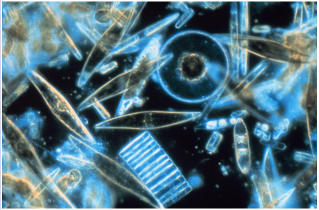
Extinction, Fixation, and Invasion in an Ecological Niche

MattheW Badali

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

Paradox of the Plankton
a problem of biodiversity



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Biodiversity: Number And Distribution Of Species

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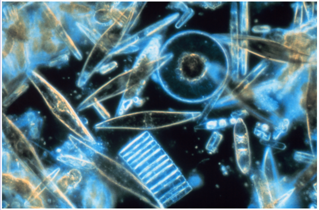

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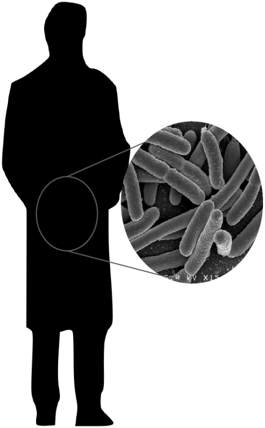
Gut Microbiome
important to health



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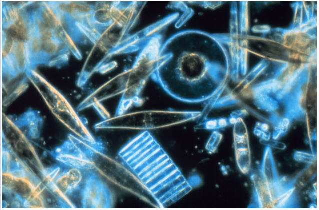

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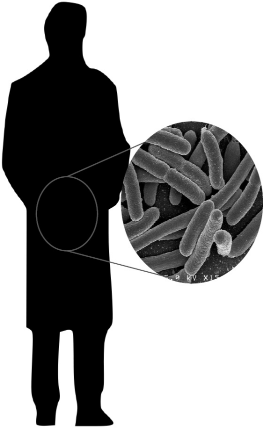

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Conservationism

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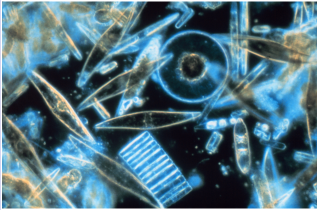

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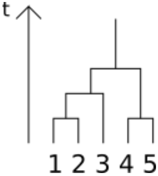
Coalescent Trees



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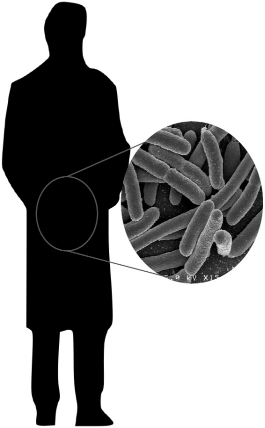

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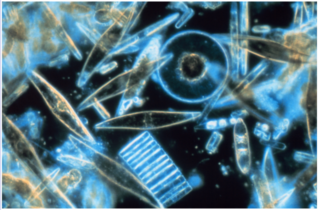

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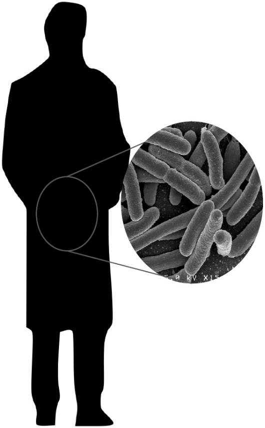

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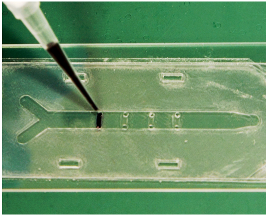
Conservationism

Small Populations
e.g. microfluidics



Microfluidic Device, Cooksey/NIST

Niche Apportionment Explains Abundance Curves

Niche Theories - each in their own niche

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

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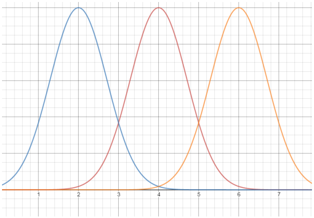

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- with stochasticity, mean time to extinction $\tau \sim e^{K}$

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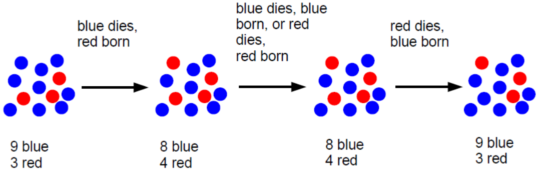

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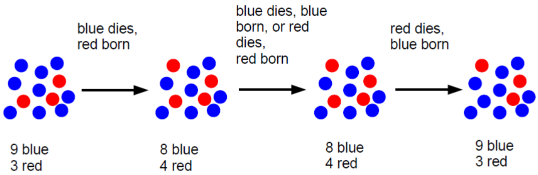

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Biodiversity comes from a balance of species exiting (fixation, extinction) and species entering (invasion) the system: what are the timescales?

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

$\rightarrow$ **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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- Fokker-Planck:
  $\partial_t P_x = -\partial_x\Big((b_x - d_x)P_x\Big) + \frac{1}{2K}\partial_x^2\Big((b_x + d_x)P_x\Big)$
  - $P_n \approx \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left\{-\frac{(n-n^*)^2}{2\sigma^2}\right\}$ with $\sigma^2 = \frac{-(b_n+d_n)|_{n^*}}{2\partial_n(b_n-d_n)|_{n^*}}$

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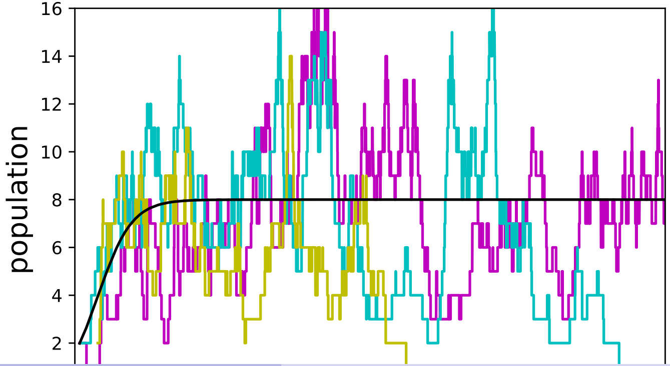
- WKB ansatz: $P_n \propto \exp\left\{K\sum_i \frac{1}{K^i} S_i(n)\right\}$ with
  $S_0(n) = \frac{1}{K}\int_0^n dx \ln\left(b_x/d_x\right)$ along extinction trajectory

Extinction within a Niche

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



Logistic Equation Has Two Hidden Parameters

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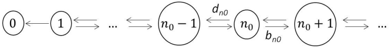

$$b_n = r\,(1+\delta)\,n - \frac{r\,q}{K} n^2$$

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

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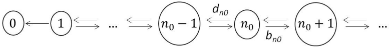

$$b_n = r\,(1+\delta)\,n - \frac{r\,q}{K}n^2$$

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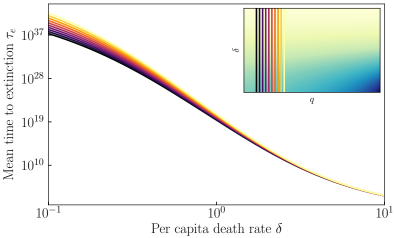
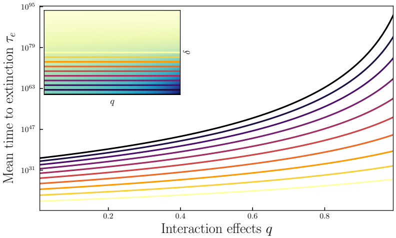
- δ gives magnitude of birth or death (rather than their average difference, the growth rate r)
- q shifts intraspecies interactions from increasing death rate ($q \sim 0$) to reducing birth rate ($q \sim 1$)

Mean Time to Extinction Depends On Interactions





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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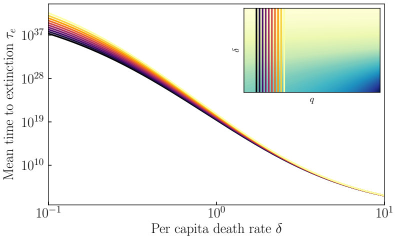
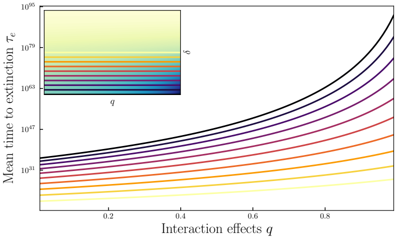
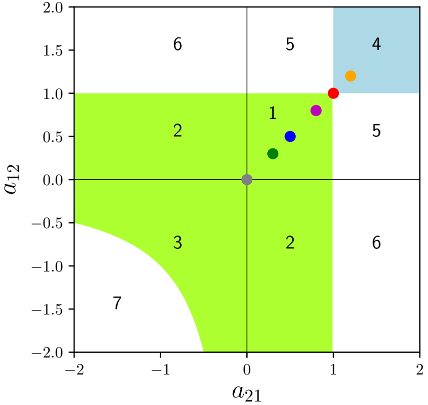




Carrying capacity $K = 100$, growth rate $r = 1$. The mean time to extinction (MTE) decreases with increased δ or decreased q.

$\rightarrow$ **increasing birth and death rates (e.g. competition increasing death rate) reduces MTE.**

Fixation versus Coexistence of Two Competing Species



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

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

2,6 = parasitism/predation,

3,7 = mutualism,

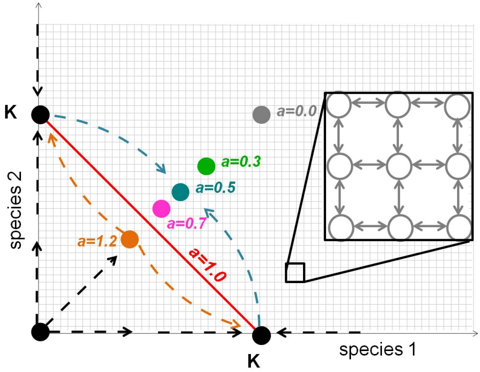
4,5 = competitive exclusion,

1 = (weak) competition

Coupled Logistic Has Niche And Neutral Limits

symmetric case: $r_1 = r_2 = r$, $K_1 = K_2 = K$, $a_{12} = a_{21} = a$

$$\dot{x}_1 = r\, x_1 \left(1 - \frac{x_1 + a\, x_2}{K}\right) \text{ and } \dot{x}_2 = r\, x_2 \left(1 - \frac{a\, x_1 + x_2}{K}\right)$$



- 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

niche theory
$\tau \sim e^K$

neutral theory
$\tau \sim K$

How The System Transitions To Neutrality

niche theory — neutral theory

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

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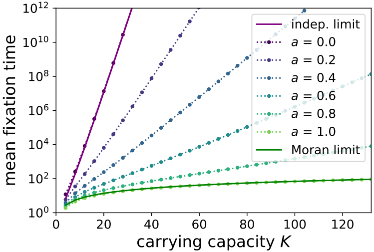

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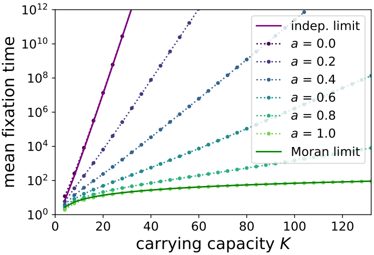

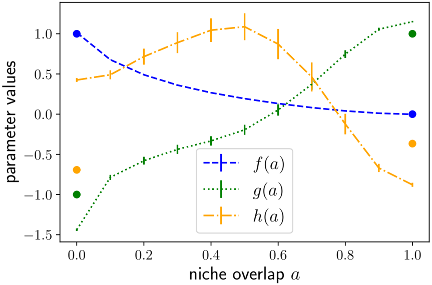

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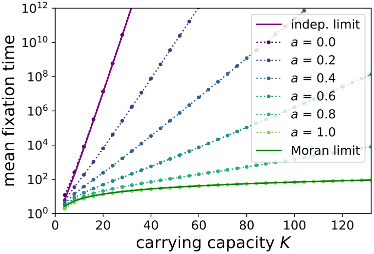
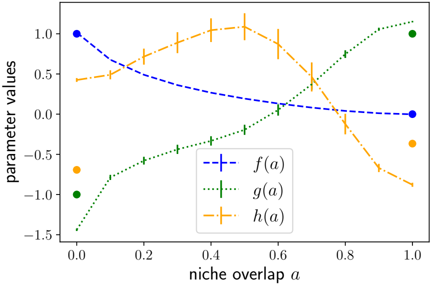
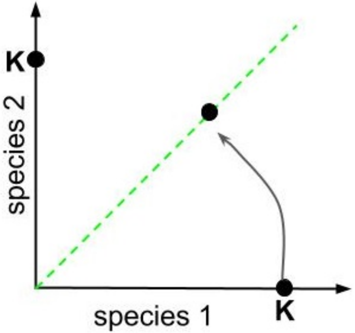




→Effective coexistence except for complete niche overlap

The Timescale of Invasion of a Second Species



- invasion balances extinction to maintain biodiversity

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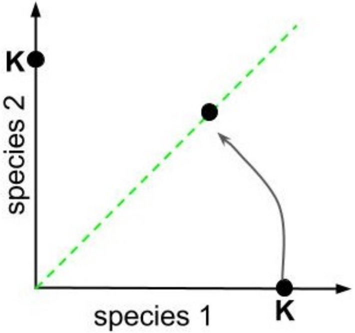
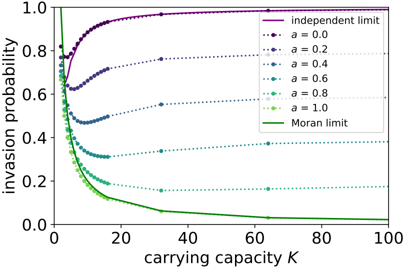
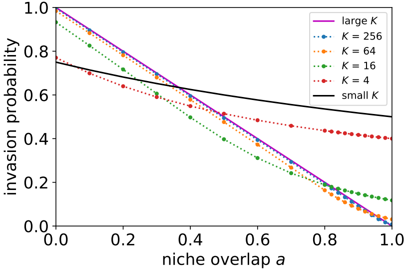


- invasion balances extinction to maintain biodiversity
- invasion is going from one organism to half the population
- invasion into a niche is deterministic, fast (logarithmic)
- invasion into Moran is linear

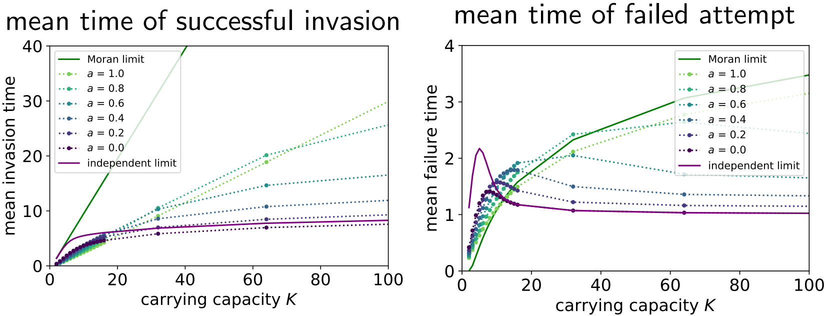
Invasion Less Probable As Niche Overlap Increases





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

Invasion Times Are Fast



$\rightarrow$ **Successful invasion times are as expected.** Scaling varies from linear in neutral limit to logarithmic in niche limit.

$\rightarrow$ **Transients die quickly.** Except for $a = 1$ the time has an asymptote of a fast time.

Conclusions

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To summarize:

- 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;
- incomplete 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

Thank You

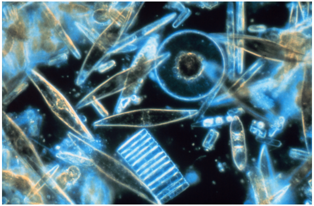
Potential Future Research

- 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)

Table of Contents

Motivation and Background

Paradox of the Plankton - a problem of biodiversity



corp2365, NOAA Corps Collection

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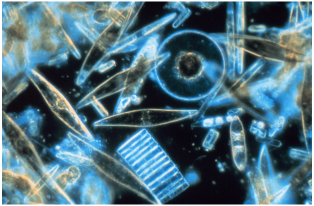

corp2365, NOAA Corps Collection

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

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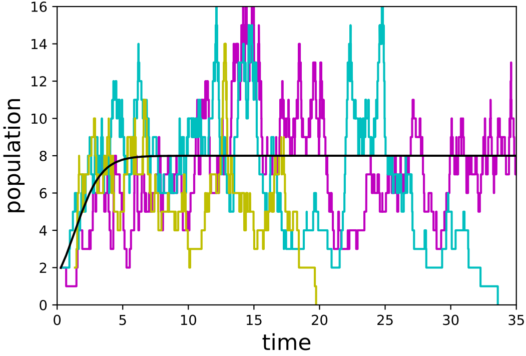
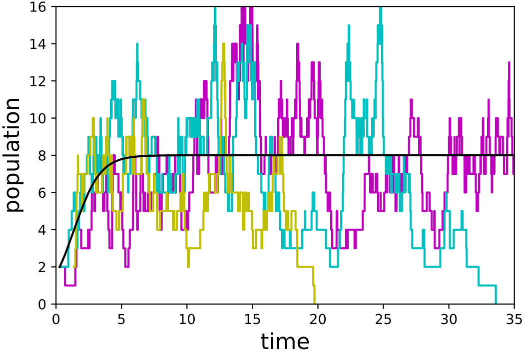


- demographic stochasticity = fluctuations, noise

Stochasticity Connects Niche and Neutral

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



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

Stochastic Analysis

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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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

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

Logistic Equation

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

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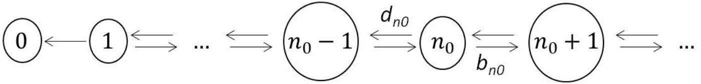
$$0 \leftarrow 1 \rightleftarrows \ldots \rightleftarrows n_0 - 1 \underset{}{\overset{d_{n0}}{\rightleftarrows}} n_0 \underset{b_{n0}}{\rightleftarrows} n_0 + 1 \rightleftarrows \ldots$$

Logistic Equation

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



derived from a stochastic model with birth/death rates:

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

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

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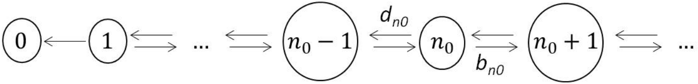

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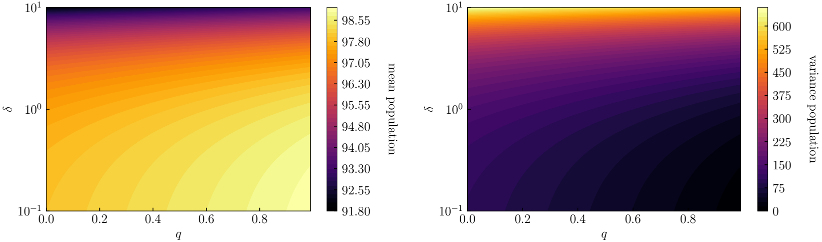
$$d_n = r\,\delta\,n + \frac{r\,(1-q)}{K}n^2$$

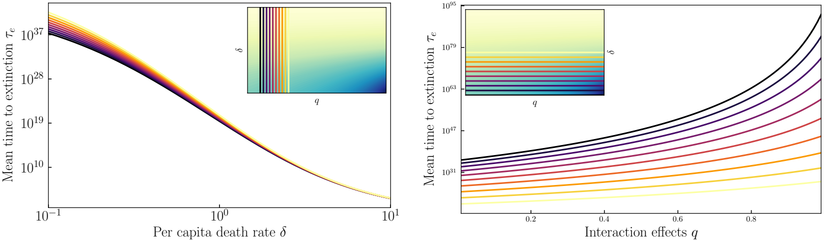
- 4 terms (2nd order in birth/death) so 4 total parameters
- δ gives magnitude of birth or death (rather than their average difference r)
- q shifts intraspecies interactions between reducing birth and increasing death

Quasi-Steady State



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



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.

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

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 $\tau(n) = \sum_{i=1}^{N} \frac{1}{d_i} \prod_{k=1}^{i-1} \frac{b_k}{d_k} + \sum_{j=1}^{n-1} \prod_{l=1}^{j} \frac{d_l}{b_l} \sum_{i=j+1}^{N} \frac{1}{d_i} \prod_{k=1}^{i-1} \frac{b_k}{d_k}$

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- Fokker-Planck equation $\partial_t P(x,t) = -\partial_x \big((b(x) - d(x))P(x,t)\big) + \frac{1}{2K}\partial_x^2 \Big((b(x) + d(x))P(x,t)\Big)$
  - 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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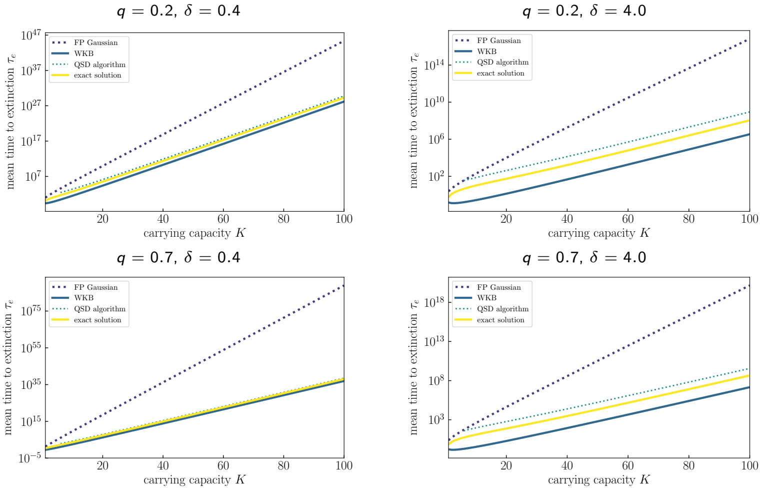
- WKB ansatz $P_n \propto \exp\left\{K\sum_i \frac{1}{K^i} S_i(n)\right\}$ with $S_0(n) = \int_{n=0}^{K} dn \ln\left(\frac{b_n}{d_n}\right)$ along extinction trajectory

† Gaussian approximation was written incorrectly in thesis.

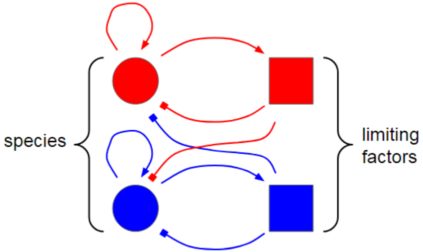
Mean Time to Extinction
Approximations



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

Fixation

Coupled Logistic Equations



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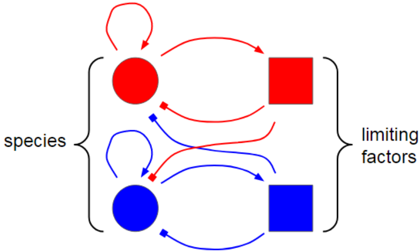

$$\dot{x}_1 = (\beta_1 - \mu_1 - e_{11} t_1 - e_{12} t_2) x_1$$
$$\dot{x}_2 = (\beta_2 - \mu_2 - e_{21} t_1 - e_{22} t_2) x_2$$

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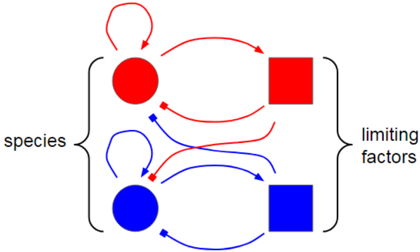

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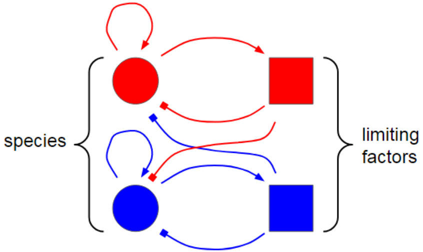

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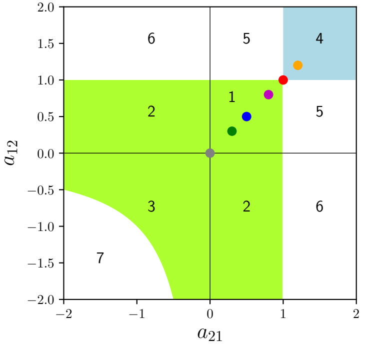
When the matrix $(\hat{E}\hat{G})$ is singular ($a_{12}a_{21} = 1$, complete niche overlap), the coexistence fixed point $\vec{x}^* = (EG)^{-1}\vec{1}$ does not exist. Coexistence is allowed only when neutral: $K_1/K_2 = a_{12} = 1/a_{21}$.

Coupled Logistic Includes Competitive Exclusion

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



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

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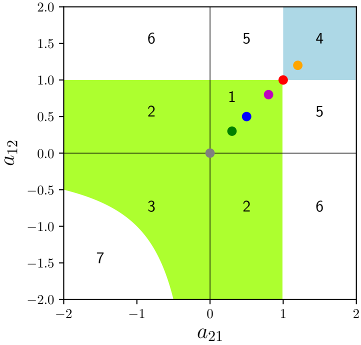

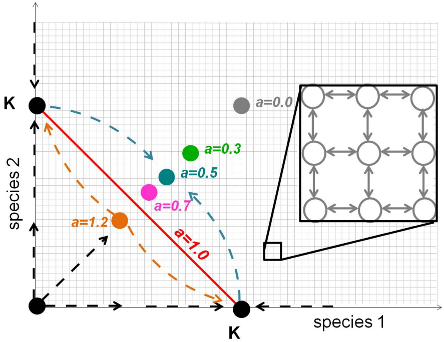

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How The System Transitions To Neutrality

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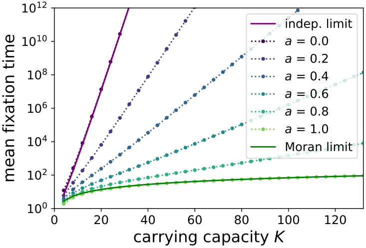

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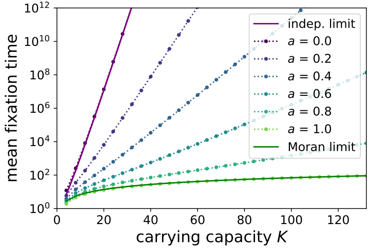

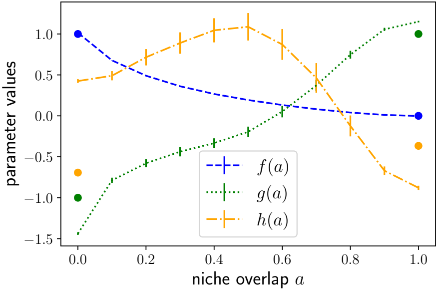

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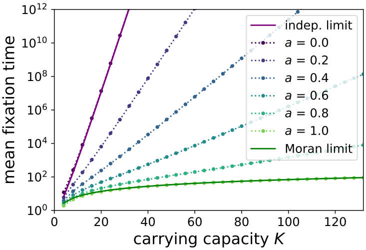
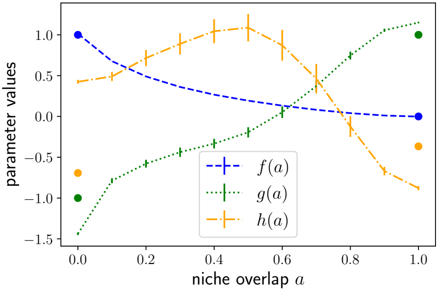
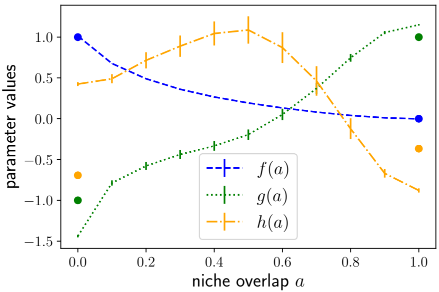


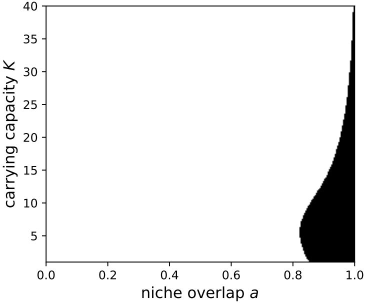


→ **Effective coexistence except with complete niche overlap.**

Exponential Scaling With K Is Long

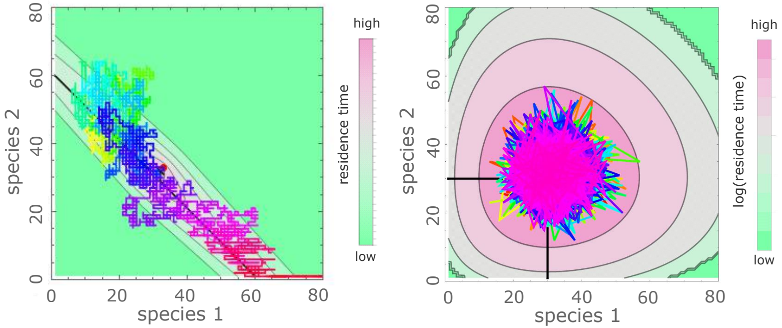
- ansatz: $\tau(a, K) = e^{h(a)} K^{g(a)} e^{f(a)K}$





Route to Fixation

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



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 $K = 32$.

Discussion

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

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- 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

Invasion

Invasion - Definition And Expectations

Invasion is going from one organism to half the population.

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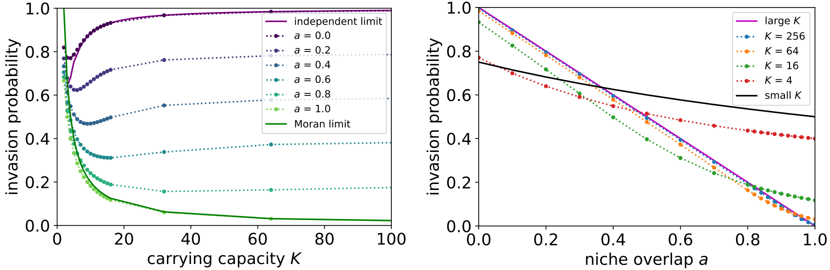
- invasion in niche/independent limit should be fast (logarithmic)
- invasion in neutral limit should be slower (linear)

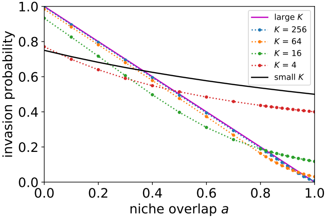
Invasion Probability



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

Invasion probability approaches $1 - a$.



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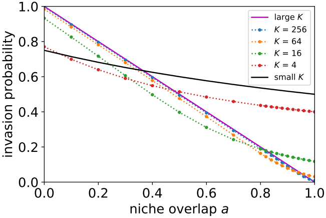
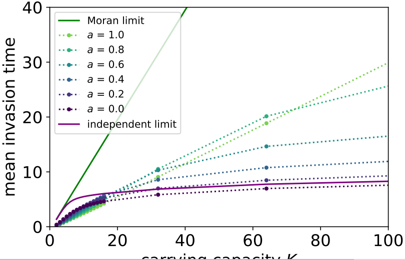
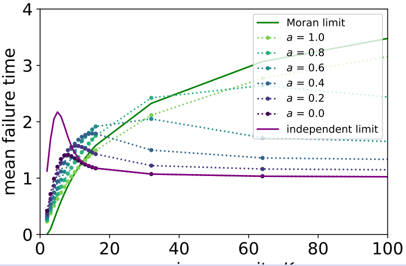


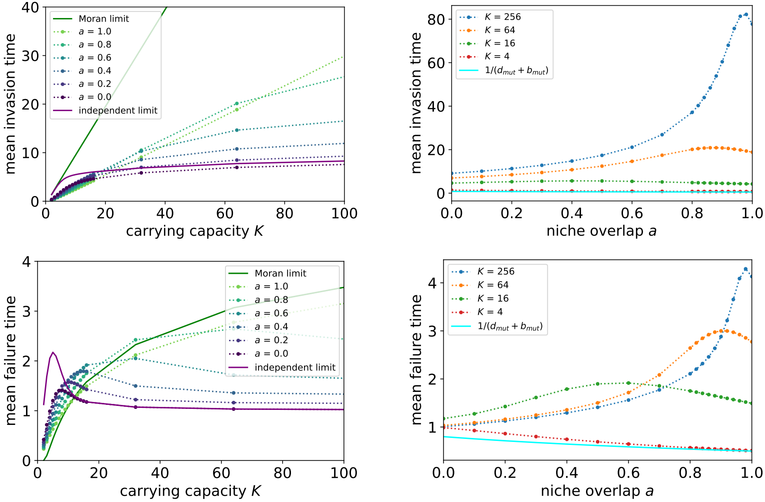
Successful invasion goes from logarithmic to linear in K.

Failed invasion attempts go from constant to logarithmic in K.





Invasion Times



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.

Discussion

- 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

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

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

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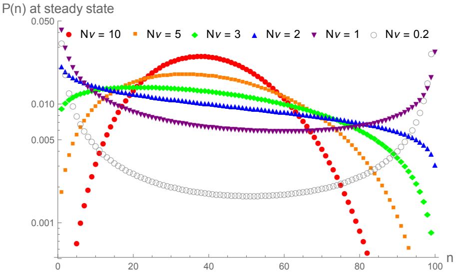
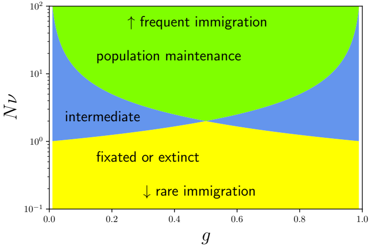
The crucial comparison for biodiversity is between $1/\nu$ and the invasion times previously described.

Steady State Results



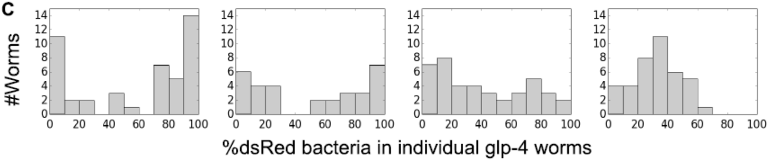


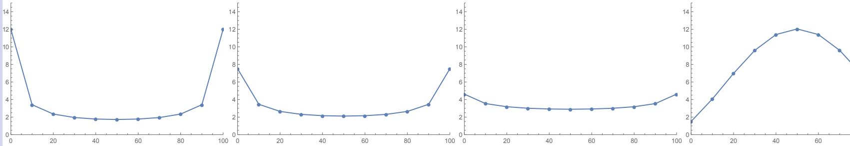
Metapopulation focal fraction is $g = 0.4$, local system size $N = 100$, immigration rate ν is given by the colour.

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.

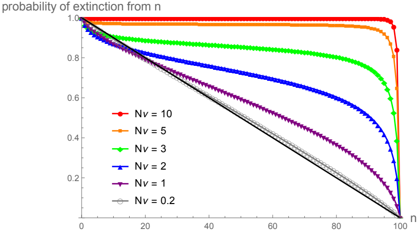
Infrequent Immigration

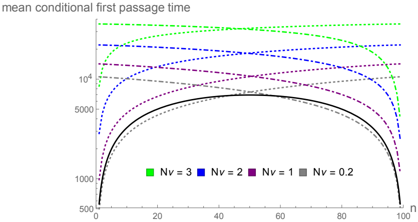
The model recovers qualitative experimental results.
(See Vega and Gore, *PLoS Biology*, 2017.)





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.

Discussion

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

Discussion

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- similarly, greater niche overlap leads to longer invasion times, and less likelihood of success of an attempt;
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- incomplete niche overlap is a niche theory with carrying capacities modified by niche overlaps;
- complete niche overlap (neutrality) 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

To reiterate:

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