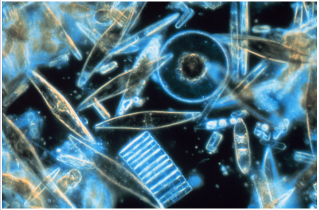
Extinction, Fixation, and Invasion in an Ecological Niche

MattheW Badali

Final defense
performed as a requirement for
the degree of Doctor of Philosophy
5 September 2019

Biodiversity: Number And Distribution Of Species

Paradox of the Plankton
a problem of biodiversity



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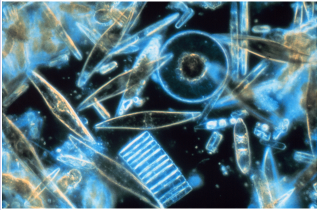

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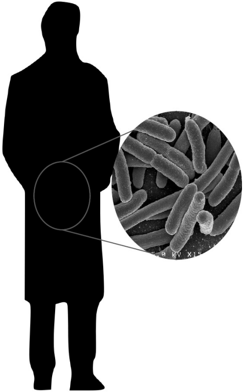
Gut Microbiome
important to health



E. coli, Rocky Mountain Laboratories, NIAID, NIH

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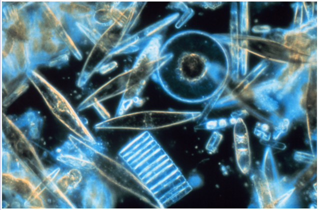

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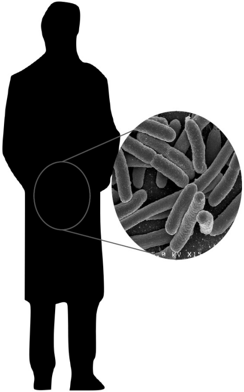

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Conservationism

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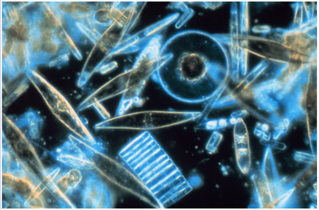

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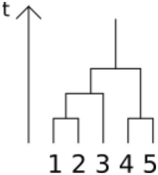
Coalescent Trees



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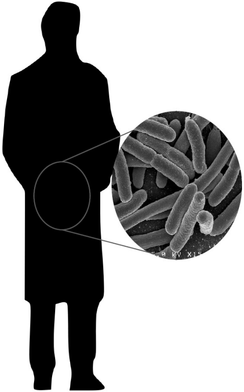

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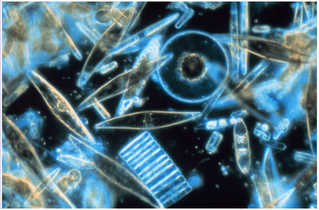

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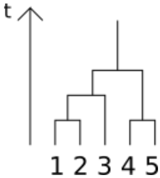

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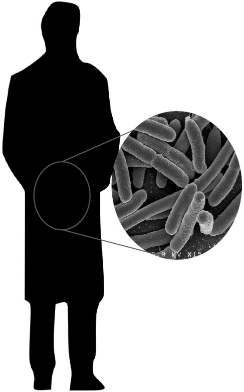

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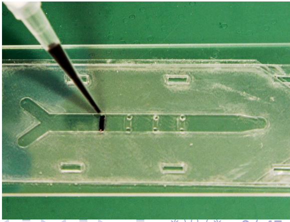
Conservationism

Small Populations
e.g. microfluidics



Microfluidic Device, Cooksey/NIST

Niche Theories - Each Species In Its Own Niche

- niche/resource apportionment explains abundance curve

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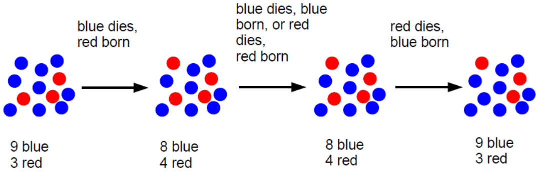

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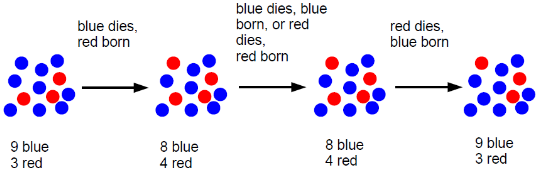

- mean time to extinction $\tau \sim K$
- problem: all species in one niche seems unphysical

Main Questions Motivating My Research

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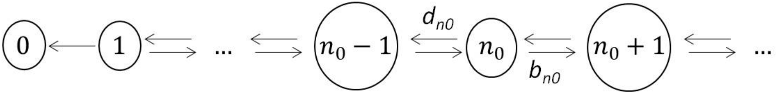
Biodiversity comes from a balance of extinction, fixation (species exiting the system) and invasion (species entering the system): what are the timescales of these processes?

$\rightarrow$ **The relevant parameter is niche overlap.**

How To Calculate The Mean Time To Extinction



Master equation: $\partial_t P_n = b_{n-1} P_{n-1} + d_{n+1} P_{n+1} - (b_n + d_n) P_n$,

in vector form $\partial_t \vec{P} = \hat{M} \vec{P}$, is solved by $\vec{P}(t) = e^{\hat{M} t} \vec{P}(0)$.

How To Calculate The Mean Time To Extinction

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

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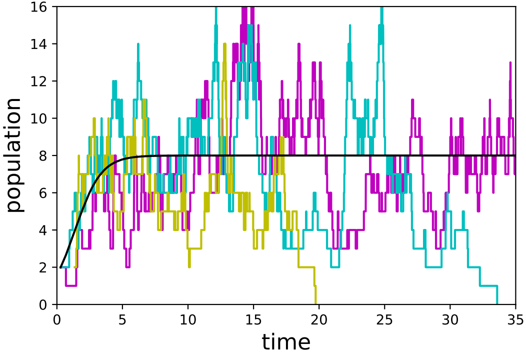
mean time to extinction $\tau_n = \frac{1}{b_n + d_n} + \frac{b_n}{b_n + d_n} \tau_{n+1} + \frac{d_n}{b_n + d_n} \tau_{n-1}$,

in vector form $\hat{M}^T \vec{T} = -\vec{1}$, is solved by $\boxed{\tau_{n^0} = -\sum_n \hat{M}^{-1}_{n^0, n}}$.

Extinction within a Niche

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



Rates Of The Stochastic 1D Logistic Model

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

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

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

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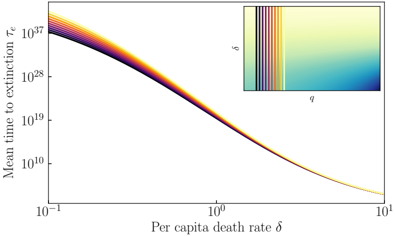
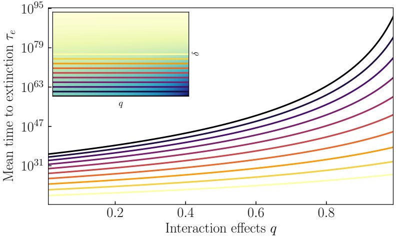
- δ gives magnitude of birth or death (rather than their average difference, the growth rate r)
- q shifts intraspecies interactions from increasing death rate ($q \sim 0$) to reducing birth rate ($q \sim 1$)

Mean Time To Extinction Depends On Interactions

(inset is heat map of mean time to extinction)





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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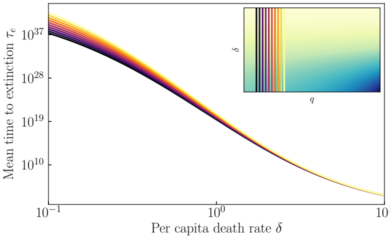
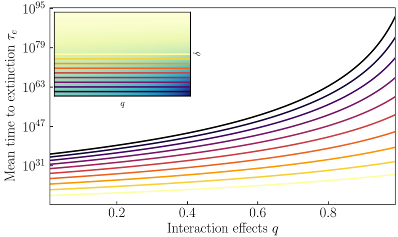
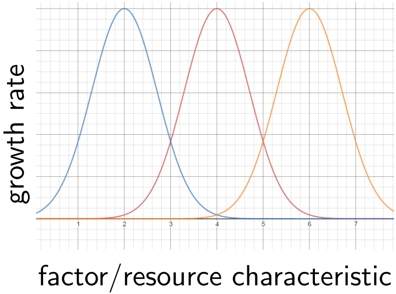




Carrying capacity $K = 100$, growth rate $r = 1$. The mean time to extinction (MTE) decreases with increased δ or decreased q.

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

Fixation versus Coexistence of Two Competing Species

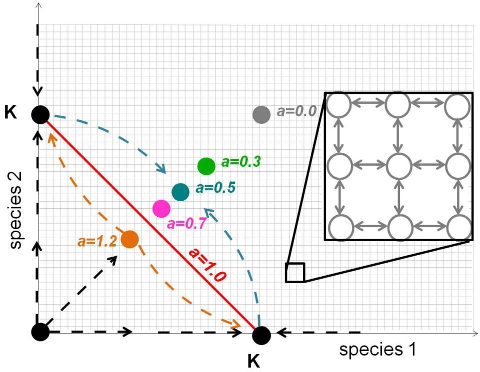


$$\dot{x}_1 = r_1 x_1 \left(1 - \frac{x_1 + a_{12} x_2}{K_1}\right)$$
$$\dot{x}_2 = r_2 x_2 \left(1 - \frac{a_{21} x_1 + x_2}{K_2}\right)$$

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
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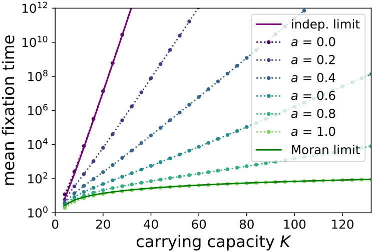

How The System Transitions To Neutrality

niche theory $\tau \sim e^K$

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

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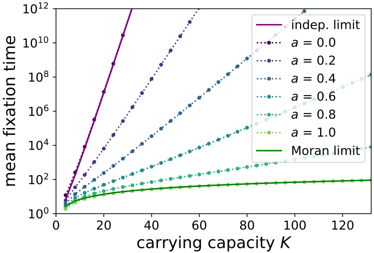

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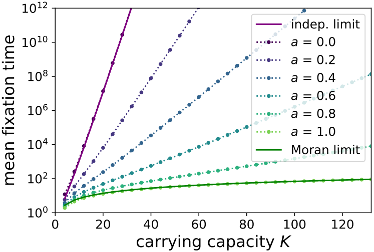

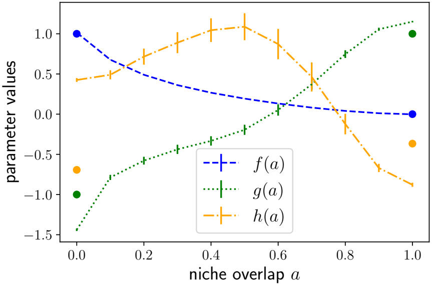

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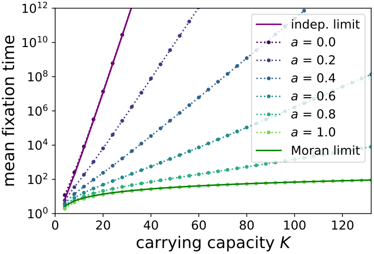
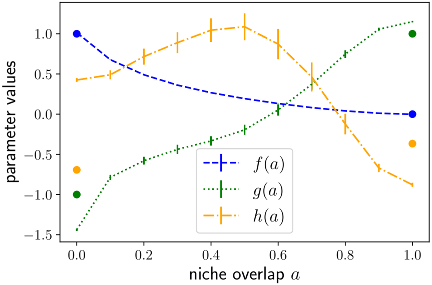
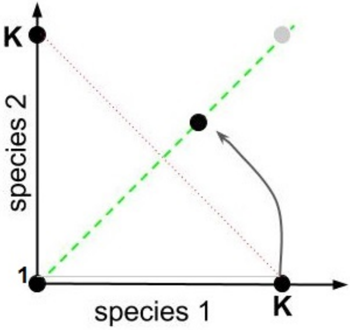




→**Effective coexistence except for complete niche overlap**

The Timescale of Invasion of a Second Species



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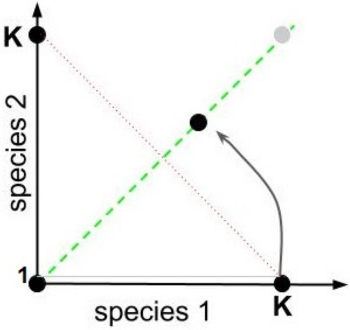
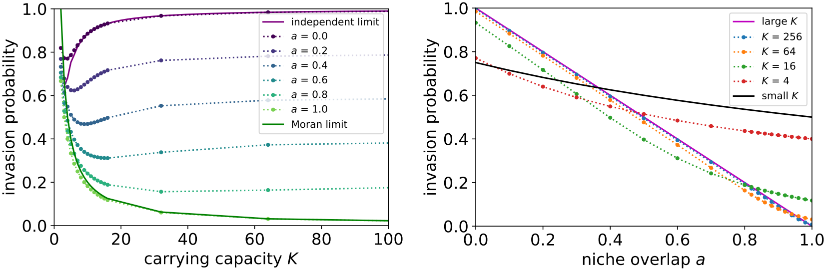


- invasion balances extinction to maintain biodiversity
- invasion is going from one organism to half the population
- invasion into a niche is deterministic, fast (logarithmic)
- invasion into Moran is linear

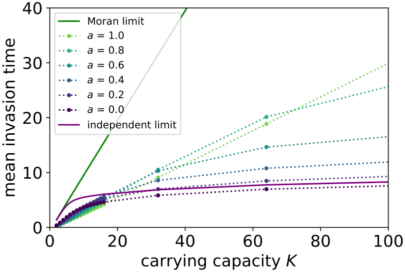
Invasion Less Probable As Niche Overlap Increases



→ **Invasion probability lessens as niche overlap increases.** The trend is more stark for large K. Dependence on K is lesser than a dependence.

Invasion Times Are Fast

mean time of successful invasion



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

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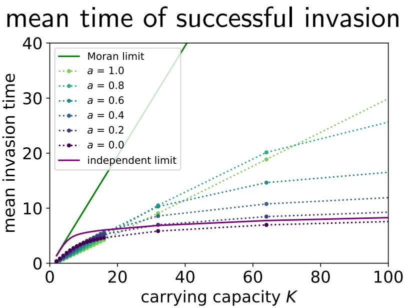

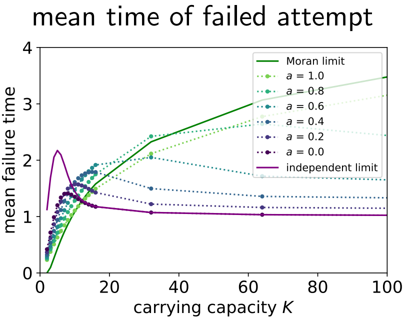

Scaling varies from linear in neutral limit to logarithmic in niche limit. → **Successful invasion times are as expected.**

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

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More generally:

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- partial niche overlap gives a niche theory with carrying capacities modified by niche overlaps $(K' = f(a)K)$

Thank You!

- 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)

Failure Of Fokker-Planck

[101] Charles R Doering, Khachik V Sargsyan, and Leonard M Sander. Extinction times for birth-death processes: exact results, continuum asymptotics, and the failure of the Fokker-Planck approximation. *Multiscale Model. Simul.*, 3(2):283–299, 2005.

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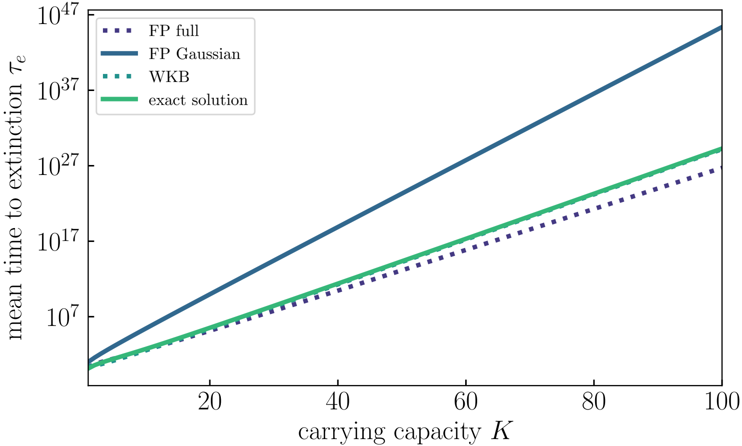
$$\tau \approx \frac{2}{V'(0)} \sqrt{\frac{2\pi}{K\,V''(x^*)}} \frac{e^{-K\,V(x^*)}}{b(x^*)+d(x^*)}$$

$$= \sqrt{\frac{4\pi(1+2\delta)^2}{K(1+\delta-q)}} e^{K\left(4(1+\delta-q)\ln 2(1+\delta-q)-2(1-2q)\right)/(1-2q)^2}$$

$$\sim e^{(4\ln 2-2)K}/\sqrt{K} \text{ and not } \sim e^K/K$$

Failure Of Fokker-Planck

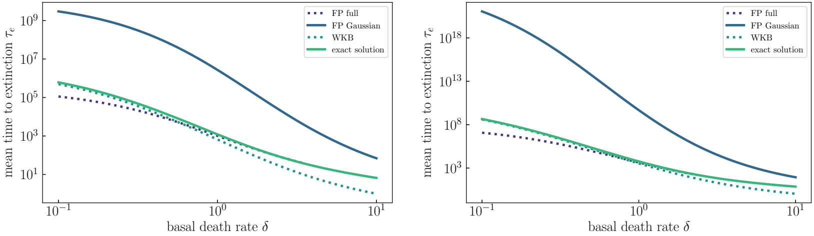


with $\delta = 0.4$ and $q = 0.2$

Approximation Methods

low q ($q = 0.2$)
competition in death rate

high q ($q = 0.7$)
competition in birth rate



appears that FP works for high δ, and WKB works for low δ

Stochastic Analysis

Master equation

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

Stochastic Analysis

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Stochastic Analysis

Master equation

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

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

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

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

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$S_0(n) = \frac{1}{K}\int_0^n dx \ln\left(b_x/d_x\right)$ along extinction trajectory

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  - 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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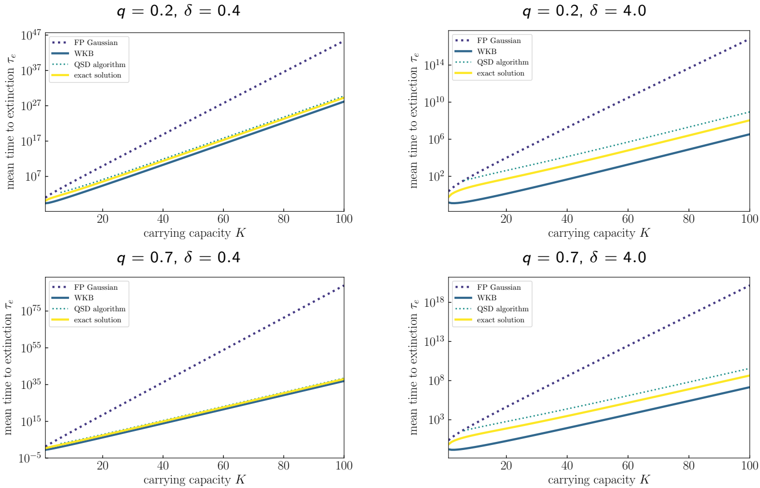
† Gaussian approximation was written incorrectly in thesis.

Mean Time to Extinction

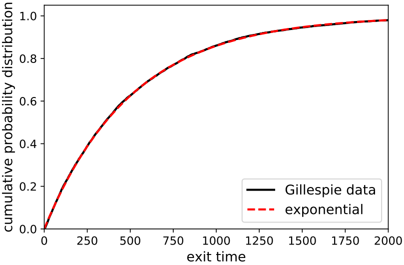
Approximations

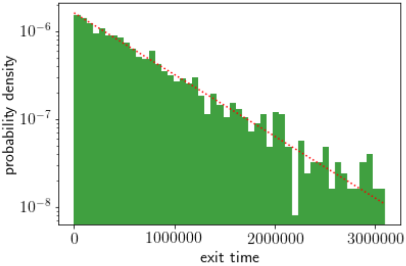


Approximations of the MTE in various regimes of parameter space. WKB is good for low δ, is otherwise poor as FP.

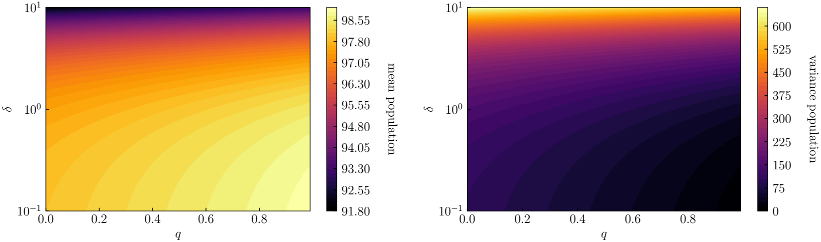
Extinction within a Niche

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





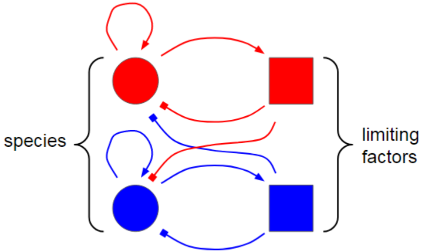
Quasi-Steady State



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.

Fixation

Coupled Logistic Equations



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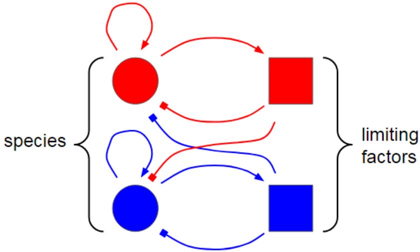

$$\dot{x}_1 = (\beta_1 - \mu_1 - e_{11} t_1 - e_{12} t_2) x_1$$
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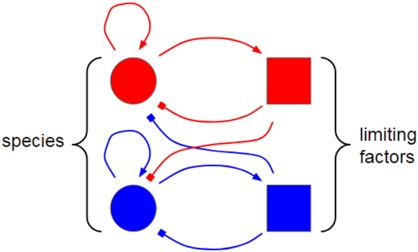

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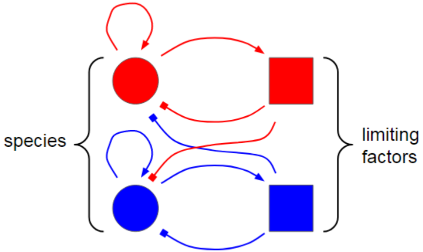

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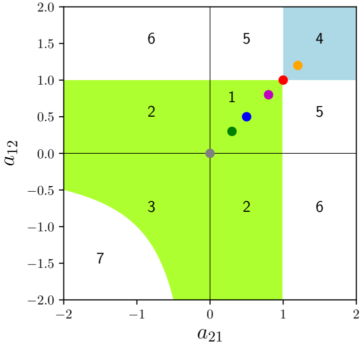
When the matrix $(\hat{E}\hat{G})$ is singular ($a_{12}a_{21} = 1$, complete niche overlap), the coexistence fixed point $\vec{x}^* = (EG)^{-1}\vec{1}$ does not exist. Coexistence is allowed only when neutral: $K_1/K_2 = a_{12} = 1/a_{21}$.

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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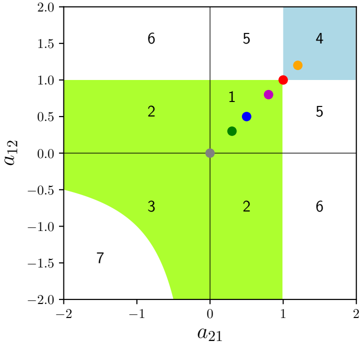

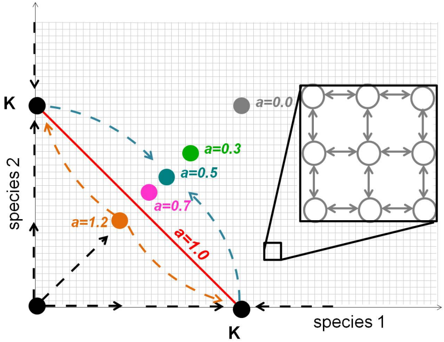

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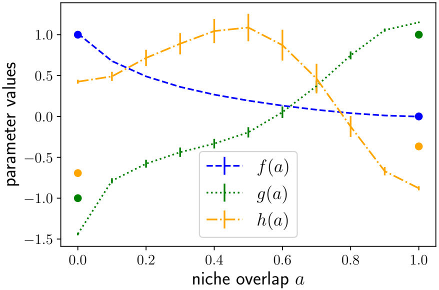
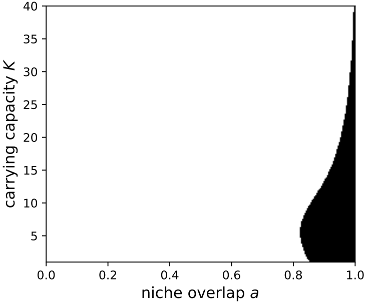
Exponential Scaling With K Is Long

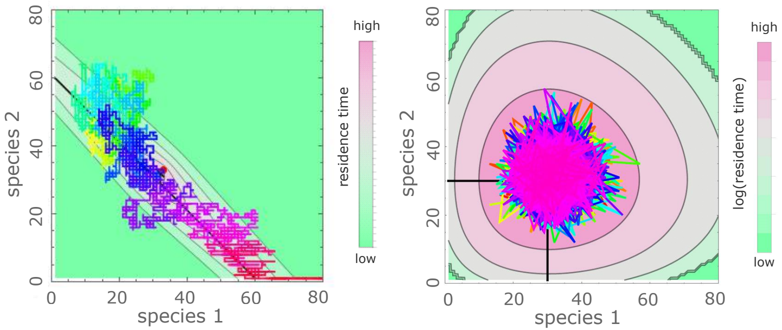
- ansatz: $\tau(a, K) = e^{h(a)} K^{g(a)} e^{f(a)K}$





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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  - any niche mismatch implies effective coexistence
- small departure from neutrality gives a niche theory

Invasion

Invasion - Definition And Expectations

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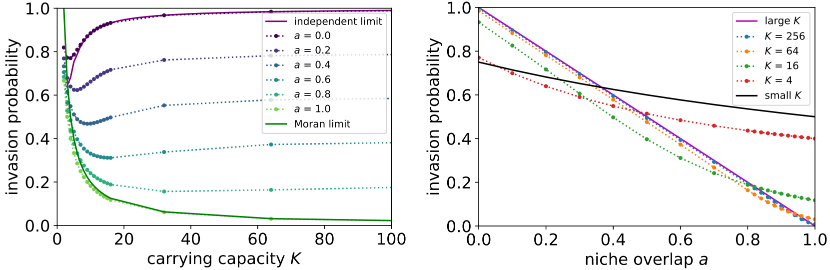
- invasion in neutral limit should be slower (linear)

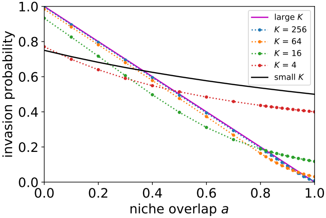
Invasion Probability



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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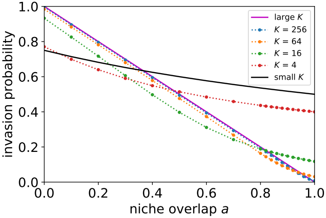
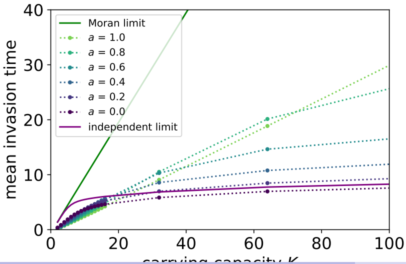
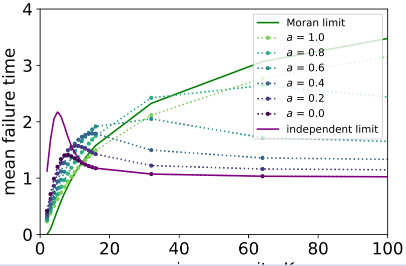


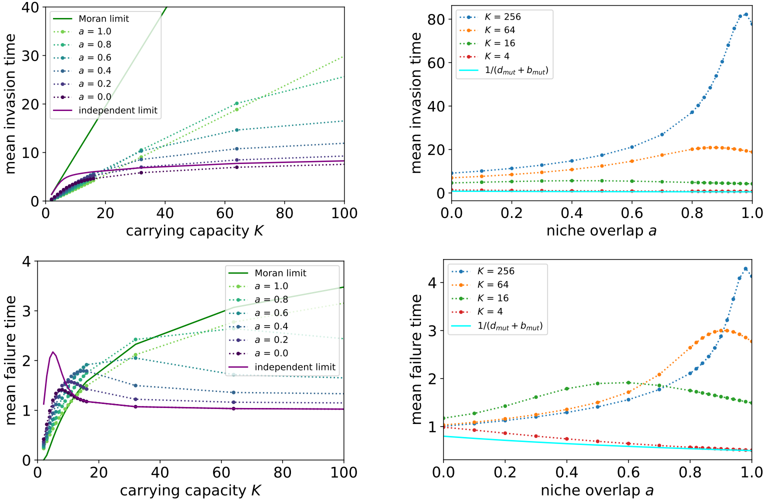
Successful invasion goes from logarithmic to linear in K.

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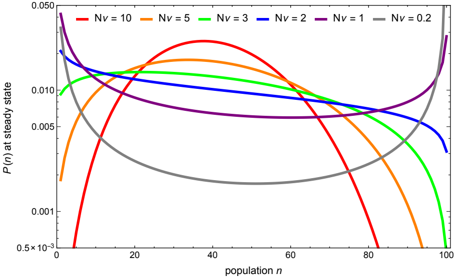
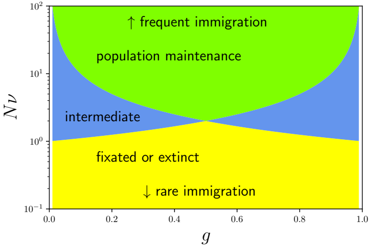
The crucial comparison for biodiversity is between $1/\nu$ and the invasion times previously described.

Steady State Results



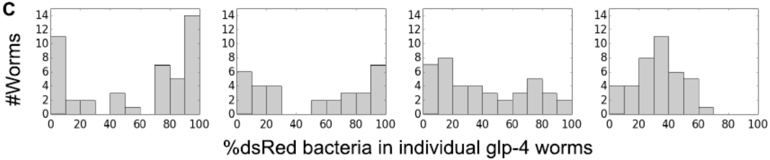


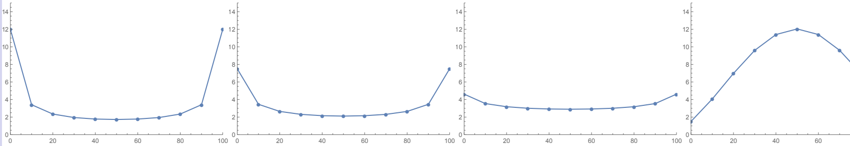
Metapopulation focal fraction is $g = 0.4$, local system size $N = 100$, immigration rate ν is given by the colour.

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.

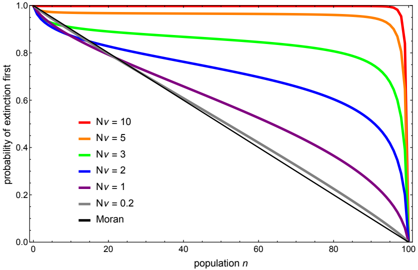
Infrequent Immigration

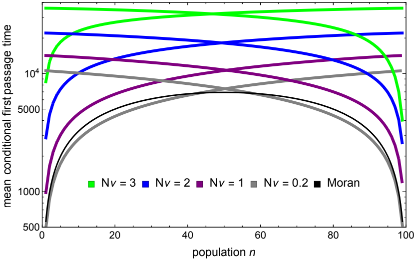
The model recovers qualitative experimental results.
(See Vega and Gore, *PLoS Biology*, 2017.)





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

Coexistence and Extinction of Competing Species

M.A.Badali

- 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

Discussion

Conclusions

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- in Moran model with immigration, a focal species at moderate size if $K\nu > 1/g$;

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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 (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