[
\frac{dx_i}{dt} = b_i x_i (1 - \sum_j x^j) - d_i x_i - \alpha_i y x_i
\]

\[
\frac{dy}{dt} = \sum \theta_i \alpha_i x^i y - \delta y
\]


Robust permanence not possible if \(n \geq 3\) as no unique internal equilibrium.
What do the models say?

\[
\frac{dx_i}{dt} = b_i x_i \left(1 - \sum_j x^j\right) - d_i x_i - \alpha_i y x^i \quad \frac{dy}{dt} = \sum \theta_i \alpha_i x^i y - \delta y
\]


Robust permanence \textbf{not possible} if \(n \geq 3\) as no unique internal equilibrium. However, replacing

\[\alpha_i \mapsto \alpha p_i(x) \text{ where } p^i(x) = 0 \text{ iff } x^i = 0\]
What do the models say?

\[
\frac{dx^i}{dt} = b_i x^i (1 - \sum_j x^j) - d_i x^i - \alpha_i y x^i
\]

frequency of prey \( i \)

\[
\frac{dy}{dt} = \sum \theta_i \alpha_i x^i y - \delta y
\]

predator consumption


Robust permanence not possible if \( n \geq 3 \) as no unique internal equilibrium. However, replacing

\[
\alpha_i \mapsto \alpha p_i(x) \text{ where } p^i(x) = 0 \text{ iff } x^i = 0
\]

Then coexistence is possible for \( n \geq 3 \) provided \( \alpha \gg 0 \).

Schreiber, unpublished notes.
What do the models say?

Replacing

\[ \alpha_i \rightarrow \alpha p_i(x) \] where \( p^i(x) = 0 \) iff \( x^i = 0 \)

Then coexistence is possible for \( n \geq 3 \) provided \( \alpha \gg 0 \).

Schreiber, unpublished notes.
Populations often structured by location, size, gender, genotype
Populations often structured by location, size, gender, genotype

Replace $x^i$ by $x^i = (x^{i1}, \ldots, x^{ik_i})$ and $r_i(x)$ by matrices

$$\frac{dx^i}{dt} = A_i(x) x^i \quad i = 1, \ldots, n$$

$k_i \times k_i$ quasi-positive matrix
\[ \frac{dx^i}{dt} = A_i(x) x^i \quad i = 1, \ldots, n \]

If \( x^i_0 = 0 \), then the solution \( z^i_t \) of \( \frac{dz^i}{dt} = A_i(x_t) z^i \) determines asymptotic tendency to increase or decrease.
\[
\frac{dx^i}{dt} = A_i(x) x^i \quad i = 1, \ldots, n
\]

If \( x_0^i = 0 \), then the solution \( z_t^i \) of \( \frac{dz^i}{dt} = A_i(x_t) z^i \) determines asymptotic tendency to increase or decrease

\[
\text{IRWR} \quad \bar{r}_i(x_0) := \limsup_{t \to \infty} \frac{1}{t} \log \frac{\|z_t^i\|}{\text{total pop size}}
\]
\[ \frac{dx^i}{dt} = A_i(x)x^i \quad i = 1, \ldots, n \]

If \( x^i_0 = 0 \), then the solution \( z^i_t \) of \( \frac{dz^i}{dt} = A_i(x_t)z^i \) determines asymptotic tendency to increase or decrease

\[ \text{IRWR} \quad \bar{r}_i(x_0) := \limsup_{t \to \infty} \frac{1}{t} \log \frac{\|z^i_t\|}{\text{total pop size}} \]

**Theorem** (Hofbauer & Schreiber (2010) JDE) If there are positive weights \( p_1, \ldots, p_n \) such that \( \sum p_i \bar{r}_i(x_0) > 0 \) for all recurrent \( x_0 \) satisfying \( \prod_i \|x^i\| = 0 \), then system is robustly permanent.

If the community on average increases when rare, then it persists robustly.
\[
\frac{dx_1}{dt} = x_1 \rho (1 - x_1 - (1 + c)x_2 - (1 - b)x_3)
\]
\[
\frac{dx_2}{dt} = x_2 \rho (1 - (1 - b)x_1 - x_2 - (1 + c)x_3)
\]
\[
\frac{dx_3}{dt} = x_3 \rho (1 - (1 + c)x_1 - (1 - b)x_2 - x_3)
\]

cost of loss

benefit of win

\(c > b \Rightarrow \) extinction of two species
\[
\frac{dx_1}{dt} = x_1 \rho (1 - x_1 - (1 + c)x_2 - (1 - b)x_3)
\]
\[
\frac{dx_2}{dt} = x_2 \rho (1 - (1 - b)x_1 - x_2 - (1 + c)x_3)
\]
\[
\frac{dx_3}{dt} = x_3 \rho (1 - (1 + c)x_1 - (1 - b)x_2 - x_3)
\]

\(c > b \Rightarrow \text{extinction of two species}\)
What if there is spatial heterogeneity?

$k$ patches $x^{ij}$ density of species $i$ in patch $j$
What if there is spatial heterogeneity?

$k$ patches  \( x_{ij} \) density of species $i$ in patch $j$

$\delta$ dispersal rate  \( d_{j\ell} \) fraction of dispersers in $j$ going to $\ell$
What if there is spatial heterogeneity?

$k$ patches $x^{ij}$ density of species $i$ in patch $j$

$\delta$ dispersal rate $d_{j\ell}$ fraction of dispersers in $j$ going to $\ell$

$$\frac{dx^{1j}}{dt} = x^{1j} \rho (1 - x^{1j} - (1 + c_j)x^{2j} - (1 - b_j)x^{3j})$$

$$\frac{dx^{2j}}{dt} = x^{2j} \rho (1 - (1 - b_j)x^{1j} - x^{2j} - (1 + c_j)x^{3j})$$

$$\frac{dx^{3j}}{dt} = x^{3j} \rho (1 - (1 + c_j)x^{1j} - (1 - b_j)x^{2j} - x^{3j})$$

**Theorem (Schreiber & Killingback (2013) TPB)**

Assume $d_{j\ell} = d_{\ell j}$ for all $j, \ell$. Then $\delta \approx 0$ max $j \ b_j > \min j \ c_j \iff$ robust permanence
What if there is spatial heterogeneity?

\( k \) patches  \( x_{ij} \) density of species \( i \) in patch \( j \)
\( \delta \) dispersal rate  \( d_{j\ell} \) fraction of dispersers in \( j \) going to \( \ell \)

\[
\frac{dx_{1j}}{dt} = x_{1j} \rho (1 - x_{1j} - (1 + c_j)x_{2j} - (1 - b_j)x_{3j}) + \delta \left( \sum_{\ell} d_{j\ell} x_{1\ell} - x_{1j} \right)
\]
\[
\frac{dx_{2j}}{dt} = x_{2j} \rho (1 - (1 - b_j)x_{1j} - x_{2j} - (1 + c_j)x_{3j}) + \delta \left( \sum_{\ell} d_{j\ell} x_{2\ell} - x_{2j} \right)
\]
\[
\frac{dx_{3j}}{dt} = x_{3j} \rho (1 - (1 + c_j)x_{1j} - (1 - b_j)x_{2j} - x_{3j}) + \delta \left( \sum_{\ell} d_{j\ell} x_{3\ell} - x_{3j} \right)
\]

Theorem (Schreiber & Killingback (2013) TPB)
Assume \( d_{j\ell} = d_{\ell j} \) for all \( j, \ell \). Then \( \delta \approx 0: \max_j b_j > \min_j c_j \iff \text{robust permanence} \)
What if there is spatial heterogeneity?

$k$ patches  \[x^{ij}\] density of species $i$ in patch $j$

\[\delta\] dispersal rate  \[d_{j\ell}\] fraction of dispersers in $j$ going to $\ell$

\[
\frac{dx^{1j}}{dt} = x^{1j} \rho (1 - x^{1j} - (1 + c_j) x^{2j} - (1 - b_j) x^{3j}) + \delta \left( \sum_{\ell} d_{j\ell} x^{1\ell} - x^{1j} \right)
\]

\[
\frac{dx^{2j}}{dt} = x^{2j} \rho (1 - (1 - b_j) x^{1j} - x^{2j} - (1 + c_j) x^{3j}) + \delta \left( \sum_{\ell} d_{j\ell} x^{2\ell} - x^{2j} \right)
\]

\[
\frac{dx^{3j}}{dt} = x^{3j} \rho (1 - (1 + c_j) x^{1j} - (1 - b_j) x^{2j} - x^{3j}) + \delta \left( \sum_{\ell} d_{j\ell} x^{3\ell} - x^{3j} \right)
\]

**Theorem** (Schreiber & Killingback (2013) TPB) Assume $d_{j\ell} = d_{\ell j}$ for all $j, \ell$. Then

\[\delta \approx 0: \max_j b_j > \min_j c_j \iff \text{robust permanence}\]
What if there is spatial heterogeneity?

$k$ patches \( x_{ij} \) density of species \( i \) in patch \( j \)

\( \delta \) dispersal rate \( d_{j\ell} \) fraction of dispersers in \( j \) going to \( \ell \)

\[
\frac{dx_{1j}}{dt} = x_{1j} \rho(1 - x_{1j} - (1 + c_{j})x_{2j} - (1 - b_{j})x_{3j}) + \delta \left( \sum_{\ell} d_{j\ell} x_{1\ell} - x_{1j} \right)
\]

\[
\frac{dx_{2j}}{dt} = x_{2j} \rho(1 - (1 - b_{j})x_{1j} - x_{2j} - (1 + c_{j})x_{3j}) + \delta \left( \sum_{\ell} d_{j\ell} x_{2\ell} - x_{2j} \right)
\]

\[
\frac{dx_{3j}}{dt} = x_{3j} \rho(1 - (1 + c_{j})x_{1j} - (1 - b_{j})x_{2j} - x_{3j}) + \delta \left( \sum_{\ell} d_{j\ell} x_{3\ell} - x_{3j} \right)
\]

**Theorem** (Schreiber & Killingback (2013) TPB) Assume \( d_{j\ell} = d_{\ell j} \) for all \( j, \ell \). Then

\( \delta \approx 0: \max_j b_j > \min_j c_j \iff \text{robust permanence} \)

\( \delta \gg 0: \frac{1}{k} \sum_j b_j > \frac{1}{k} \sum_j c_j \iff \text{robust permanence} \)
RPS with E. coli*

* Kerr et al. (2002) Nature
How do species interactions and population structure impact species coexistence?

- keystone predation
- spatial heterogeneity

How does demographic and environmental stochasticity impact species coexistence?

- metastability
- storage effect
Lest men suspect your tale untrue, Keep probability in view. –John Gay
Lest biologicals suspect your model untrue, Keep probability in view.
Lest biologists suspect your model untrue, Keep probability in view.

Demographic stochasticity (intrinsic noise)

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. –Peter Jagers (2010) JMB
Lest biologists suspect your model untrue, Keep probability in view.

Demographic stochasticity (intrinsic noise)

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

—Peter Jagers (2010) JMB
Lest **biologists** suspect your **model** untrue, Keep probability in view.

**Demographic stochasticity** (intrinsic noise)

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

—Peter Jagers (2010) JMB

*The future’s uncertain and the end is always near –*Jim Morrison (1970) Roadhouse Blues
Lest biologists suspect your model untrue, keep probability in view.

Demographic stochasticity (intrinsic noise)

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...Any population allowing individual variation in reproduction, ultimately dies out–unless it grows beyond all limits, an impossibility in a bounded world. Deterministic population mathematics on the contrary allows stable asymptotics. Are these artifacts or do they tell us something interesting about quasi-stationary stages of real or stochastic populations?—Peter Jagers (2010) JMB

The future’s uncertain and the end is always near—Jim Morrison (1970) Roadhouse Blues
Poisson processes

$N^i_t$ - number of individuals of species $i$ at time $t$

$1/\varepsilon$ - habitat size

$X^i_t = \varepsilon N^i_t$ - species density
Poisson processes

\( N^i_t \) - number of individuals of species \( i \) at time \( t \)

\( 1/\varepsilon \) - habitat size

\( X^i_t = \varepsilon N^i_t \) - species density

\( N^i_{t+1} \sim \text{Poisson with mean } N^i_t r_i(X_t) \)
Poisson processes

\( N^i_t \) - number of individuals of species \( i \) at time \( t \)
1/\( \varepsilon \) - habitat size
\( X^i_t = \varepsilon N^i_t \) - species density

\[ N^i_{t+1} \sim \text{Poisson with mean } N^i_t r_i(X^i_t) \]
Poisson processes

\[ N_t^i \] - number of individuals of species \( i \) at time \( t \)
\[ 1/\varepsilon \] - habitat size
\[ X_t^i = \varepsilon N_t^i \] - species density

\[ N_{t+1}^i \sim \text{Poisson with mean } N_t^i \overbrace{r_i(X_t)}^{\text{fitness}} \]
Poisson processes

\( N^i_t \) - number of individuals of species \( i \) at time \( t \)

\( 1/\varepsilon \) - habitat size

\( X^i_t = \varepsilon N^i_t \) - species density

\( N^i_{t+1} \sim \text{Poisson with mean } N^i_t r_i(X_t) \)
Poisson processes

\( N^i_t \) - number of individuals of species \( i \) at time \( t \)
\( 1/\varepsilon \) - habitat size
\( X^i_t = \varepsilon N^i_t \) - species density

\[ N^i_{t+1} \sim \text{Poisson with mean } N^i_t \overbrace{r_i(X^i_t)}^{\text{fitness}} \]

What can we say about the metastable behavior of \( \{X^\varepsilon_t\} \)?
Quasi-stationary distributions If $x \mapsto (x_1 r_1(x), \ldots, x_n r_n(x)) =: f(x)$ is pre-compact and $\varepsilon > 0$,
Quasi-stationary distributions  If $x \mapsto (x_1 r_1(x), \ldots, x_n r_n(x)) =: f(x)$ is pre-compact and $\varepsilon > 0$, then there a probability measure $\mu_\varepsilon$ on $(0, \infty)^n$ and $e_\varepsilon > 0$ such that

$$\lim_{t \to \infty} \mathbb{P} \left[ X_t^\varepsilon \in A \mid \prod_i X_t^{\varepsilon,i} > 0 \right] = \mu_\varepsilon(A) \text{ for all } A \subset (0, \infty)^n$$


$\mu_\varepsilon$ describes the long-term statistical behavior of $X_t^\varepsilon$ conditioned on non-extinction
Quasi-stationary distributions If \( x \mapsto (x_1 r_1(x), \ldots, x_n r_n(x)) =: f(x) \) is pre-compact and \( \varepsilon > 0 \), then there a probability measure \( \mu_\varepsilon \) on \((0, \infty)^n\) and \( e_\varepsilon > 0 \) such that

\[
\lim_{t \to \infty} \mathbb{P} \left[ X_t^\varepsilon \in A \mid \prod_i X_t^{\varepsilon,i} > 0 \right] = \mu_\varepsilon(A) \text{ for all } A \subset (0, \infty)^n
\]

and

\[
\lim_{t \to \infty} \frac{1}{t} \log \mathbb{P} \left[ \prod_i X_t^{\varepsilon,i} > 0 \right] = -e_\varepsilon
\]


\( \mu_\varepsilon \) describes the long-term statistical behavior of \( X_t^\varepsilon \) conditioned on non-extinction

\( e_\varepsilon \) is the asymptotic rate of extinction
Mestability Theorem (Faure & Schreiber (2014) Ann.Appl.Prob) *If there exists at least one attractor in $\mathbb{R}^n$ for the mean field map $f$*,
Mestability Theorem (Faure & Schreiber (2014) Ann.Appl.Prob) If there exists at least one attractor in $(0, \infty)^n$ for the mean field map $f$, then

(i) there exists $C > 0$ such that $e_\varepsilon \leq \exp(-C/\varepsilon)$

Persistence time increases exponentially with system size $1/\varepsilon$
Mestability Theorem (Faure & Schreiber (2014) Ann.Appl.Prob) *If there exists at least one attractor in $(0, \infty)^n$ for the mean field map $f$, then*

(i) there exists $C > 0$ such that $e^\varepsilon \leq \exp(-C/\varepsilon)$

(ii) weak* limit point of $\{\mu_\varepsilon\}_{\varepsilon > 0}$ are $f$-invariant and supported by the positive attractors of $f$.

Persistence time increases exponentially with system size $1/\varepsilon$

Metastable behavior supported by the attractors of $f$. 
**Mestability Theorem** (Faure & Schreiber (2014) Ann. Appl. Prob) *If there exists at least one attractor in $(0, \infty)^n$ for the mean field map $f$, then*

(i) there exists $C > 0$ such that $e_\varepsilon \leq \exp(-C/\varepsilon)$

(ii) weak* limit point of $\{\mu_\varepsilon\}_{\varepsilon > 0}$ are $f$-invariant and supported by the positive attractors of $f$.

Persistence time increases exponentially with system size $1/\varepsilon$

Metastable behavior supported by the attractors of $f$.

host-parasite dynamics

\[ N_{t+1}^1 \sim \text{Poisson}(N_t^1 \lambda \exp(-aX_t^1 - bX_t^2)) \]

\[ N_{t+1}^2 \sim \text{Poisson}(N_t^1 \lambda (1 - \exp(-bX_t^2))) \]

\[ 1/\varepsilon = 10^2 \]
host-parasite dynamics

\[ N_{t+1}^1 \sim \text{Poisson}(N_t^1 \lambda \exp(-aX_t^1 - bX_t^2)) \]
\[ N_{t+1}^2 \sim \text{Poisson}(N_t^1 \lambda (1 - \exp(-bX_t^2))) \]
host-parasite dynamics

\[ N_{t+1}^1 \sim \text{Poisson}(N_t^1 \lambda \exp(-aX_t^1 - bX_t^2)) \]

\[ N_{t+1}^2 \sim \text{Poisson}(N_t^1 \lambda (1 - \exp(-bX_t^2))) \]
host-parasite dynamics

\[ N_{t+1}^1 \sim \text{Poisson}(N_t^1 \lambda \exp(-aX_t^1 - bX_t^2)) \]
\[ N_{t+1}^2 \sim \text{Poisson}(N_t^1 \lambda (1 - \exp(-bX_t^2))) \]
host-parasite dynamics

\[ N_{t+1}^1 \sim \text{Poisson}(N_t^1 \lambda \exp(-aX_t^1 - bX_t^2)) \]

\[ N_{t+1}^2 \sim \text{Poisson}(N_t^1 \lambda (1 - \exp(-bX_t^2))) \]
Lest **biologists** suspect your **model** untrue, Keep probability in view.

**Environmental stochasticity** (extrinsic noise)
Lest biologists suspect your model untrue, keep probability in view.

Environmental stochasticity (extrinsic noise)

- fluctuations in temperature, precipitation, etc.

![BML Air Temperature (deg C), Hourly Averages for 2011](image_url)
Lest biologists suspect your model untrue, keep probability in view.

**Environmental stochasticity (extrinsic noise)**

- fluctuations in temperature, precipitation, etc.
- demographic rates correlated to environmental conditions

![Graph](image-url)
Lest **biologists** suspect your **model** untrue, keep probability in view.

**Environmental stochasticity** *(extrinsic noise)*
- fluctuations in temperature, precipitation, etc.
- demographic rates correlated to environmental conditions

---

*One day is fine, the next is black.* — *The Clash* (1981) *Should I stay or should I go?*
The environment-community dynamic:

\[ \xi_1, \xi_2, \xi_3, \ldots \text{ ergodic, stationary sequence} \]

\[ X_{t+1}^i = A_i(X_t, \xi_{t+1})X_t^i \quad i = 1, \ldots, n \]
The environment-community dynamic:

\[ \xi_1, \xi_2, \xi_3, \ldots \text{ ergodic, stationary sequence} \]

\[ X_{t+1}^i = A_i(X_t, \xi_{t+1})X_t^i \quad i = 1, \ldots, n \]

What ensures the long-term persistence of the community?
The environment-community dynamic:

\[ \xi_1, \xi_2, \xi_3, \ldots \text{ ergodic, stationary sequence} \]

\[ X_{t+1}^i = A_i(x_t, \xi_{t+1})X_t^i \quad i = 1, \ldots, n \]

What ensures the long-term persistence of the community?

The system is **stochastically persistent** if for all $\varepsilon > 0$ there exists $\delta > 0$ such that

$$\limsup_{T \to \infty} \frac{\# \{ 1 \leq t \leq T \text{ such that } \|X^i_t\| \leq \delta \text{ for some } i \}}{T} \leq \varepsilon$$

with probability one.
The system is **stochastically persistent** if for all $\varepsilon > 0$ there exists $\delta > 0$ such that

$$\limsup_{T \to \infty} \frac{\#\{1 \leq t \leq T \text{ such that } \|X^i_t\| \leq \delta \text{ for some } i\}}{T} \leq \varepsilon$$

with probability one.

**An arbitrarily small fraction of time is spent below arbitrarily small densities**
If $X^i_0 = 0$, then

$$\text{IRWR } \bar{r}_i(X_0) = \limsup_{t \to \infty} \frac{1}{t} \log \|A_i(X_{t-1}, \xi_t) \cdots A_i(X_0, \xi_1)\|$$

determines growth of species $i$ when introduced at low densities.
If $X_0^i = 0$, then

$$\mathrm{IRWR} \quad \bar{r}_i(X_0) = \limsup_{t \to \infty} \frac{1}{t} \log \|A_i(X_{t-1}, \xi_t) \cdots A_i(X_0, \xi_1)\|$$

determines growth of species $i$ when introduced at low densities.

**Stochastic Persistence Theorem.** (Roth & S. (2014) J.Math.Bio.) If there exist weights $p_i > 0$ such that $\sum_i p_i \bar{r}_i(X_0) > 0$ with probability one for $X_0$ with $\prod_i \|X_0^i\| = 0$, then the system stochastically persists.
If $X_0^i = 0$, then

$$\text{IRWR } \bar{r}_i(X_0) = \limsup_{t \to \infty} \frac{1}{t} \log \|A_i(X_{t-1}, \xi_t) \ldots A_i(X_0, \xi_1)\|$$

determines growth of species $i$ when introduced at low densities.

**Stochastic Persistence Theorem.** (Roth & S. (2014) J.Math.Bio.) If there exist weights $p_i > 0$ such that $\sum_i p_i \bar{r}_i(X_0) > 0$ with probability one for $X_0$ with $\prod_i \|X_0^i\| = 0$, then the system stochastically persists.

*If the community on average increases when rare, then it stochastically persists*
Chesson’s Lottery Model
Chesson’s Lottery Model
Chesson’s Lottery Model
Chesson’s Lottery Model
Chesson’s Lottery Model
Chesson’s Lottery Model
What about species coexistence?

\[ X^i_{t+1} \]

fraction space occupied by \( i \)

What about species coexistence?

\[ X_{t+1}^i = (1 - d)X_t^i \]

fraction space occupied by \( i \)

fraction dying

What about species coexistence?

\[
X^i_{t+1} = (1 - d)X^i_t + d \frac{\xi^i_{t+1}X^i_t}{\sum_j \xi^j_{t+1}X^j_t}
\]

fraction space occupied by \( i \)

fraction dying

fecundity of \( i \)

What about species coexistence?

\[ X_{t+1}^i = (1 - d)X_t^i + d \frac{\xi_i^{t+1}X_t^i}{\sum_j \xi_j^{t+1}X_t^j} \]

fraction space occupied by \( i \)

fraction dying

\( \xi_i \equiv \bar{\xi}_i \) and \( \bar{\xi}_1 > \bar{\xi}_i \) for all \( i > 1 \) \( \Rightarrow \) species 1 displaces all others.

Assume $\log \xi^1_t, \ldots, \log \xi^n_t$ are multivariate normals
Assume $\log \xi_t^1, \ldots, \log \xi_t^n$ are multivariate normals

**Theorem** (Schreiber, unpublished notes) If $d \approx 0$ and

$$ \mathbb{E}[\log \xi_t^i - \log \xi_t^j] < \text{Var}[\log \xi_t^i - \log \xi_t^j] \text{ for all } j \neq i $$

then the system is stochastically persistent.
Assume \( \log \xi^1_t, \ldots, \log \xi^n_t \) are multivariate normals

**Theorem** (Schreiber, unpublished notes) If \( d \approx 0 \) and

\[
\mathbb{E}[\log \xi^i_t - \log \xi^j_t] < \text{Var}[\log \xi^i_t - \log \xi^j_t] \quad \text{for all } j \neq i
\]

then the system is stochastically persistent. If \( d \approx 1 \) and \( \mathbb{E}[\log \xi^1_t] > \mathbb{E}[\log \xi^i_t] \) for \( i \geq 2 \), then \( \lim_{t \to \infty} X^i_t = 0 \) for all \( i \geq 2 \) whenever \( X^1_0 > 0 \).
Assume $\log \xi_t^1, \ldots, \log \xi_t^n$ are multivariate normals

**Theorem** (Schreiber, unpublished notes) If $d \approx 0$ and

$$\mathbb{E}[\log \xi_t^i - \log \xi_t^j] < \text{Var}[\log \xi_t^i - \log \xi_t^j]$$

for all $j \neq i$, then the system is stochastically persistent. If $d \approx 1$ and $\mathbb{E}[\log \xi_t^1] > \mathbb{E}[\log \xi_t^i]$ for $i \geq 2$, then $\lim_{t \to \infty} X_t^i = 0$ for all $i \geq 2$ whenever $X_0^1 > 0$. 

![Graph showing frequency and fraction of time over time and best competitor](image_url)
Assume $\log \xi^1_t, \ldots, \log \xi^n_t$ are multivariate normals

**Theorem** (Schreiber, unpublished notes) If $d \approx 0$ and

$$\mathbb{E}[\log \xi^i_t - \log \xi^j_t] < \text{Var}[\log \xi^i_t - \log \xi^j_t] \text{ for all } j \neq i$$

then the system is stochastically persistent. If $d \approx 1$ and $\mathbb{E}[\log \xi^1_t] > \mathbb{E}[\log \xi^i_t]$ for $i \geq 2$, then $\lim_{t \to \infty} X^i_t = 0$ for all $i \geq 2$ whenever $X^1_0 > 0$. 

---

![Graph showing time-frequency analysis and fraction of time for best competitor](image-url)
Assume $\log \xi^1_t, \ldots, \log \xi^n_t$ are multivariate normals

**Theorem** (Schreiber, unpublished notes) If $d \approx 0$ and

$$E[\log \xi^i_t - \log \xi^j_t] < Var[\log \xi^i_t - \log \xi^j_t]$$

for all $j \neq i$, then the system is stochastically persistent. If $d \approx 1$ and $E[\log \xi^1_t] > E[\log \xi^i_t]$ for $i \geq 2$, then $\lim_{t \to \infty} X^i_t = 0$ for all $i \geq 2$ whenever $X^1_0 > 0$.
Assume $\log \xi^1_t, \ldots, \log \xi^n_t$ are multivariate normals.

**Theorem** (Schreiber, unpublished notes) If $d \approx 0$ and

$$\mathbb{E}[\log \xi^i_t - \log \xi^j_t] < \text{Var}[\log \xi^i_t - \log \xi^j_t] \text{ for all } j \neq i$$

then the system is stochastically persistent. If $d \approx 1$ and $\mathbb{E}[\log \xi^1_t] > \mathbb{E}[\log \xi^i_t]$ for $i \geq 2$, then $\lim_{t \to \infty} X^i_t = 0$ for all $i \geq 2$ whenever $X^1_0 > 0$. 
Assume $\log \xi^1_t, \ldots, \log \xi^n_t$ are multivariate normals

**Theorem** (Schreiber, unpublished notes) If $d \approx 0$ and

$$E[\log \xi^i_t - \log \xi^j_t] < \text{Var}[\log \xi^i_t - \log \xi^j_t] \quad \text{for all } j \neq i$$

then the system is stochastically persistent. If $d \approx 1$ and $E[\log \xi^1_t] > E[\log \xi^i_t]$ for $i \geq 2$, then $\lim_{t \to \infty} X^i_t = 0$ for all $i \geq 2$ whenever $X^1_0 > 0$.
Assume $\log \xi^1_t, \ldots, \log \xi^n_t$ are multivariate normals

**Theorem** (Schreiber, unpublished notes) If $d \approx 0$ and

$$\mathbb{E}[\log \xi^i_t - \log \xi^j_t] < \text{Var}[\log \xi^i_t - \log \xi^j_t] \text{ for all } j \neq i$$

then the system is stochastically persistent. If $d \approx 1$ and $\mathbb{E}[\log \xi^1_t] > \mathbb{E}[\log \xi^i_t]$ for $i \geq 2$, then $\lim_{t \to \infty} X^i_t = 0$ for all $i \geq 2$ whenever $X^1_0 > 0$. 
Assume $\log \xi_t^1, \ldots, \log \xi_t^n$ are multivariate normals.

**Theorem** (Schreiber, unpublished notes) If $d \approx 0$ and

$$\mathbb{E}[\log \xi_t^i - \log \xi_t^j] < \text{Var}[\log \xi_t^i - \log \xi_t^j]$$

for all $j \neq i$, then the system is stochastically persistent. If $d \approx 1$ and $\mathbb{E}[\log \xi_t^1] > \mathbb{E}[\log \xi_t^i]$ for $i \geq 2$, then $\lim_{t \to \infty} X_t^i = 0$ for all $i \geq 2$ whenever $X_0^1 > 0$. 

![Graph showing frequency and fraction of time against time and best competitor](image)
Storage effect in Kansas prairies

Adler et al. 2006 PNAS
Storage effect in Kansas prairies

Adler et al. 2006 PNAS

- Fit a dynamic, stochastic model using a hierarchical Bayesian approach
Storage effect in Kansas prairies

Adler et al. 2006 PNAS

- Fit a dynamic, stochastic model using a hierarchical Bayesian approach
- Computed $\bar{r}_i$ for fluctuating and constant environments
Storage effect in Kansas prairies

Adler et al. 2006 PNAS

- Fit a dynamic, stochastic model using a hierarchical Bayesian approach
- Computed $\bar{r}_i$ for fluctuating and constant environments
Storage effect in Kansas prairies

Adler et al. 2006 PNAS

- Fit a dynamic, stochastic model using a hierarchical Bayesian approach
- Computed $\bar{r}_i$ for fluctuating and constant environments
- Reduction in climactic variability predicted to reduce diversity by $\frac{2}{3}$ rds
If nothing else, take this to the bank...

Permanence or stochastic persistence

- is a tendency of populations to stay away from low densities for all positive initial conditions

Thank you for listening and the U.S. National Science Foundation for funding. Questions?
If nothing else, take this to the bank...

Permanence or stochastic persistence

- is a tendency of populations to stay away from low densities for all positive initial conditions
- implies extinction times of order $\exp(\text{system size})$ for the discrete-population counterparts of deterministic models.
If nothing else, take this to the bank...

Permanence or stochastic persistence

- is a tendency of populations to stay away from low densities for all positive initial conditions
- implies extinction times of order $\exp($system size$)$ for the discrete-population counterparts of deterministic models.

For many model types, this persistence occurs provided that

$$\sum_i p_i \bar{r}_i(x_0) > 0 \text{ for } x_0 \text{ with } \prod_i \|x_0^i\| = 0$$
If nothing else, take this to the bank...

Permanence or stochastic persistence

- is a tendency of populations to stay away from low densities for all positive initial conditions
- implies extinction times of order $\exp(\text{system size})$ for the discrete-population counterparts of deterministic models.

For many model types, this persistence occurs provided that

$$\sum_i p_i \tilde{r}_i(x_0) > 0 \text{ for } x_0 \text{ with } \prod_i \|x_0^i\| = 0$$

Many coexistence mechanisms including

- keystone species
- population structure - spatial heterogeneity + dispersal
- storage effect
If nothing else, take this to the bank...

Permanence or stochastic persistence

- is a tendency of populations to stay away from low densities for all positive initial conditions
- implies extinction times of order $\exp(\text{system size})$ for discrete-population counterparts of deterministic models.

For many model types, this persistence occurs provided that

$$\sum_i p_i \bar{r}_i(x_0) > 0 \quad \text{for } x_0 \text{ with } \prod_i \|x_0^i\| = 0$$

Many coexistence mechanisms including

- keystone species
- population structure - spatial heterogeneity + dispersal
- storage effect
If nothing else, take this to the bank...

Permanence or stochastic persistence

▶ is a tendency of populations to stay away from low densities for all positive initial conditions
▶ implies extinction times of order $\exp(\text{system size})$ for the discrete-population counterparts of deterministic models.

For many model types, this persistence occurs provided that

$$\sum p_i \bar{r}_i(x_0) > 0 \text{ for } x_0 \text{ with } \prod_i \|x_0^i\| = 0$$

Many coexistence mechanisms including

▶ keystone species
▶ population structure - spatial heterogeneity + dispersal
▶ storage effect

Thank you for listening and the U.S. National Science Foundation for funding. Questions?