Extinction, Fixation, and Invasion in an Ecological Niche

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

Motivation and Background

- biodiversity is the number of species in an ecosystem
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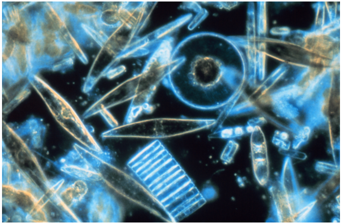
Paradox of the Plankton
a problem of biodiversity



corp2365, NOAA Corps Collection

Niche Theories

Competitive Exclusion

- niche apportionment explains abundance distribution
- classic niche theory is Lotka-Volterra/logistic

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Competitive Exclusion

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- "two species cannot coexist if they share a single [ecological] niche"[1]
- species: group with the same birth and death rates
- niche: survivable values of those factors which affect the birth and death rates

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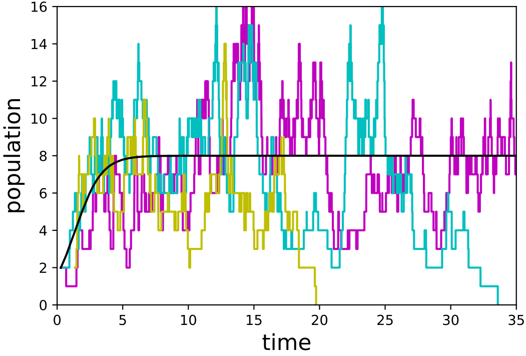
Stochastic Analysis

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



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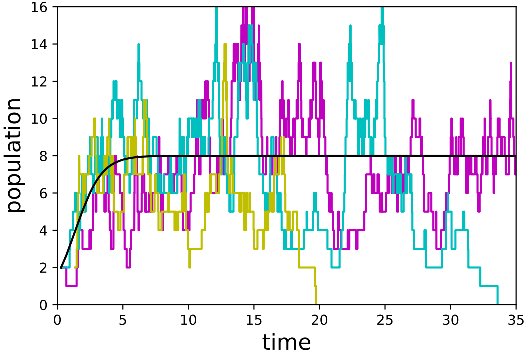

- demographic stochasticity = fluctuations, noise
- probability of population n: P_n
- mean time to extinction: $\tau \sim e^K$

Neutral Theories

- better prediction of abundance curves (Hubbell), also allele frequencies (Kimura), fixation (Moran)
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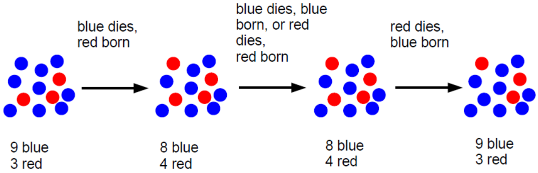

- $\tau \sim K$

Structure of Thesis

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

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

Extinction

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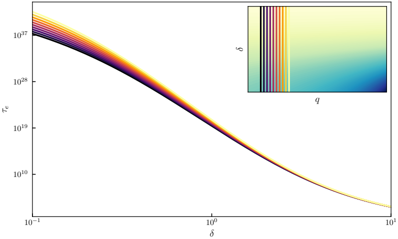
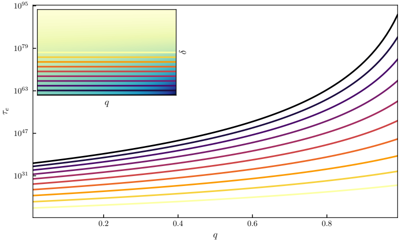
- 4 terms (2nd order in birth/death) so 4 total parameters
- δ gives magnitude of birth or death (rather than their average difference r)
- q shifts intraspecies interactions between reducing birth and increasing death

Mean Time to Extinction



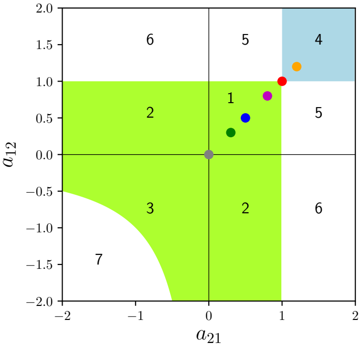


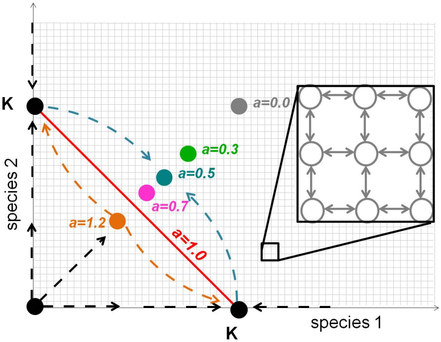
Mean time to extinction for varying δ and q. Lightness of the line indicates an increase of q or δ in left and right respectively. Carrying capacity $K = 100$. The MTE decreases with increased δ or decreased q.

Fixation

Coupled Logistic Equations

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





$O = (0,0),\ A = (0, K_2),\ B = (K_1, 0),\ C = \left(\frac{K_1 - a_{12}K_2}{1 - a_{12}a_{21}}, \frac{K_2 - a_{21}K_1}{1 - a_{12}a_{21}}\right)$

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

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

Transition to Neutrality

- Recall for niches $\tau \sim e^K$
- $a_{12} = a_{21} = 1$ limit recovers Moran results $\tau \sim K$: **neutral limit**

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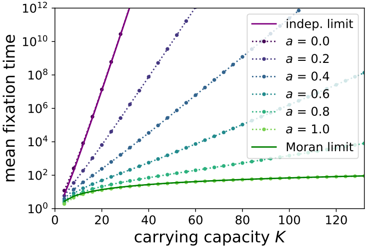

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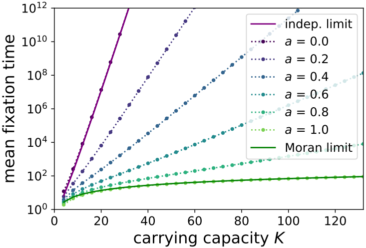

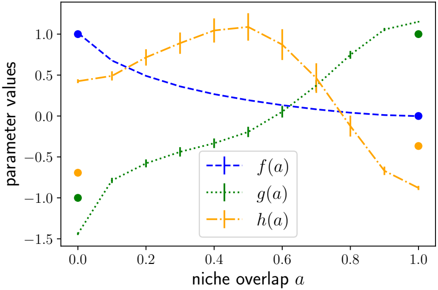

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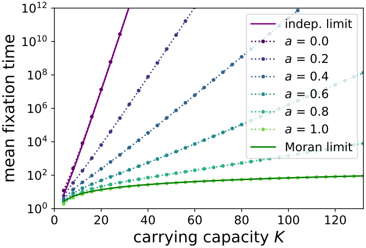

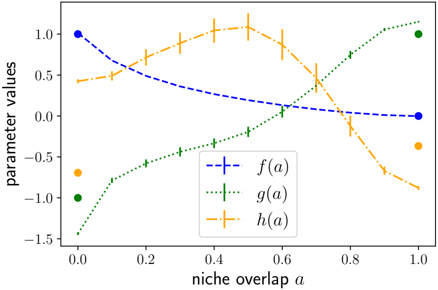

Effective coexistence except with complete niche overlap!

Invasion

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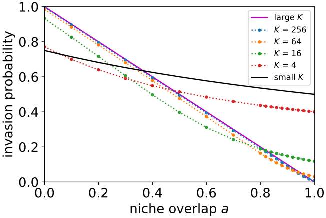
- invasion is the other part of maintenance of biodiversity
- invasion with a fixed point should be fast (logarithmic)
- invasion on the line should be slower (linear)
- effects of a and K are not trivial
- invasion attempts characterized by invasion probability E_s, successful invasion time τ_s, and failed invasion time τ_f

Invasion Probability

Invasion probability approaches $1 - a$.



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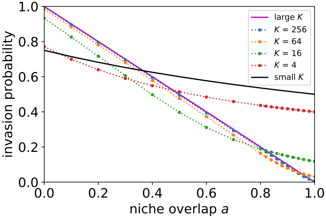
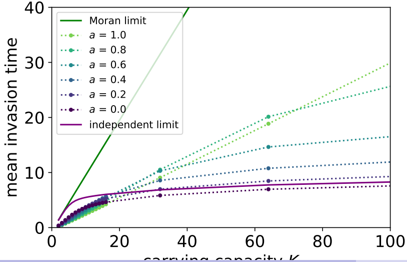
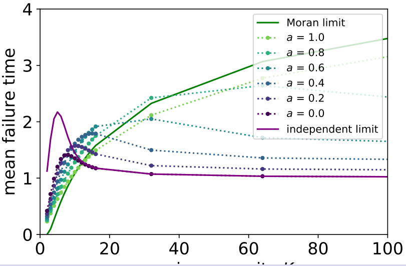


Successful invasion goes from logarithmic to linear in K.

Failed invasion attempts go from constant to logarithmic in K.





Maintenance

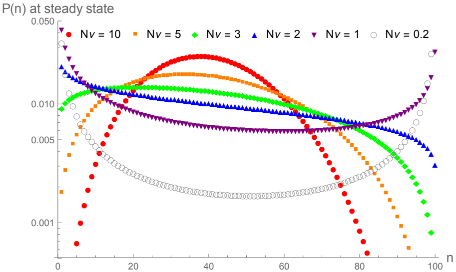
Moran Model with Immigration

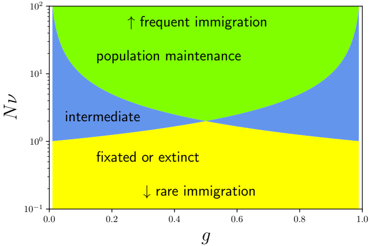
Immigration comes from a constant reservoir of focal species fraction $g = n_{reservoir}/K_{reservoir}$ at a rate ν. Defining $f = n/K$, we have the following transition rates.

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

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

Steady State Results





PDF of stationary Moran process with immigration. 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.

Discussion

Testable Systems

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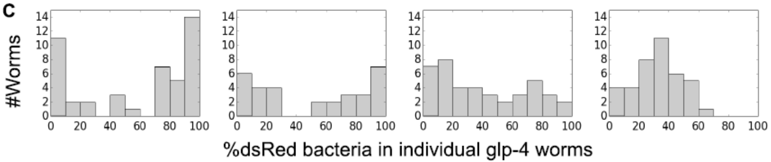
Vega and Gore, *PLoS Biology*, 2017.



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- two species will effectively coexist unless they have exactly the same niche;
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- 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.

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- evolving parameters (ecology and evolutionary biology)

Thank You

Table of Contents

Motivation and Background

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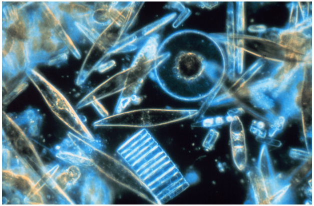

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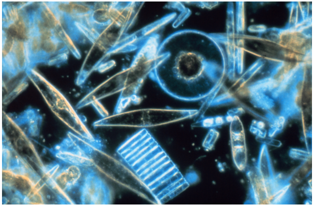

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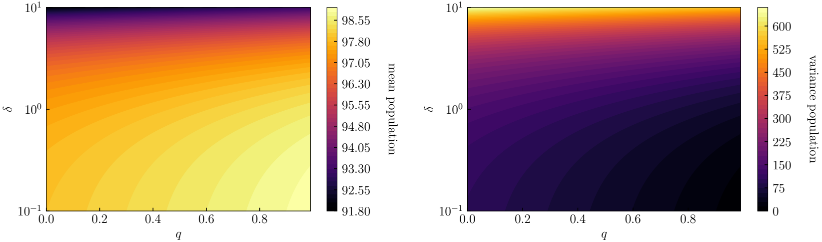
With a stable fixed point $\tau \sim e^K$ (actually e^K/K)

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
Approximations

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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.

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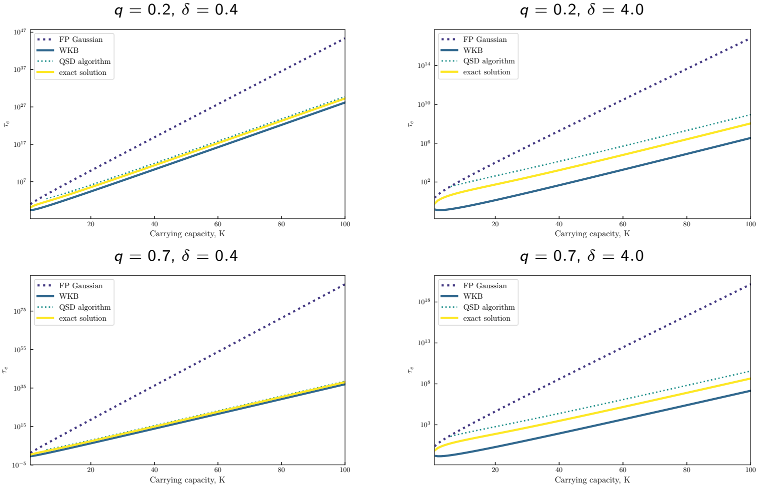
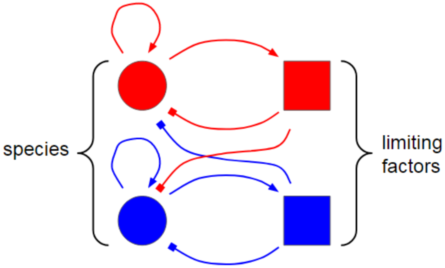


Approximations of the MTE in various regimes of parameter space. WKB is good for low δ, is otherwise poor as FP.

Coupled Logistic Equations



Each of the two species reproduces (arrows to self) and produces a toxin (arrows to limiting factors) which inhibits its own growth (square-ending lines to self) and the growth of the other (square-ending lines to other colour).

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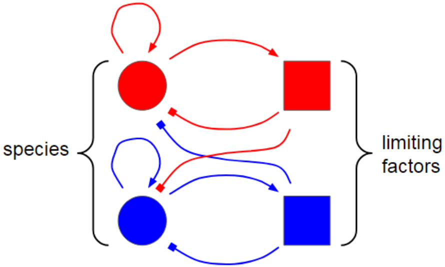
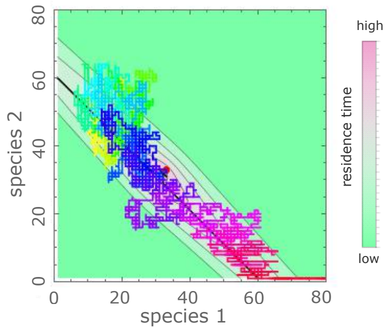


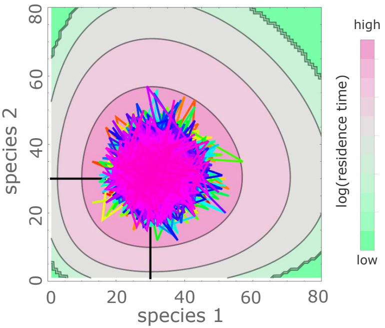
Each of the two species reproduces (arrows to self) and produces a toxin (arrows to limiting factors) which inhibits its own growth (square-ending lines to self) and the growth of the other (square-ending lines to other colour). The deterministic coupled logistic equations are

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

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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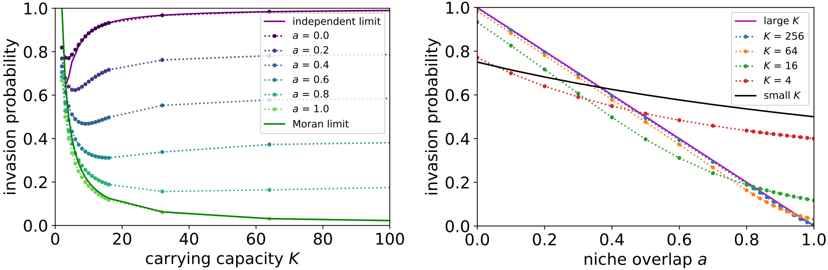
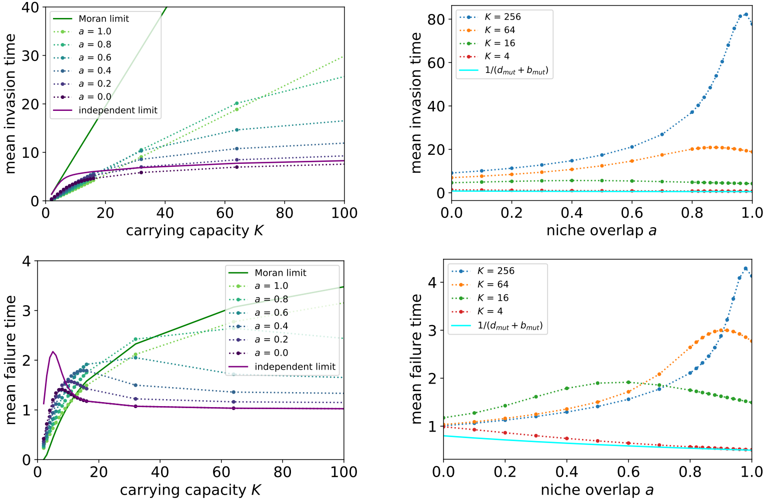
- any niche mismatch allows for exponential dependence on K, which is typically large
  - any niche mismatch implies effective coexistence
- small departure from neutrality gives a niche theory

Invasion 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 Times



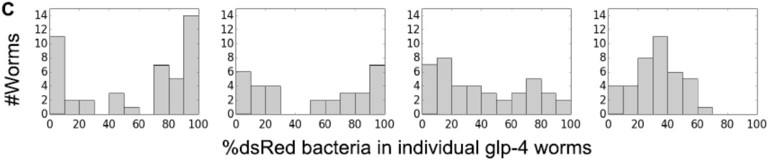
Mean time of a successful or failed invasion attempt. Left: Mean time vs K. *Right:* Mean line vs a. *Upper:* Mean time conditioned on eventual invasion success. *Lower:* Mean time conditioned on failed attempt.

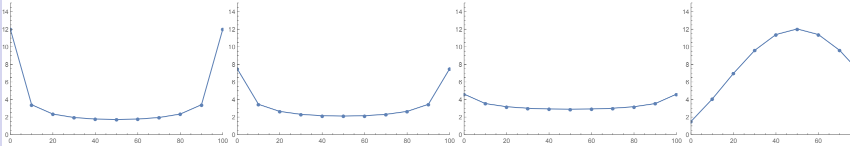
Discussion

- 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

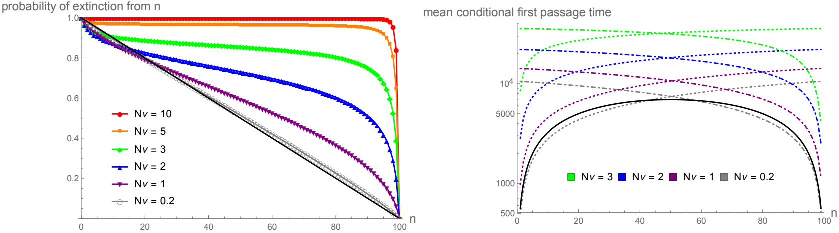
Infrequent Immigration

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





First Passage Results



Probability and conditional times of the focal species reaching temporary extinction before fixation, as a function of initial population. 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 ($N\nu < \min\left(1/g, 1/(1-g)\right)$), focal species either fixated or extinct most of the time
- when immigration is common ($N\nu > \max\left(1/g, 1/(1-g)\right)$), focal species is maintained at moderate abundance in the system, specifically gN
- immigration increases the times to (temporary) fixation or extinction

Conclusions

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- 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.

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