

Extinction, Fixation, and Invasion in an Ecological Niche

MattheW Badali

Internal defense
performed as a requirement for
the degree of Doctor of Philosophy
4 July 2019

Biodiversity: Number And Distribution Of Species

Coexistence
and
Extinction of
Competing
Species

M.A.Badali

Background

Extinction

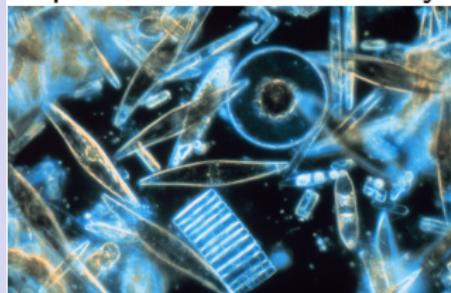
Fixation

Invasion

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Extra Slides

Paradox of the Plankton a problem of biodiversity



corp2365, NOAA Corps Collection

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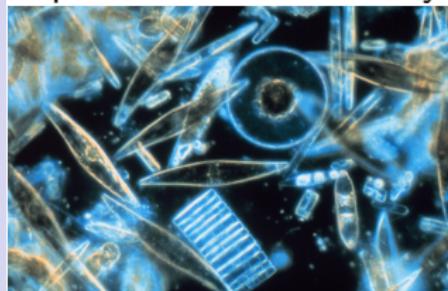
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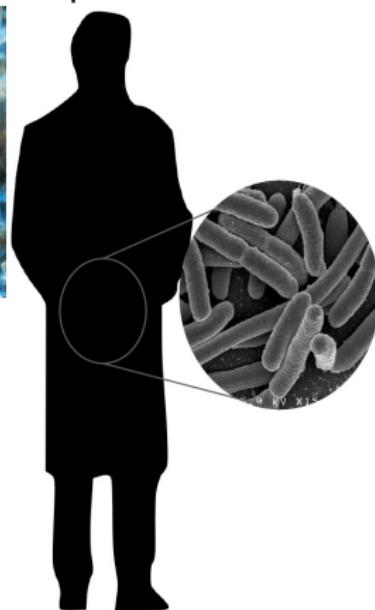
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Gut Microbiome
important to health



E. coli, Rocky Mountain
Laboratories, NIAID, NIH

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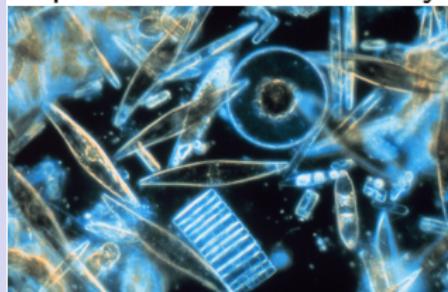
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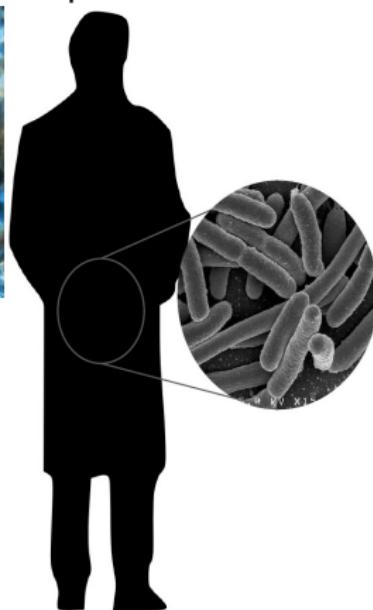
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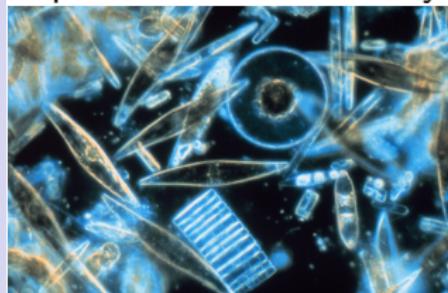
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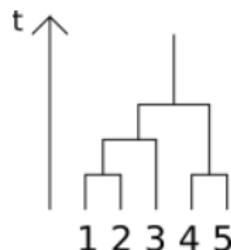
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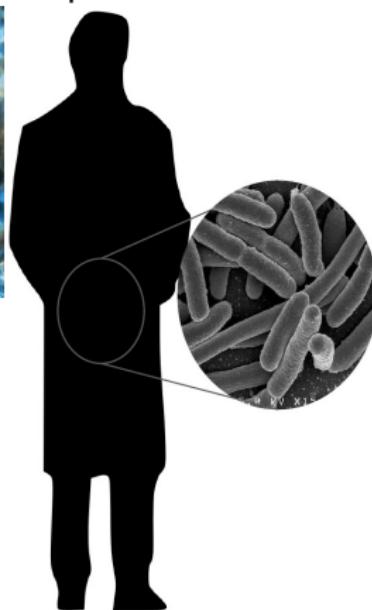


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Coalescent Trees



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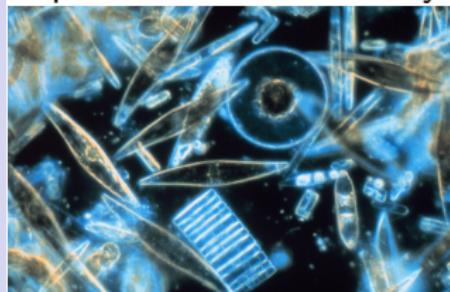
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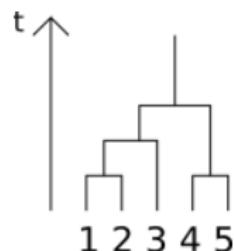
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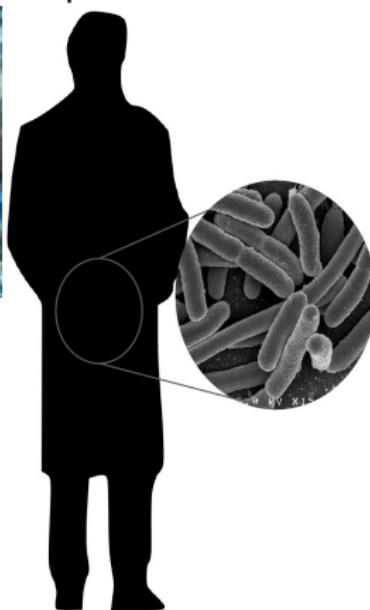


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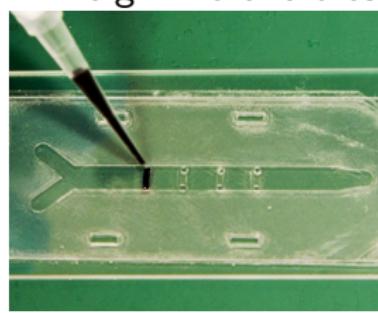


E. coli, Rocky Mountain
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Conservationism



Small Populations
e.g. microfluidics



Microfluidic Device, Cooksey/NIST

Niche Apportionment Explains Abundance Curves

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Niche Theories - each in their own niche

- niche/resource apportionment explains abundance curve
- use logistic equation $\dot{x} = rx(1 - x/K)$

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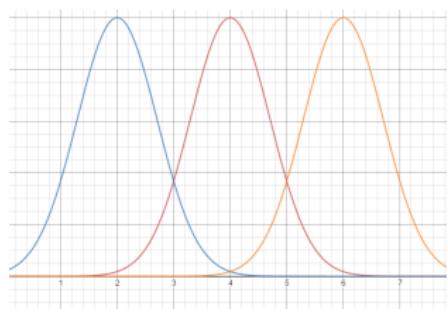
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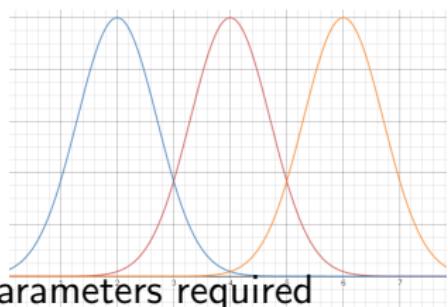
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- niche: survivable values of those factors which affect the birth and death rates



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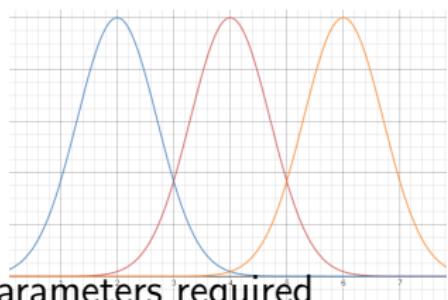
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- problem: too many resources, parameters required
- with stochasticity, mean time to extinction $\tau \sim e^K$

Neutral Theory Explains Abundance Curves Better

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Neutral Theories - all in one niche

- better prediction of abundance curves (Hubbell),
also allele frequencies (Kimura), fixation (Moran)
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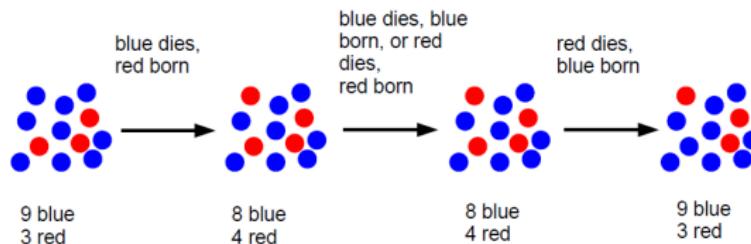
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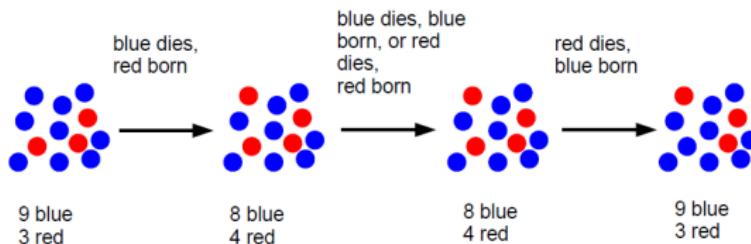
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- problem: all species in one niche seems unphysical

Main Goals Of My Research

Coexistence
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Stochasticity connects niche and neutral theories:
what is the nature of that connection?

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Biodiversity comes from a balance of species
existing (fixation, extinction) and species entering
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Stochasticity connects niche and neutral theories:
what is the nature of that connection?

Biodiversity comes from a balance of species exiting (fixation, extinction) and species entering (invasion) the system: what are the timescales?

→ **The relevant parameter is niche overlap.**

How To Calculate The Mean Time To Extinction

Master equation $\dot{\vec{P}}(t) = \hat{M}\vec{P}(t)$ is solved by $\vec{P}(t) = e^{\hat{M}t}\vec{P}(0)$.

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Residence time $= \int_0^\infty dt P(s|s^0) = \hat{M}_{s,s^0}^{-1}$ so $\hat{M}\vec{T} = -\vec{1}$.

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- $\tau \approx \frac{1}{d_1 P_1}$

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- Fokker-Planck:

$$\partial_t P_x = -\partial_x ((b_x - d_x)P_x) + \frac{1}{2K} \partial_x^2 ((b_x + d_x)P_x)$$

- $P_n \approx \frac{1}{\sqrt{2\pi\sigma^2}} \exp \left\{ -\frac{(n-n^*)^2}{2\sigma^2} \right\}$ with $\sigma^2 = \frac{-(b_n+d_n)|_{n^*}}{2\partial_n(b_n-d_n)|_{n^*}}$

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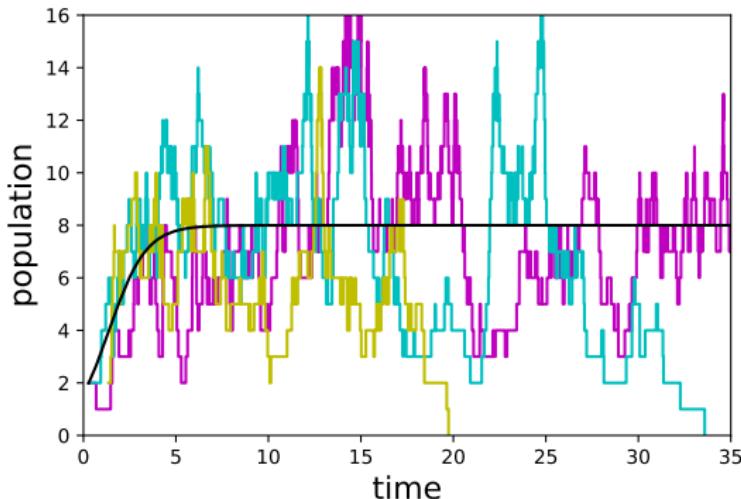
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- WKB ansatz: $P_n \propto \exp\left\{K \sum_i \frac{1}{K^i} S_i(n)\right\}$ with $S_0(n) = \frac{1}{K} \int_0^n dx \ln(b_x/d_x)$ along extinction trajectory

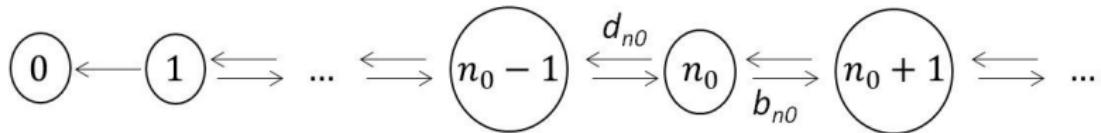
Extinction within a Niche

deterministic logistic equation $\dot{x} = r x \left(1 - \frac{x}{K}\right)$



Logistic Equation Has Two Hidden Parameters

deterministic logistic equation $\dot{x} = rx(1 - \frac{x}{K})$

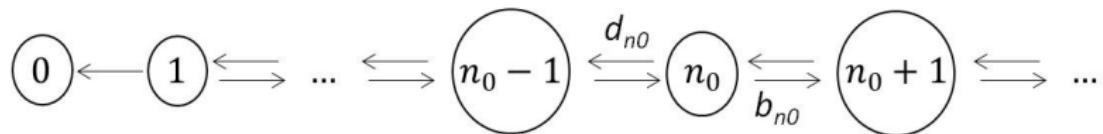


$$b_n = r(1 + \delta) n - \frac{r q}{K} n^2$$

$$d_n = r \delta n + \frac{r(1 - q)}{K} n^2$$

Logistic Equation Has Two Hidden Parameters

deterministic logistic equation $\dot{x} = rx \left(1 - \frac{x}{K}\right)$



$$b_n = r(1 + \delta)n - \frac{r q}{K} n^2$$

$$d_n = r\delta n + \frac{r(1 - q)}{K} n^2$$

- δ gives magnitude of birth or death (rather than their average difference, the growth rate r)
- q shifts intraspecies interactions from increasing death rate ($q \sim 0$) to reducing birth rate ($q \sim 1$)

Mean Time to Extinction Depends On Interactions

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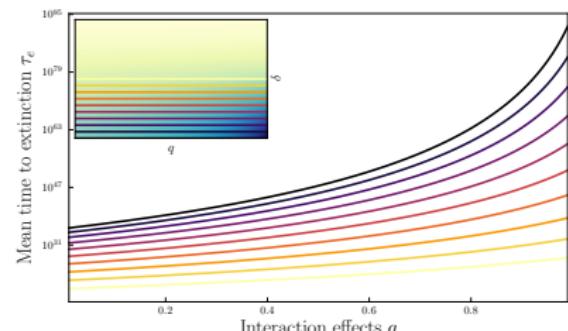
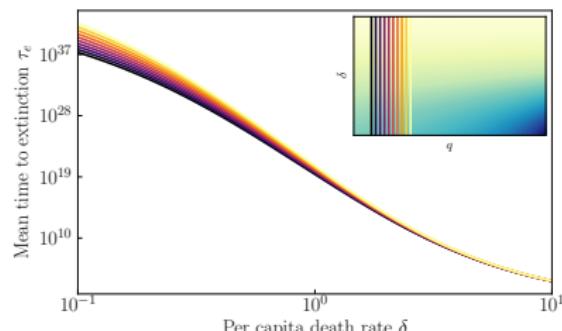
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Carrying capacity $K = 100$, growth rate $r = 1$. The mean time to extinction (MTE) decreases with increased δ or decreased q .

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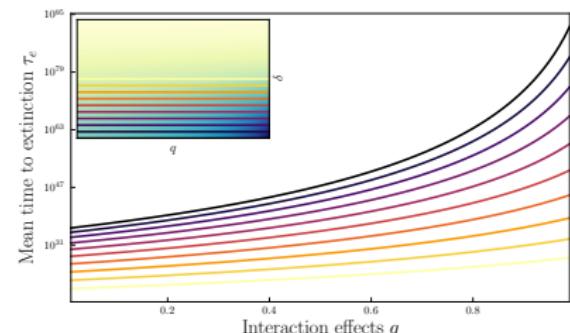
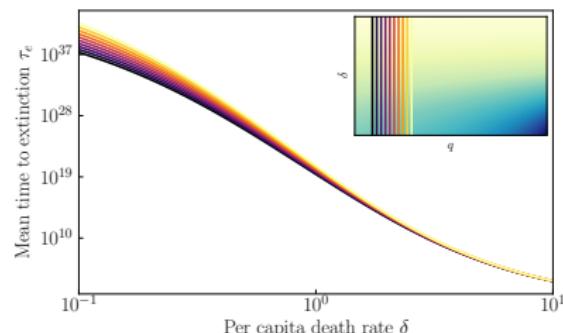
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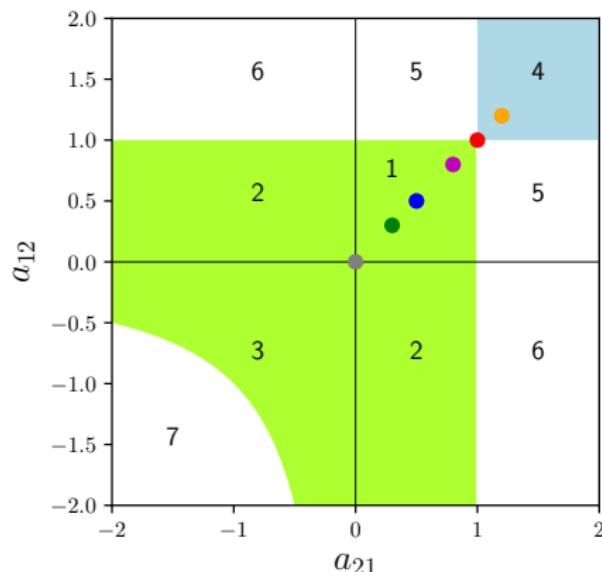
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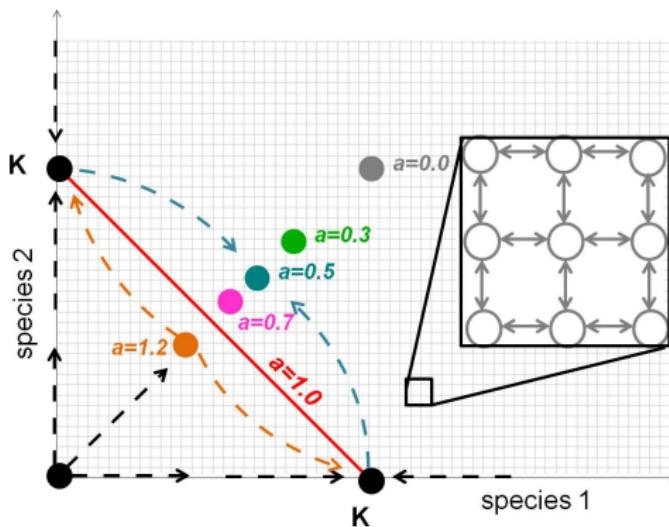
→ **increasing birth and death rates (e.g. competition increasing death rate) reduces the mean time to extinction**



$$\dot{x}_1 = r_1 x_1 \left(1 - \frac{x_1 + a_{12}x_2}{K_1}\right)$$
$$\dot{x}_2 = r_2 x_2 \left(1 - \frac{a_{21}x_1 + x_2}{K_2}\right)$$

2,6 = parasitism/predation,
3,7 = mutualism,
4,5 = competitive exclusion,
1 = (weak) competition

Coupled Logistic Has Niche And Neutral Limits



- for niche theory (independent limit):
 $a = 0$,
 $\tau \sim e^K$
- for neutral theory (Moran limit):
 $a = 1$,
 $\tau \sim K$

How The System Transitions To Neutrality

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niche theory

$$\tau \sim e^K$$

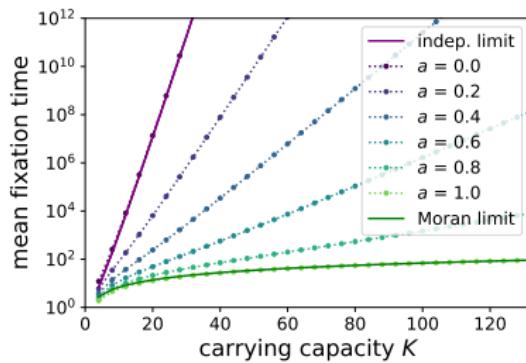
neutral theory

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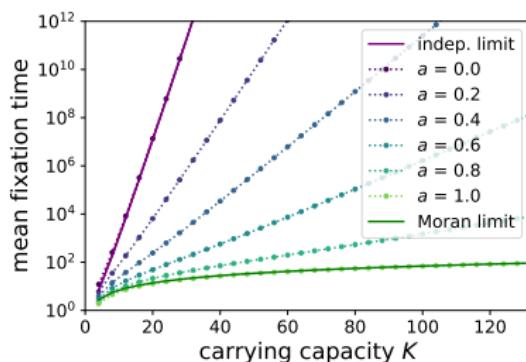
niche theory

$$\tau \sim e^K$$

ansatz: $\tau(a, K) = e^{h(a)} K^{g(a)} e^{f(a)K}$

neutral theory

$$\tau \sim K$$



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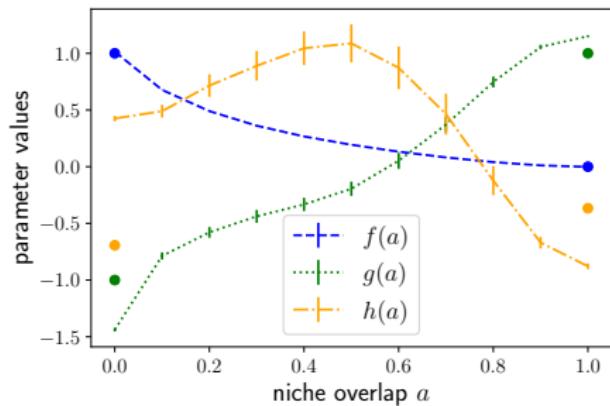
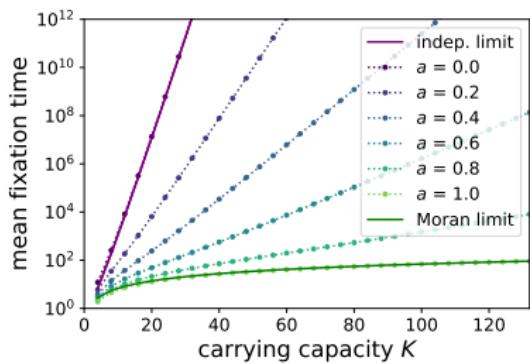
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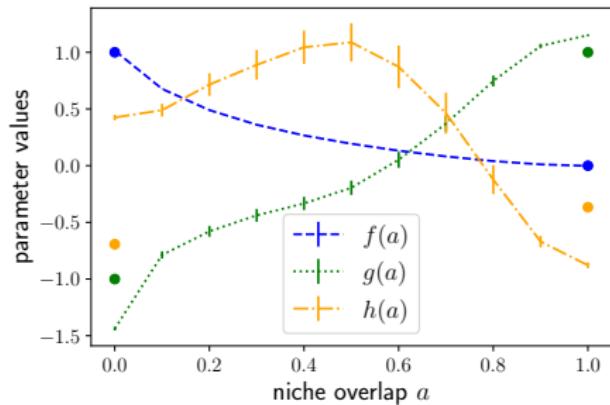
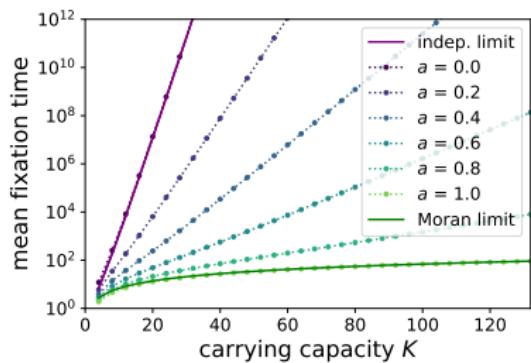
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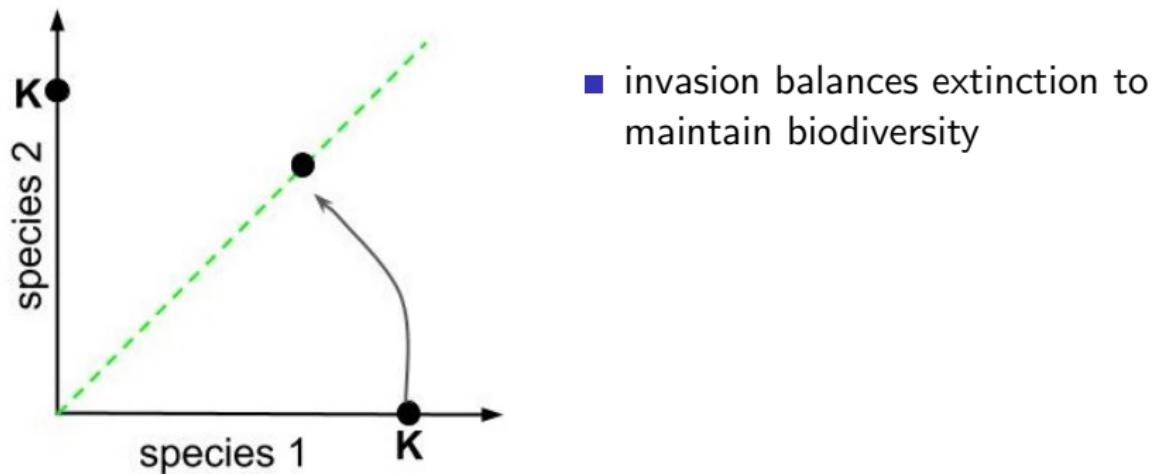
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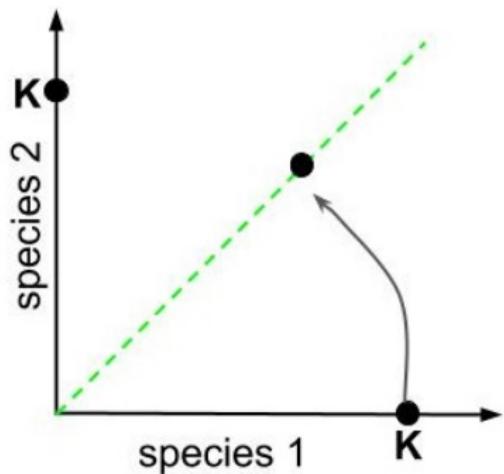


→ Effective coexistence except for complete niche overlap

The Timescale of Invasion of a Second Species



The Timescale of Invasion of a Second Species



- invasion balances extinction to maintain biodiversity
- invasion is going from one organism to half the population
- invasion into a niche is deterministic, fast (logarithmic)
- invasion into Moran is linear

Invasion Less Probable As Niche Overlap Increases

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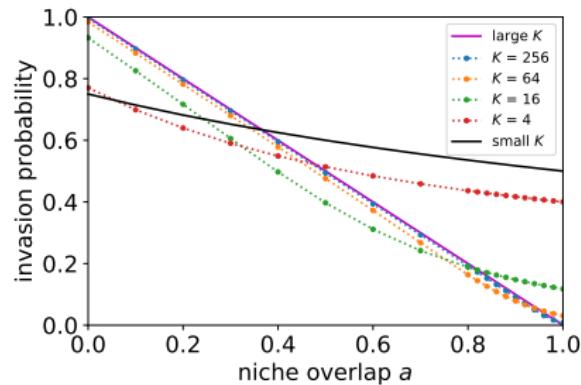
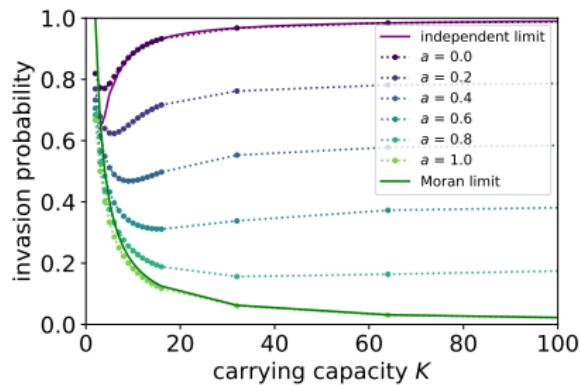
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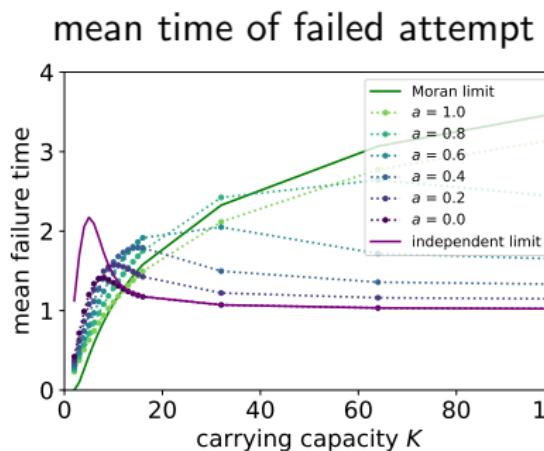
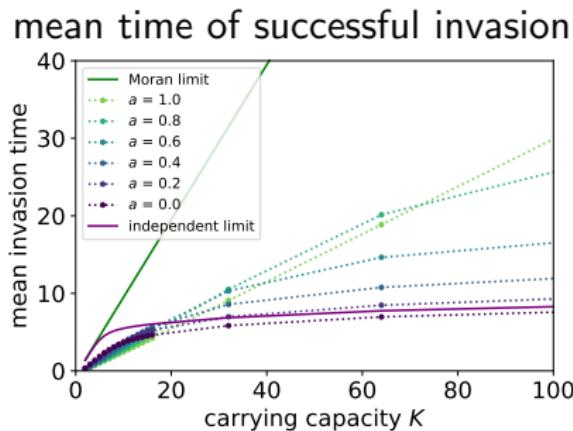
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→ **Invasion probability lessens as niche overlap increases.**
The trend is more stark for large K .

Invasion Times Are Fast



- **Successful invasion times are as expected.** Scaling varies from linear in neutral limit to logarithmic in niche limit.
- **Transients die quickly.** Except for $a = 1$ the time has an asymptote of a fast time.

Conclusions

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In particular:

- the mechanism of competition is important: faster extinction with higher birth and death rates (higher δ), competition leading to death (lower q);

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In particular:

- the mechanism of competition is important: faster extinction with higher birth and death rates (higher δ), competition leading to death (lower q);
- two species will effectively coexist unless they have exactly the same niche;
- greater niche overlap leads to longer invasion times, and less likelihood of success of an attempt;

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In general:

- with partial niche overlap exit (extinction) is slow and entrance (invasion) is fast so we expect high biodiversity

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- partial niche overlap gives a niche theory with carrying capacities modified by niche overlaps
 - that is, the time for a species to exit a system is long, and the time to enter is short, unless niches completely overlap

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Thank You

Potential Future Research

- experimental systems (microfluidics, plasmids, mitochondria)
- predator-prey model (centre fixed point)
- rock-paper-scissors model (limit cycle)
- other 3D models (e.g. chaos)
- SIR model (epidemics)
- evolving parameters (ecology and evolutionary biology)

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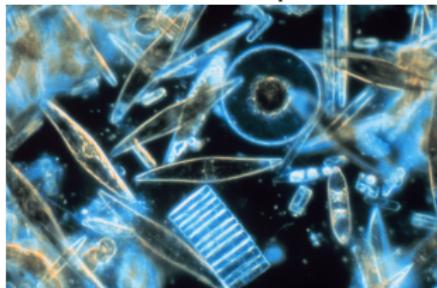
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Invasion

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Extra Slides

Paradox of the Plankton - a problem of biodiversity



corp2365, NOAA Corps Collection

- biodiversity is the number of species in an ecosystem

¹Amor, Ratzke, and Gore. *bioRxiv*, 2019

Motivation and Background

Coexistence
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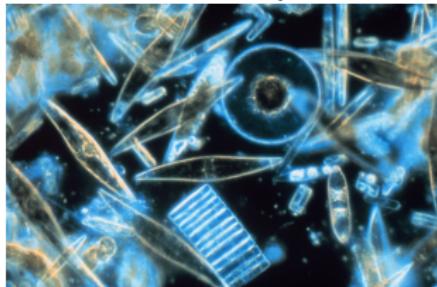
Fixation

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Extra Slides

Paradox of the Plankton - a problem of biodiversity



corp2365, NOAA Corps Collection

- biodiversity is the number of species in an ecosystem
- applications:
 - human health (gut microbiome)¹
 - planet health (conservation)
 - minimal working models
 - coalescent theory

¹Amor, Ratzke, and Gore. *bioRxiv*, 2019

Niche Theories

Coexistence
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- Competitive Exclusion: “two species cannot coexist if they share a single [ecological] niche”²

²Gause. *Science*, 1934

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- Competitive Exclusion: “two species cannot coexist if they share a single [ecological] niche”²
- Lotka-Volterra/coupled logistic

$$\begin{aligned}\frac{\dot{x}_1}{r_1 x_1} &= 1 - \frac{(x_1 + a_{12}x_2)}{K_1} \\ \frac{\dot{x}_2}{r_2 x_2} &= 1 - \frac{(a_{21}x_1 + x_2)}{K_2}.\end{aligned}$$

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Niche Theories

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- Niche Apportionment

²Gause. *Science*, 1934

Stochasticity Connects Niche and Neutral

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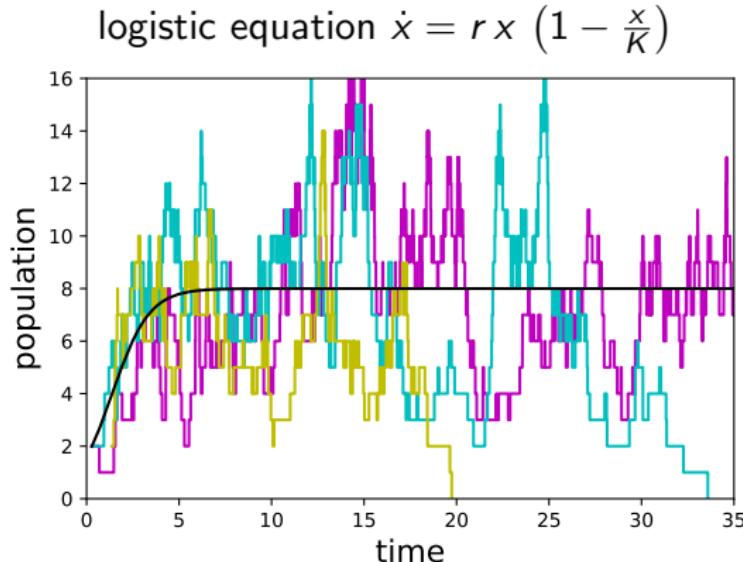
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- demographic stochasticity = fluctuations, noise

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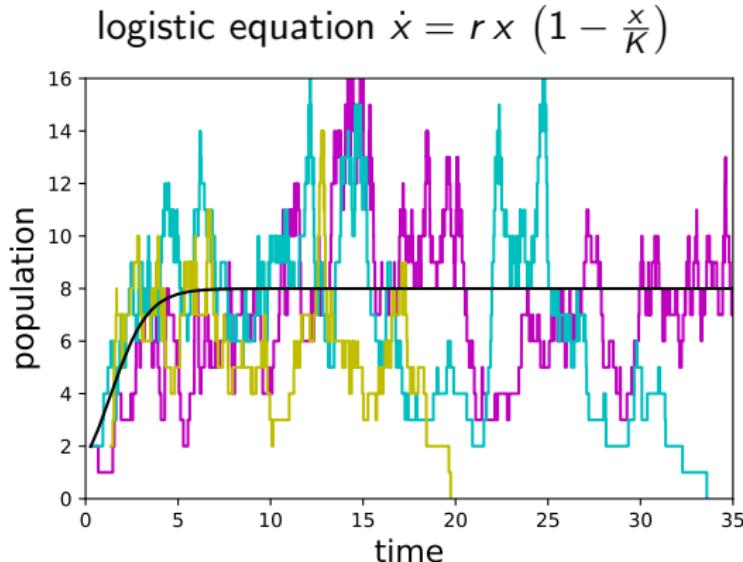
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- demographic stochasticity = fluctuations, noise
- probability of population n : P_n
- mean time to extinction: $\tau \sim e^K$

Stochastic Analysis

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Master equation

$$\frac{dP_n}{dt} = b_{n-1}P_{n-1}(t) + d_{n+1}P_{n+1}(t) - (b_n + d_n)P_n(t).$$

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Master equation

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$$\dot{\vec{P}}(t) = \hat{M}\vec{P}(t) \text{ is solved by } \vec{P}(t) = \exp\left(\hat{M}t\right)\vec{P}(0)$$

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$\dot{\vec{P}}(t) = \hat{M}\vec{P}(t)$ is solved by $\vec{P}(t) = \exp(\hat{M}t)\vec{P}(0)$

Residence time is $\langle t(s^0) \rangle_s = \int_0^\infty dt P(s, t | s^0, 0) = \hat{M}_{s, s^0}^{-1}$

so MTE given by $\hat{M}\vec{T} = -\vec{1}$

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so MTE given by $\hat{M}\vec{T} = -\vec{1}$

With a stable fixed point $\tau \sim e^K$ (actually e^K/K)

Structure of Thesis

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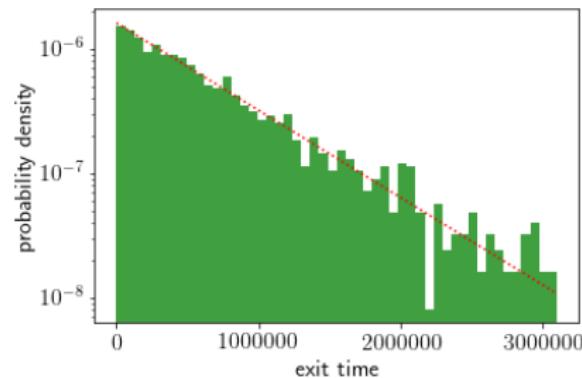
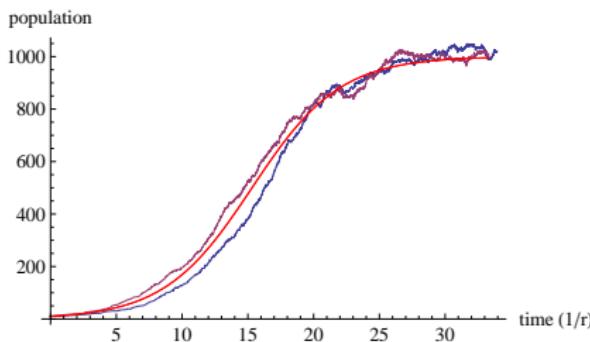
Biodiversity comes from a balance of species exiting (extinction, fixation) and species entering (invasion, immigration) the system.

Tell them what you'll tell them

- Fixation - Coupled Logistic System/LV
- Invasion - Coupled Logistic System/LV
- Maintenance - Moran with Immigration
- Discussion

Extinction within a Niche

deterministic logistic equation $\dot{x} = rx(1 - \frac{x}{K})$



Logistic Equation

deterministic logistic equation $\dot{x} = rx(1 - \frac{x}{K})$

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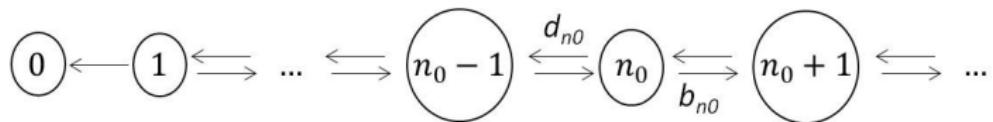
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Logistic Equation

deterministic logistic equation $\dot{x} = rx(1 - \frac{x}{K})$



Logistic Equation

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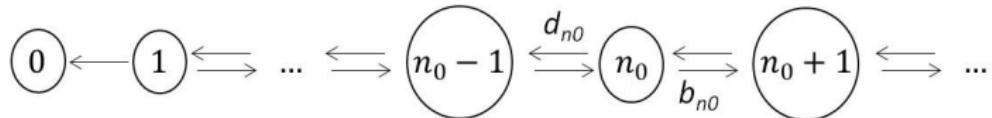
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deterministic logistic equation $\dot{x} = rx \left(1 - \frac{x}{K}\right)$



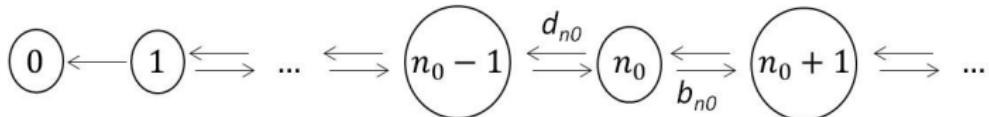
derived from a stochastic model with birth/death rates:

$$b_n = r(1 + \delta)n - \frac{r q}{K} n^2$$

$$d_n = r\delta n + \frac{r(1 - q)}{K} n^2$$

Logistic Equation

deterministic logistic equation $\dot{x} = rx \left(1 - \frac{x}{K}\right)$



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$$b_n = r(1 + \delta)n - \frac{r q}{K} n^2$$

$$d_n = r\delta n + \frac{r(1 - q)}{K} n^2$$

- 4 terms (2nd order in birth/death) so 4 total parameters
- δ gives magnitude of birth or death (rather than their average difference r)
- q shifts intraspecies interactions between reducing birth and increasing death

Quasi-Steady State

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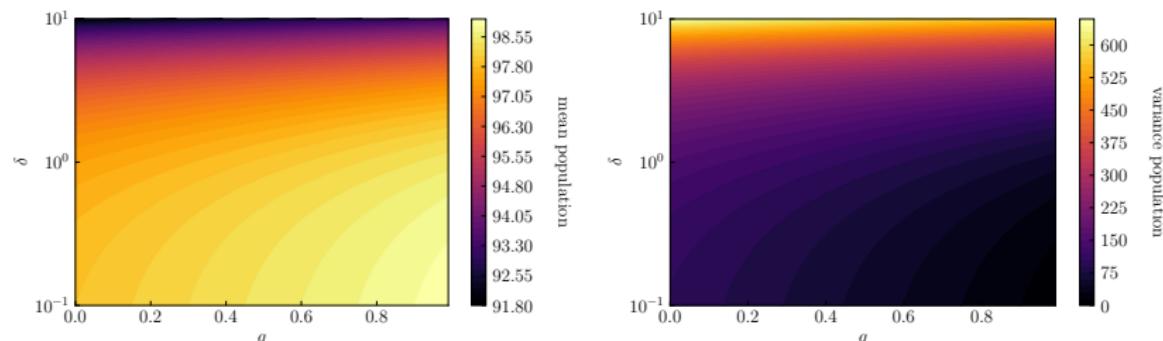
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Characterizing the quasi-stationary probability distribution function for varying δ and q . Lightness indicates an increased mean or variance in left and right respectively. Carrying capacity $K = 100$. The QSD has decreasing mean and increasing variance with increased δ or decreased q .

Mean Time to Extinction

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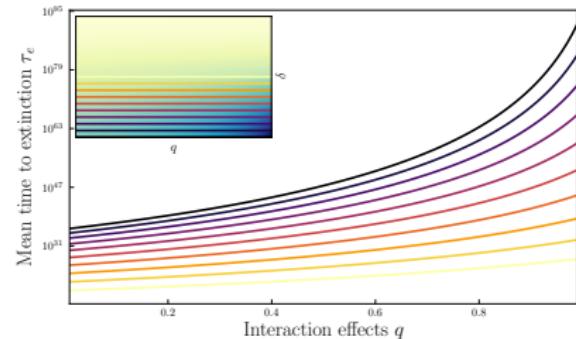
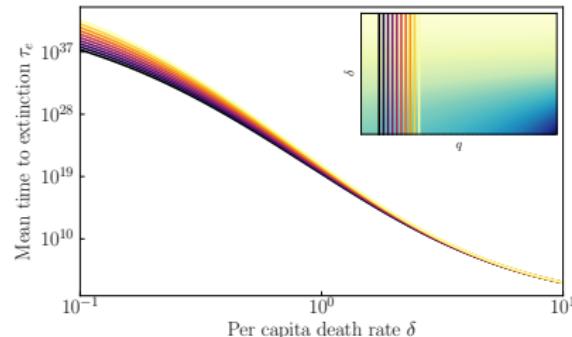
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Mean time to extinction for varying δ and q . Lightness of the line indicates an increase of q or δ in left and right respectively. Carrying capacity $K = 100$. The MTE decreases with increased δ or decreased q .

Mean Time to Extinction

Approximations

- larger fluctuations lead to shorter MTE: $\tau \approx \frac{1}{d_1 P_1}$

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Mean Time to Extinction

Approximations

- larger fluctuations lead to shorter MTE: $\tau \approx \frac{1}{d_1 P_1}$
- $\hat{M} \vec{T} = -\vec{1}$ is equivalent to $\tau(n) = \sum_{i=1}^N \frac{1}{d_i} \prod_{k=1}^{i-1} \frac{b_k}{d_k} + \sum_{j=1}^{n-1} \prod_{l=1}^j \frac{d_l}{b_l} \sum_{i=j+1}^N \frac{1}{d_i} \prod_{k=1}^{i-1} \frac{b_k}{d_k}$

Mean Time to Extinction

Approximations

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- Fokker-Planck equation $\partial_t P(x, t) = -\partial_x((b(x) - d(x))P(x, t)) + \frac{1}{2K} \partial_x^2((b(x) + d(x))P(x, t))$
- Gaussian approximation[†] $p(n) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left\{-\frac{(n-n^*)^2}{2\sigma^2}\right\}$
with $\sigma^2 = \frac{-(b_n+d_n)|_{n=n^*}}{2\partial_n(b_n-d_n)|_{n=n^*}}$

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Approximations

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 - WKB ansatz $P_n \propto \exp\left\{K \sum_i \frac{1}{K^i} S_i(n)\right\}$
with $S_0(n) = \int_{n=0}^K dn \ln\left(\frac{b_n}{d_n}\right)$ along extinction trajectory

[†]Gaussian approximation was written incorrectly in thesis.

Mean Time to Extinction Approximations

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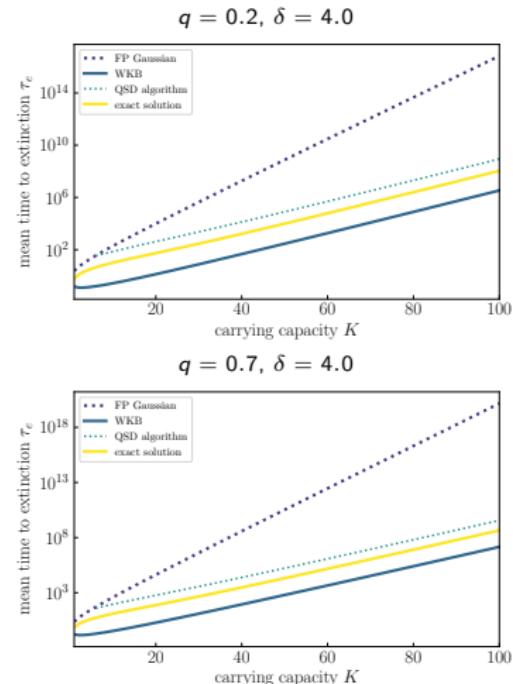
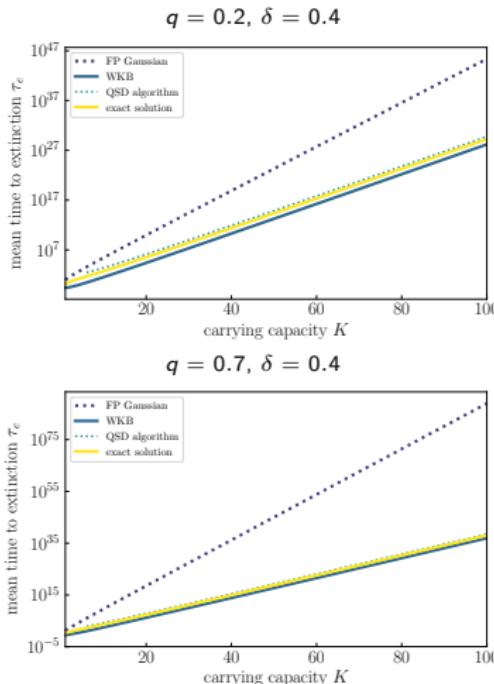
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Approximations of the MTE in various regimes of parameter space. WKB is good for low δ , is otherwise poor as FP.

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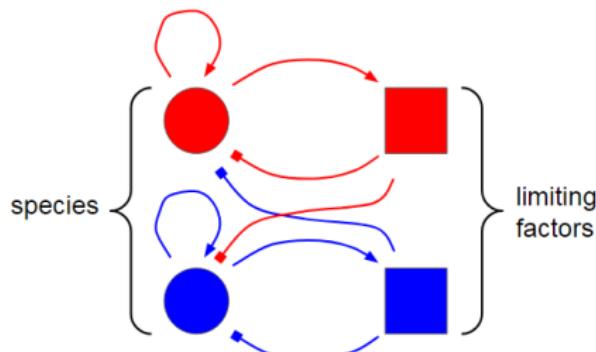
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Coupled Logistic Equations

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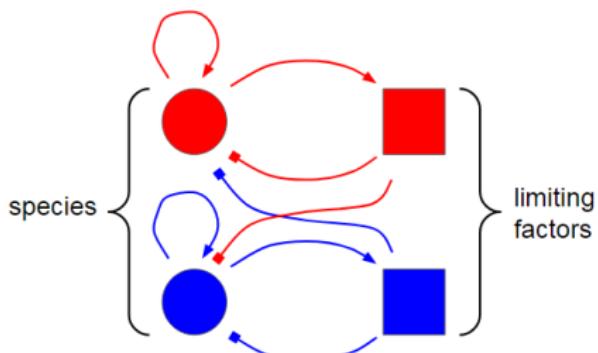
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$$\dot{x}_1 = (\beta_1 - \mu_1 - e_{11}t_1 - e_{12}t_2)x_1$$

$$\dot{x}_2 = (\beta_2 - \mu_2 - e_{21}t_1 - e_{22}t_2)x_2$$

$$\dot{t}_1 = g_{11}x_1 + g_{12}x_2 - \lambda_1 t_1$$

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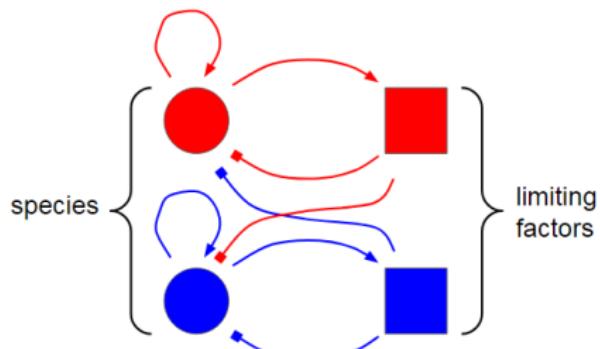
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$$\dot{\vec{x}} = \hat{R}\hat{X} \left(\vec{1} - (\hat{E}\hat{G})\vec{x} \right)$$

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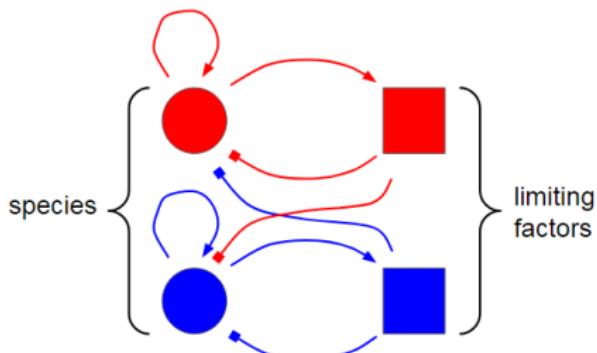
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$$\dot{\vec{x}} = \hat{R}\hat{X} \left(\vec{1} - (\hat{E}\hat{G})\vec{x} \right)$$

When the matrix $(\hat{E}\hat{G})$ is singular ($a_{12}a_{21} = 1$, complete niche overlap), the coexistence fixed point $\vec{x}^* = (EG)^{-1}\vec{1}$ does not exist. Coexistence is allowed only when neutral: $K_1/K_2 = a_{12} = 1/a_{21}$.

Coupled Logistic Includes Competitive Exclusion

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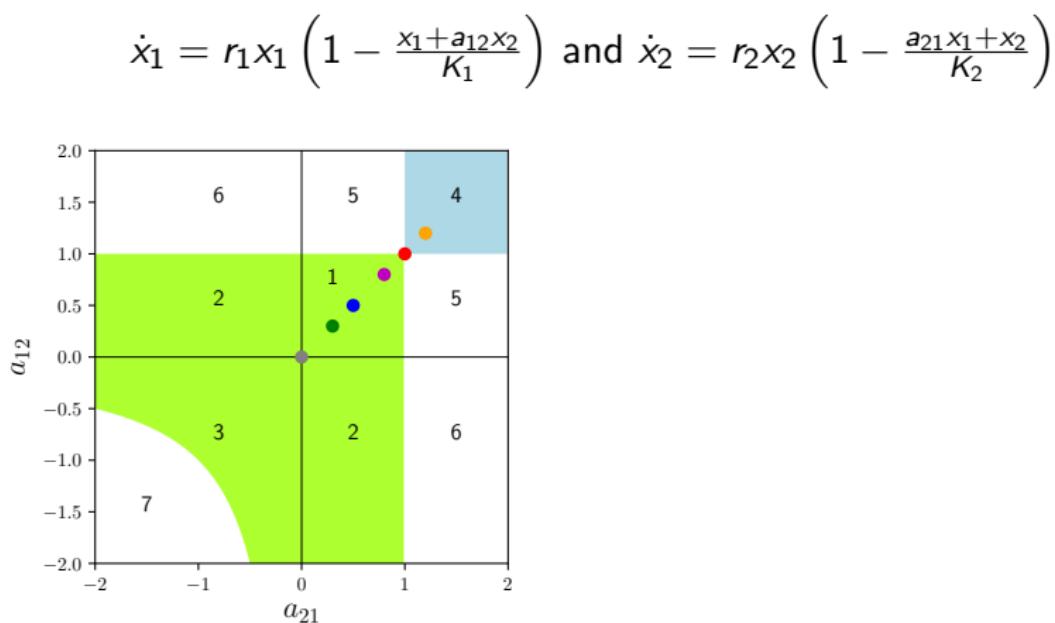
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2,6 = parasitism/predation/antagonism, 3,7 = mutualism,
4,5 = competitive exclusion, 1 = (weak) competition

Coupled Logistic Includes Competitive Exclusion

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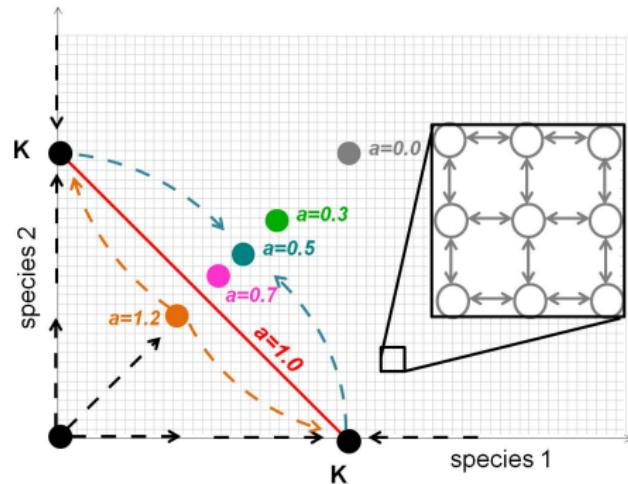
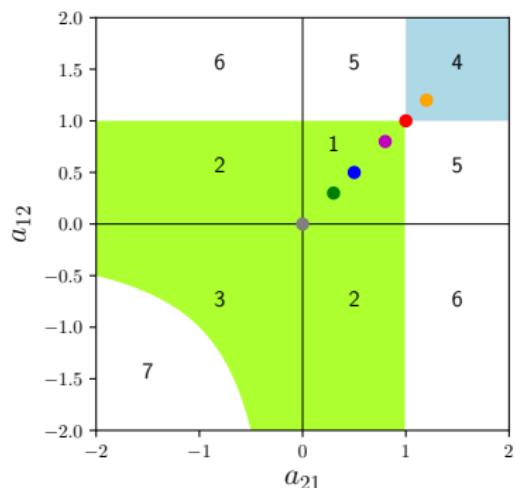
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$2, 6 =$ parasitism/predation/antagonism, $3, 7 =$ mutualism,

$4, 5 =$ competitive exclusion, $1 =$ (weak) competition

How The System Transitions To Neutrality

- for niche theory $a = 0$ (independent limit) $\tau \sim e^K$
- for neutral theory $a = 1$ (Moran limit) $\tau \sim K$

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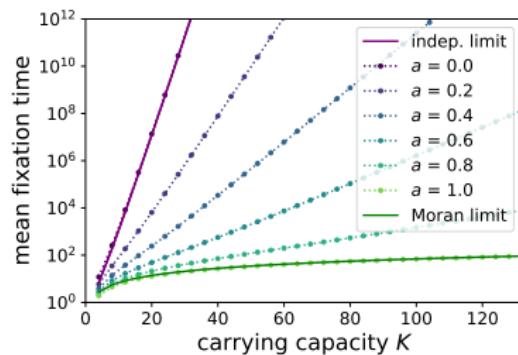
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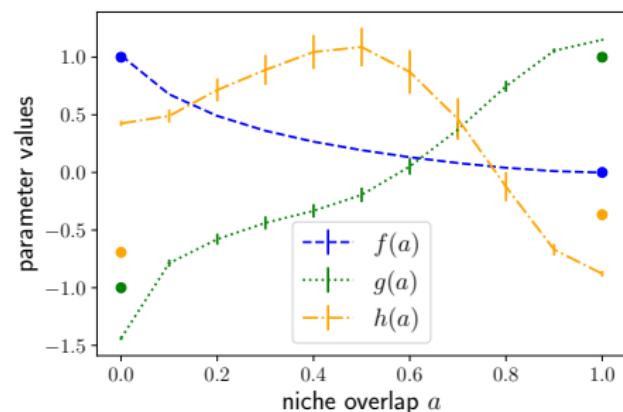
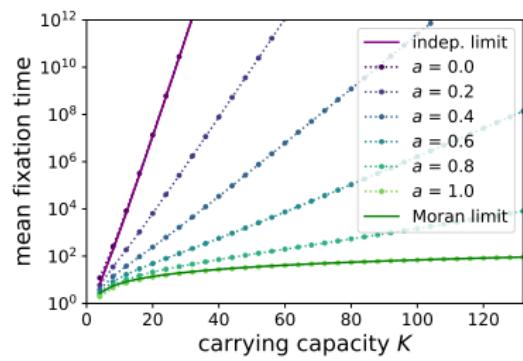
How The System Transitions To Neutrality

- for niche theory $a = 0$ (independent limit) $\tau \sim e^K$
- for neutral theory $a = 1$ (Moran limit) $\tau \sim K$
- ansatz: $\tau(a, K) = e^{h(a)} K^{g(a)} e^{f(a)K}$

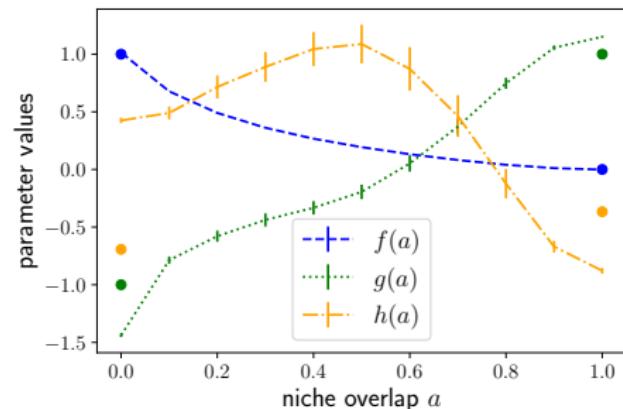
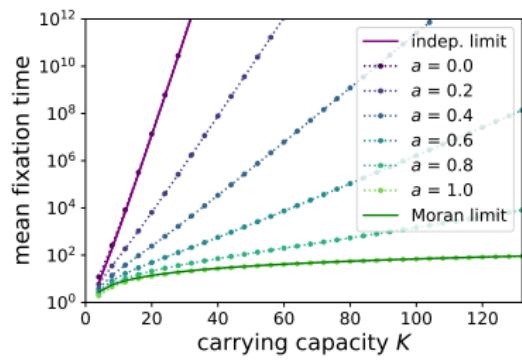
How The System Transitions To Neutrality



How The System Transitions To Neutrality



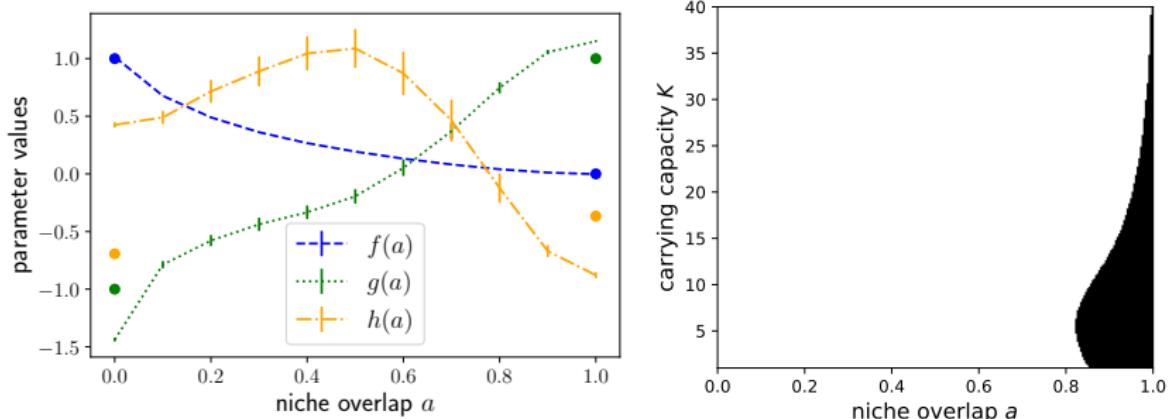
How The System Transitions To Neutrality



→ Effective coexistence except with complete niche overlap.

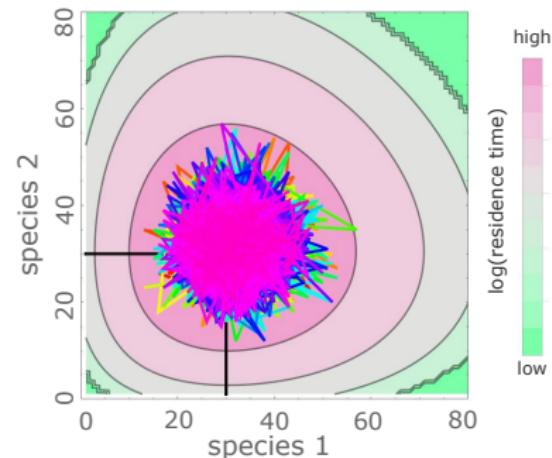
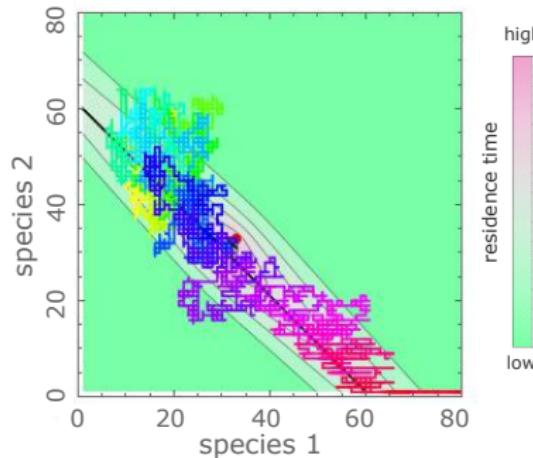
Exponential Scaling With K Is Long

■ ansatz: $\tau(a, K) = e^{h(a)} K^{g(a)} e^{f(a)K}$



Route to Fixation

$$\text{Residence time } \langle t(s^0) \rangle_s = \int_0^\infty dt P(s, t | s^0, 0) = \hat{M}_{s, s^0}^{-1}$$



The system samples multiple trajectories on its way to fixation.
Left: Complete niche overlap limit, $a = 1$, for $K = 64$.
Right: Independent limit with $a = 0$ and $K = 32$.

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$f(a)$ (exponential dependence of MTE) approaches zero monotonically as niche overlap reaches Moran limit $a = 1$

- only for complete niche overlap will there be no exponential dependence: fixation will be rapid

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$f(a)$ (exponential dependence of MTE) approaches zero monotonically as niche overlap reaches Moran limit $a = 1$

- only for complete niche overlap will there be no exponential dependence: fixation will be rapid
- any niche mismatch allows for exponential dependence on K , which is typically large
 - any niche mismatch implies effective coexistence

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$f(a)$ (exponential dependence of MTE) approaches zero monotonically as niche overlap reaches Moran limit $a = 1$

- only for complete niche overlap will there be no exponential dependence: fixation will be rapid
- any niche mismatch allows for exponential dependence on K , which is typically large
 - any niche mismatch implies effective coexistence
- small departure from neutrality gives a niche theory

**Coexistence
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Invasion

Invasion - Definition And Expectations

Invasion is going from one organism to half the population.

- invasion balances extinction to maintain biodiversity

Invasion - Definition And Expectations

Invasion is going from one organism to half the population.

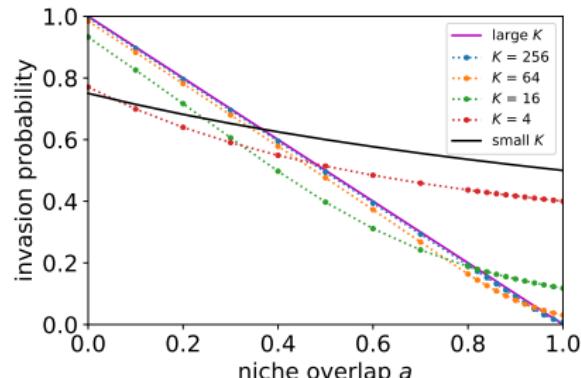
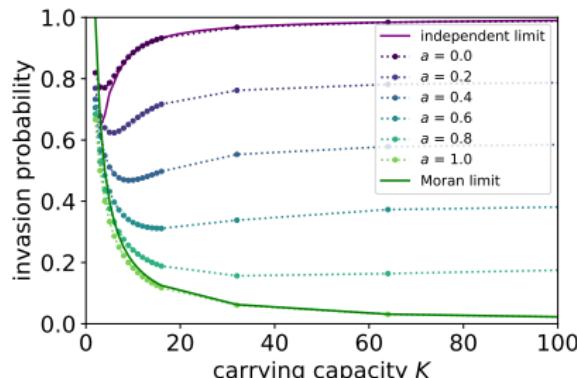
- invasion balances extinction to maintain biodiversity
- invasion in niche/independent limit should be fast (logarithmic)

Invasion - Definition And Expectations

Invasion is going from one organism to half the population.

- invasion balances extinction to maintain biodiversity
- invasion in niche/independent limit should be fast (logarithmic)
- invasion in neutral limit should be slower (linear)

Invasion Probability



Probability of a successful invasion. Left: Numerical results, from $a = 0$ at the top to $a = 1$ at the bottom. The purple solid line is the expected analytical solution in the independent limit. The green solid line is the prediction of the Moran model in the complete niche overlap case. Right: The red data show the results for carrying capacity $K = 4$, and suggest the solid black line $\frac{b_{mut}}{b_{mut} + d_{mut}}$ is an appropriate small carrying capacity limit. Successive lines are at larger system size, and approach the solid magenta line of $1 - d_{mut}/b_{mut} \approx 1 - a$.

Invasion Probability

Coexistence
and
Extinction of
Competing
Species

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Extinction

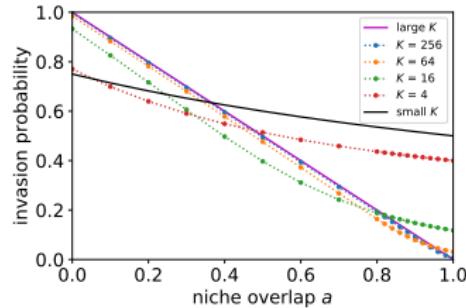
Fixation

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Invasion probability
approaches $1 - a$.



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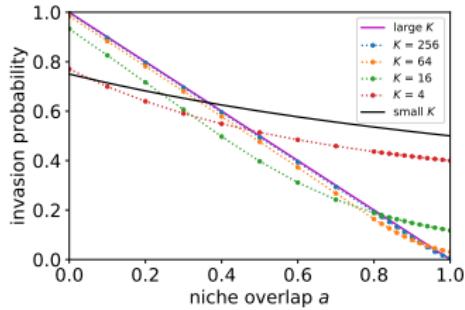
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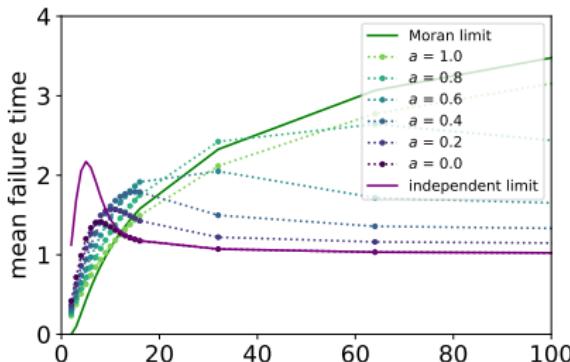
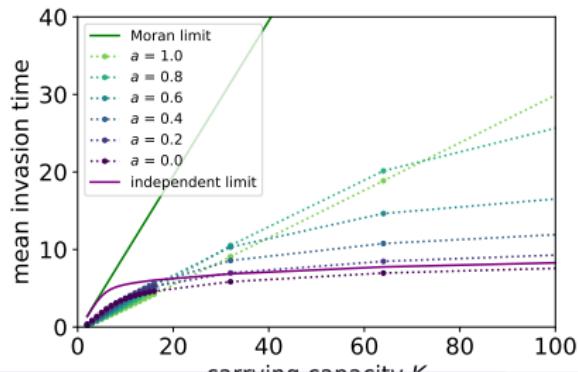
Extra Slides

Invasion probability
approaches $1 - a$.

Successful invasion
goes from logarithmic
to linear in K .



Failed invasion
attempts go
from constant to
logarithmic in K .



Invasion Times

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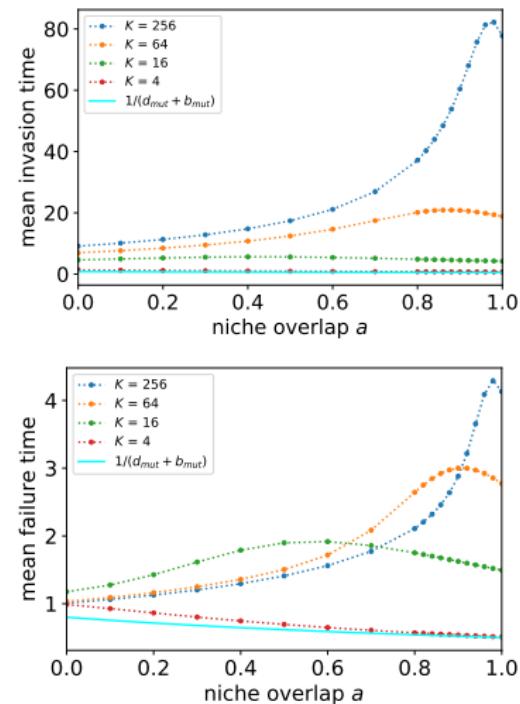
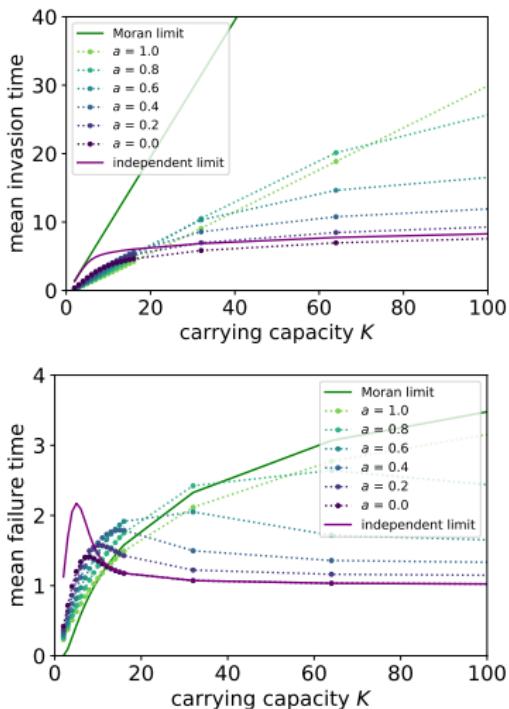
Extinction

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Mean time of a successful or failed invasion attempt. Left: Mean time vs K . Right: Mean line vs a . Upper: Mean time conditioned on eventual invasion success. Lower: Mean time conditioned on failed attempt.

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- we can rationalize most of the behaviour
- some questions remain (why is there a max time for failed attempts, why do probabilities remain intermediate for large K)
- implication is that any invasion attempt (whether successful or not) is faster than fixation times
- comparison of interest is invasion attempt times with immigration rate

Maintenance of a Species with Repeated Immigration

Moran Model With Immigration

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Immigration comes from a constant reservoir of focal species fraction $g = n_{\text{reservoir}}/K_{\text{reservoir}}$ at a rate ν . Defining $f = n/K$, we have the following transition rates.

transition	function	value
$n \rightarrow n + 1$	$b(n)$	$f(1 - f)(1 - \nu) + \nu g(1 - f)$
$n \rightarrow n - 1$	$d(n)$	$f(1 - f)(1 - \nu) + \nu(1 - g)f$
$n \rightarrow n$	$1 - b - d$	$(f^2 + (1 - f)^2)(1 - \nu) + \nu(gf + (1 - g)(1 - f))$

Moran Model With Immigration

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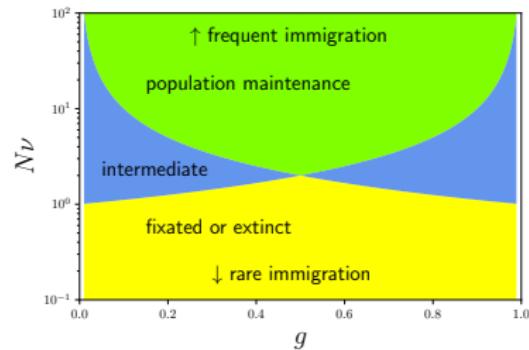
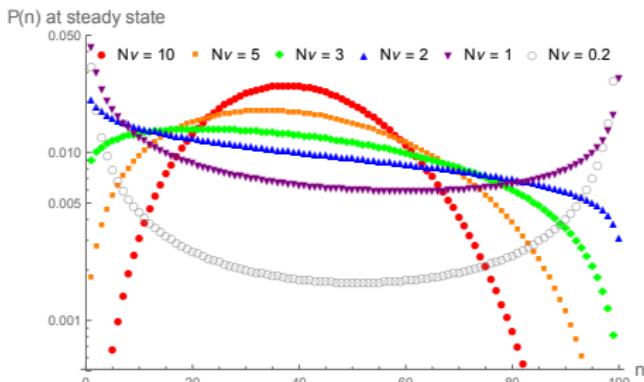
The crucial comparison for biodiversity is between $1/\nu$ and the invasion times previously described.

Steady State Results

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Metapopulation focal fraction is $g = 0.4$, local system size $N = 100$, immigration rate ν is given by the colour.

For high immigration rate the distribution should be centered near the metapopulation fraction $g N$ whereas for low immigration the system spends most of its time fixated. What is "high" and "low" depends on g .

Infrequent Immigration

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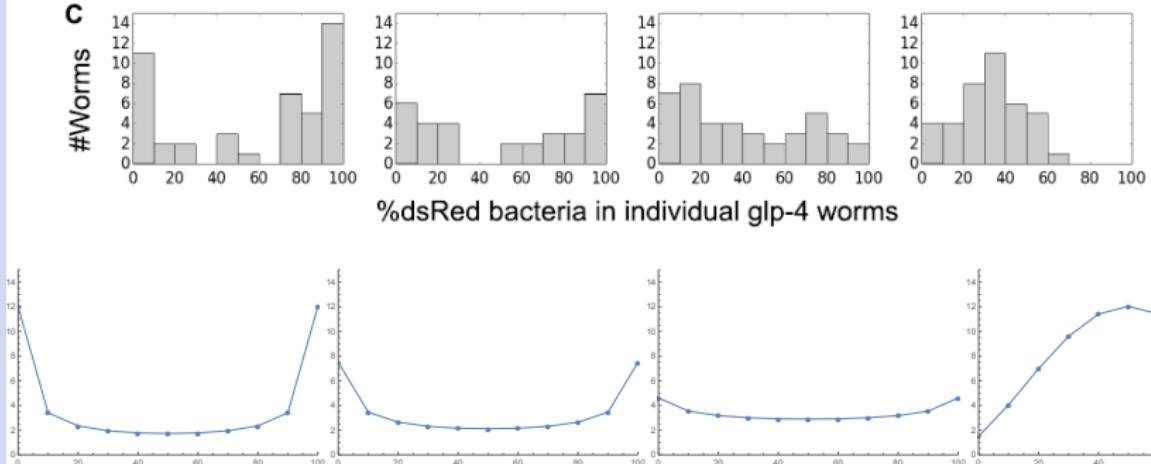
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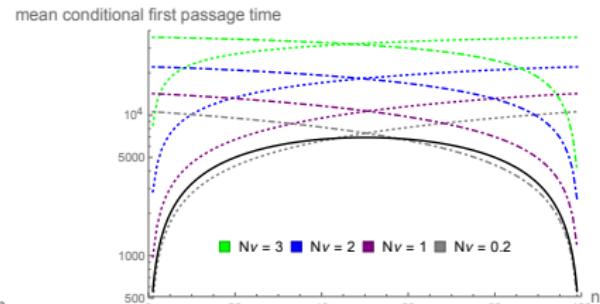
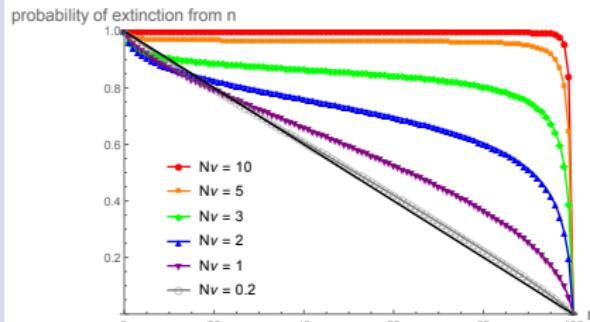
Extra Slides

The model recovers qualitative experimental results.
(See Vega and Gore, *PLoS Biology*, 2017.)

C



First Passage Results



Metapopulation focal fraction is $g = 0.4$, local system size $N = 100$, immigration rate ν is given by the colour. The black line is the regular Moran result without immigration.

When the immigrant is mostly not from the focal species ($g < 0.5$) immigration increases the likelihood of the focal species going extinct before fixating. Conditioned first passage times are longer when immigration is more frequent, rare events take even longer still.

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- when immigration is uncommon
 $(N\nu < \min(1/g, 1/(1-g)))$, focal species either fixated or extinct most of the time
- when immigration is common
 $(N\nu > \max(1/g, 1/(1-g)))$, focal species is maintained at moderate abundance in the system, specifically gN
- immigration increases the times to (temporary) fixation or extinction

**Coexistence
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Competing
Species**

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Conclusions

- higher commensurate birth and death rates (*i.e.* higher δ , lower q) leads to faster extinction;

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- higher commensurate birth and death rates (*i.e.* higher δ , lower q) leads to faster extinction;
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- similarly, greater niche overlap leads to longer invasion times, and less likelihood of success of an attempt;

Conclusions

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Conclusions

- higher commensurate birth and death rates (*i.e.* higher δ , lower q) leads to faster extinction;
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- two species will effectively coexist unless they have exactly the same niche;
- similarly, greater niche overlap leads to longer invasion times, and less likelihood of success of an attempt;
- in Moran model with immigration, a focal species at moderate size if $K\nu > 1/g$;
- incomplete niche overlap is a niche theory with carrying capacities modified by niche overlaps;
- complete niche overlap (neutralism) on an island with immigration has abundance curve like mainland for species with $g_i > 1/K\nu$; other species are transients.

Utility Of My Results

Coexistence
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Extra Slides

To reiterate:

- human health (gut microbiome)
- planet health (conservation)
- minimal working models
- coalescent theory
- small population systems like:
 - microfluidics
 - plasmids
 - mitochondria