Extinction, Fixation, and Invasion in an Ecological Niche

MattheW Badali

Internal defense
performed as a requirement for
the degree of Doctor of Philosophy
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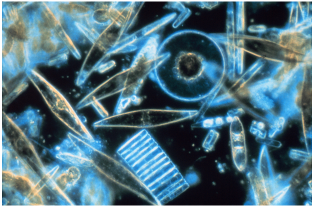
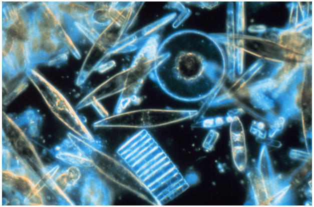
Paradox of the Plankton - a problem of biodiversity



corp2365, NOAA Corps Collection

Motivation and Background

Paradox of the Plankton - a problem of biodiversity

corp2365, NOAA Corps Collection 

- human health (gut)
- planet health (conservation)
- minimal working models
- coalescent theory

Niche Theories

- Competitive Exclusion: "two species cannot coexist if they share a single [ecological] niche"[1]

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- Lotka-Volterra

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

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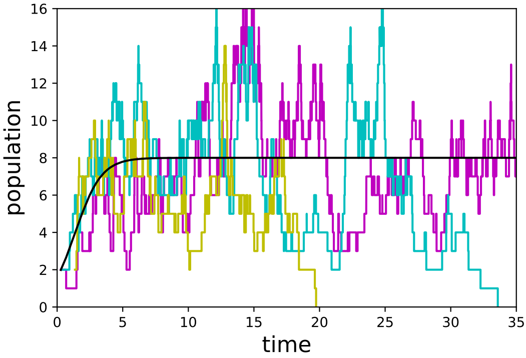
Stochastic Analysis



- Demographic Stochasticity: fluctuations

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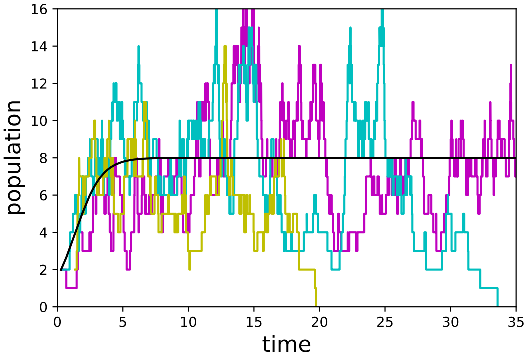

- Demographic Stochasticity: fluctuations
- Probability of being in state, Extinction

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

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

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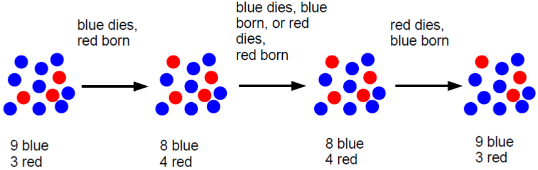
With a stable fixed point $\tau \sim e^K$ (actually e^K/K)

Neutral Theories

- inherently stochastic
- used for allele frequencies (Kimura), fixation (Moran), abundance curves (Hubbell)
- Moran model



$$\tau(n) = -\Delta t\, K^2 \left(\frac{n}{K} \ln\left(\frac{n}{K}\right) + \frac{K-n}{K} \ln\left(\frac{K-n}{K}\right)\right) \sim K.$$

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- Biodiversity is balance of species out and species in to system

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- Discussion

Extinction

Logistic Equation

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$$0 \longleftarrow 1 \rightleftarrows \cdots \rightleftarrows n_0 - 1 \underset{}{\overset{b_{n0}}{\leftrightarrows}} n_0 \underset{d_{n0}}{\rightleftarrows} n_0 + 1 \rightleftarrows \cdots$$

can be derived from a stochastic model with birth/death rates

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

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

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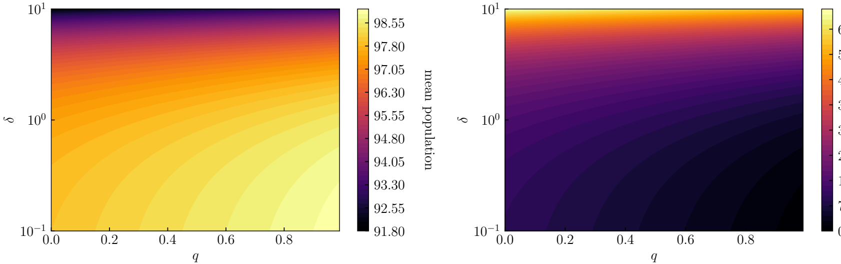
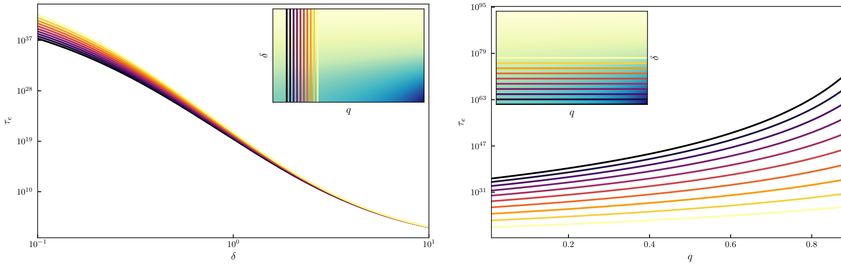
- 4 terms (2nd order in birth/death) so 4 total parameters
- note that $b_n > 0$ implies a maximum population size, N

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.

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

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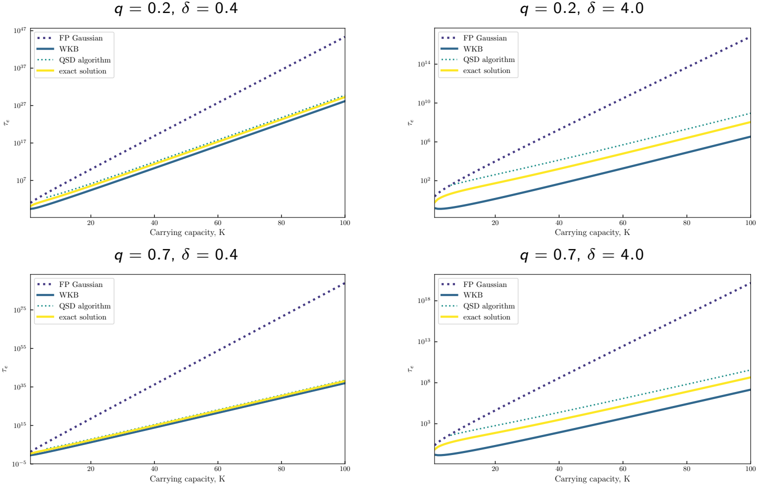
- WKB ansatz $P_n \propto \exp\left\{K \sum_i \frac{1}{K^i} S_i(n)\right\}$ with $S_0(n) = \int_{n=0}^{K} dn \ln\left(\frac{b_n}{d_n}\right)$ along extinction trajectory

†Gaussian approximation was written incorrectly in thesis.

Mean Time to Extinction

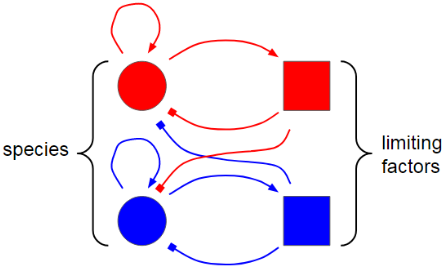
Approximations



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



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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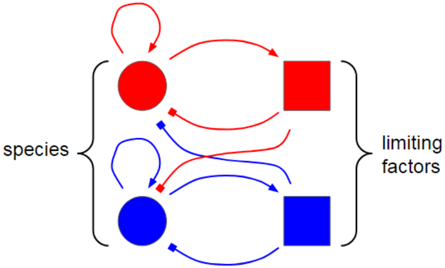

Each of the two species reproduces (arrows to self) and produces a toxin (arrows to limiting factors) which inhibits its own growth (square-ending lines to self) and the growth of the other (square-ending lines to other colour). The deterministic coupled logistic equations are $\dot{x}_1 = r_1 x_1 \left(1 - \frac{x_1 + a_{12} x_2}{K_1}\right)$ and $\dot{x}_2 = r_2 x_2 \left(1 - \frac{a_{21} x_1 + x_2}{K_2}\right)$

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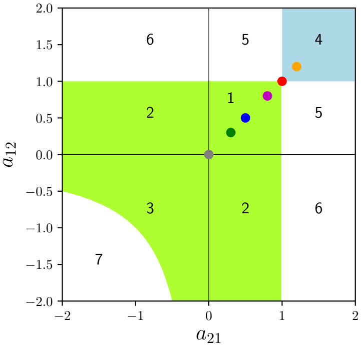

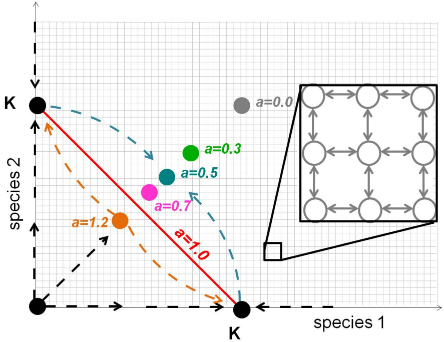

$$O = (0,0),\ A = (0, K_2),\ B = (K_1, 0),\ C = \left(\frac{K_1 - a_{12}K_2}{1 - a_{12}a_{21}}, \frac{K_2 - a_{21}K_1}{1 - a_{12}a_{21}}\right)$$

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[2] $\tau \sim K$

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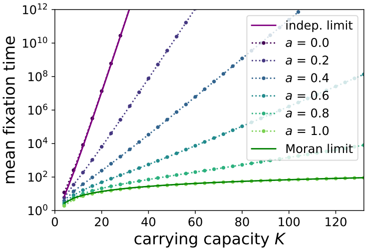

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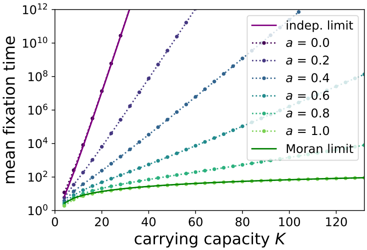
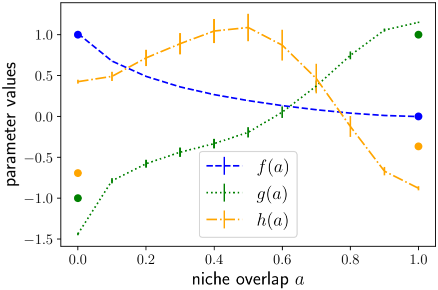


$$\tau(a, K) = e^{h(a)} K^{g(a)} e^{f(a)K}$$



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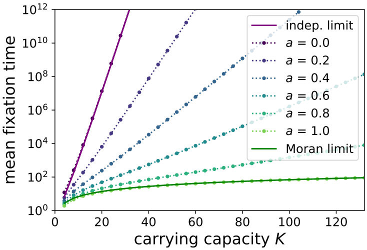

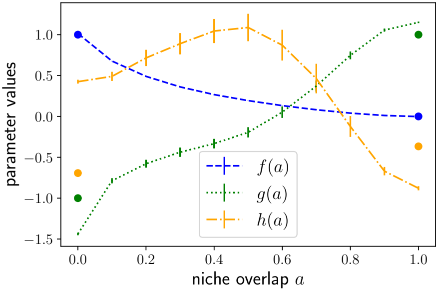

Effective coexistence except with complete niche overlap!

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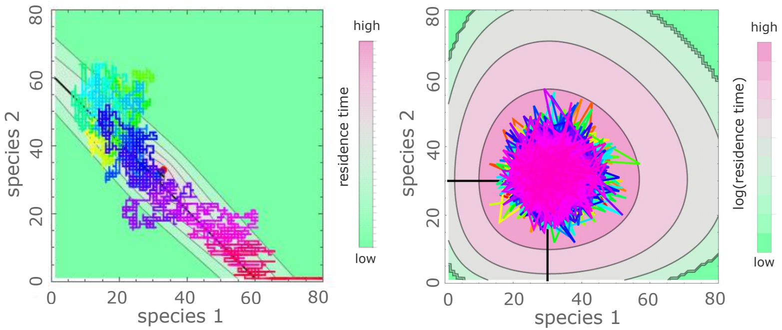
Route to Fixation

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

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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

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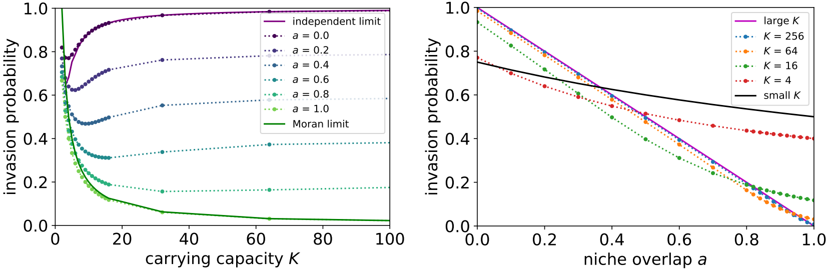
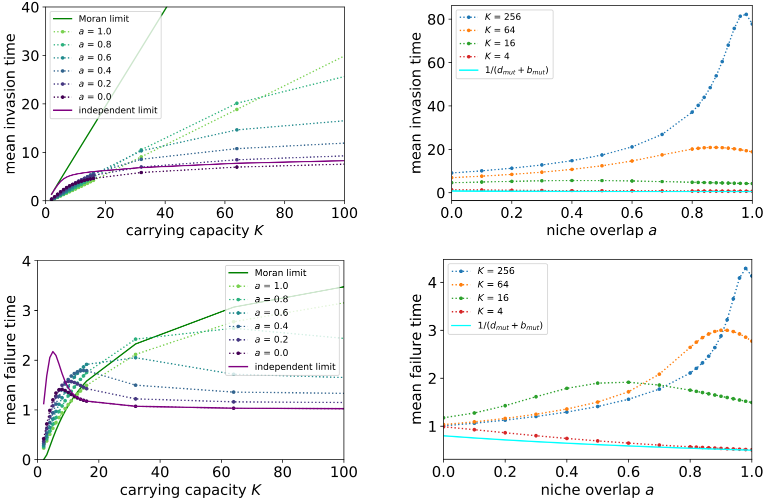
- invasion is the other part of maintenance of biodiversity
- invasion with a fixed point should be fast (logarithmic)
- invasion on the line should be slower (linear)
- effects of a and K are not trivial
- invasion attempts characterized by in invasion probability E_s, successful invasion time τ_s,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

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.

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

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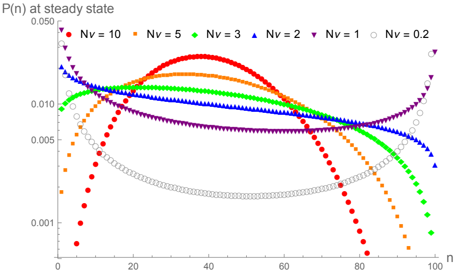
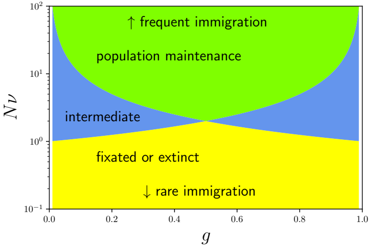
The crucial comparison is between $1/\nu$ and the invasion times previously described.

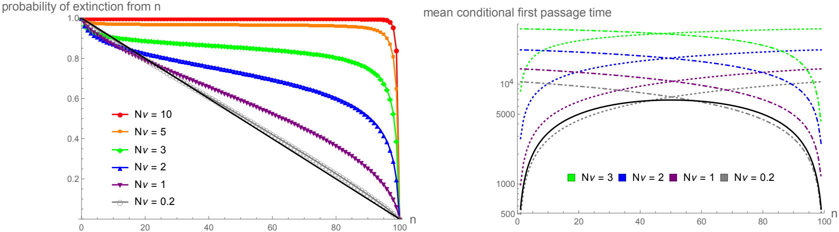
Steady State Results





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.

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.

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- 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

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- 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

Testable Systems

- microfluidics

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- microfluidics
- plasmids

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- microfluidics
- plasmids
- mitochondria

Testable Systems

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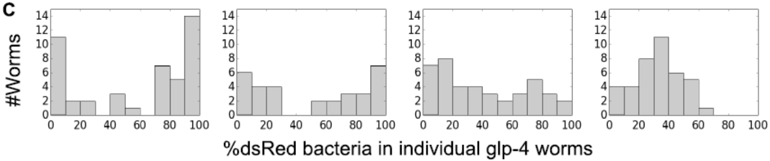
Vega and Gore, *PLoS Biology*, 2017.



Conclusions

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

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