Minimizing extinction risk by migration

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Collaborators

- With
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- arXiv.org
  1201.5204v2 [q-bio.PE]

Extinction risk & rare events

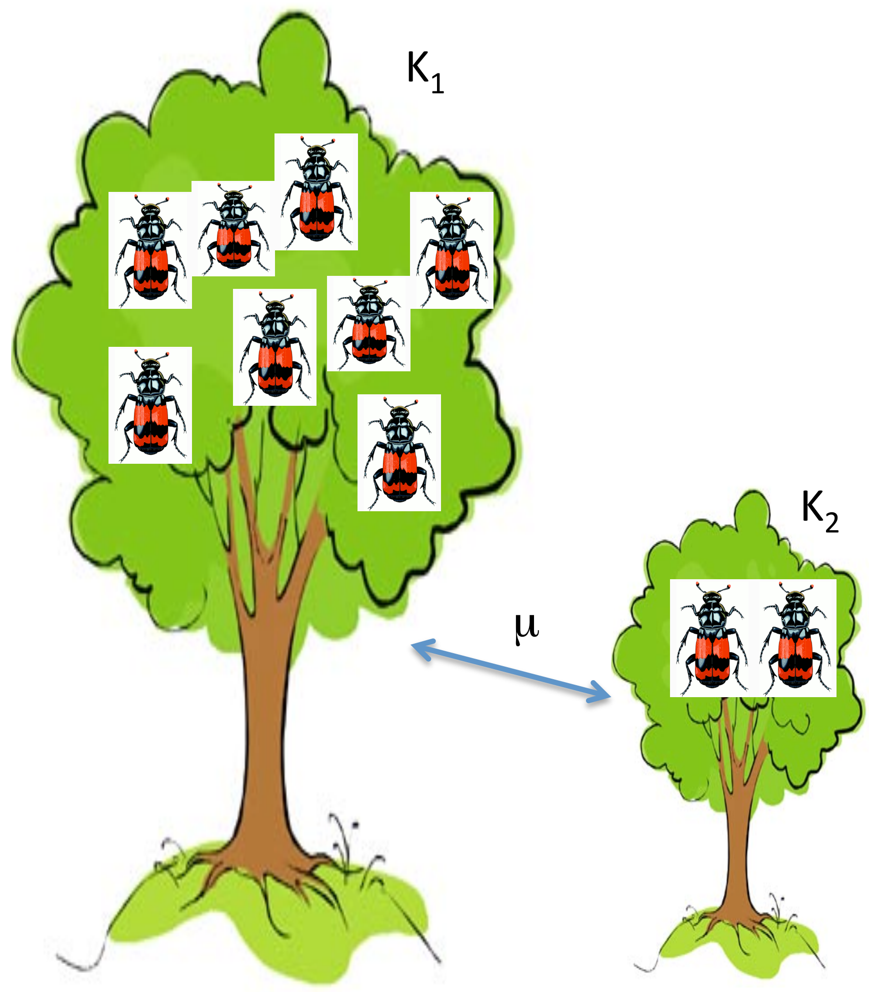
- We will introduce a model that may be interesting in population biology and ecology with a surprising result.
  - Like many population problems, this one *lacks detailed balance*.
- We are interested in a rare event, extinction of a metapopulation.
- We do the problem numerically and, in the limit of large populations, in the WKB (eikonal) approximation.
- The most interesting results are *not given by WKB.*

Ecological motivation

- Populations of animals and plants are often fragmented and live on small patches of habitat. (Meta-population)
- A local population is prone to extinction because of the shot noise of birth and death processes.
- The whole meta-population, however, might persist much longer in a balance between local extinctions and re-colonizations
- Is there an optimal migration rate that maximizes the mean time to extinction (MTE) of the meta-population?

A tale of two trees (or a forest)

- Suppose the same species lives on two patches of habitat.
- The two patches differ only by how favorable they are: i.e. one has a larger *carrying capacity* (steady state population) than the other.
- Question: what is the best strategy for long-term survival? Migrate or not?
  - '*Always stay home*' seems better for the better patch.
  - '*Migrate often*' seems better for the worse patch.
- What is better for the population as a whole?
- We will generalize to a network of N trees.



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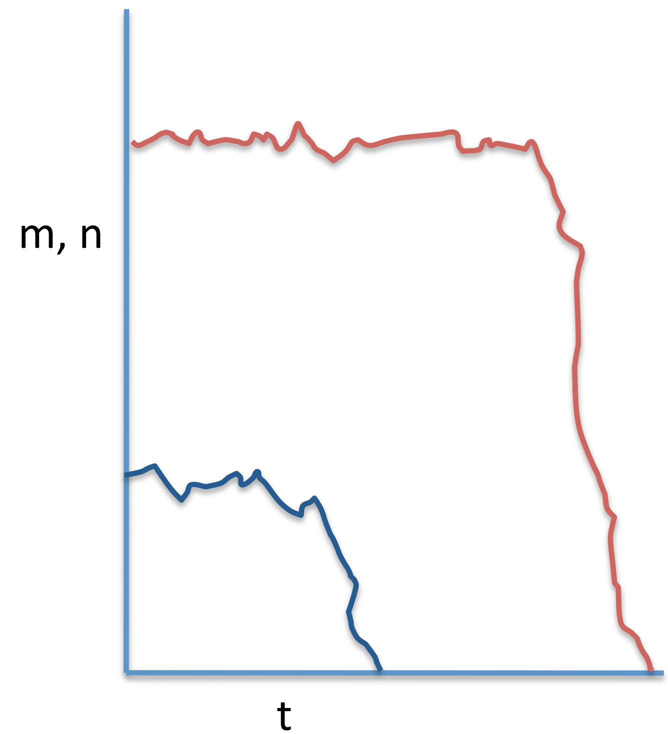
Minimizing extinction risk, 2 sites

- When the patches are uncoupled, each is expected to have a steady state population:
  $K_1 = K,\ K_2 = \kappa K,\ K >> 1,\ \kappa < 1$
  (one good place, one bad place).
- Populations go extinct as a result of rare, large fluctuations in birth/death rates.
- T = mean time to extinction obeys
  $T \sim \exp(K_i S)$, S of order unity, see below.
  - Thus the 'bad' patch has *much faster extinction.*
  - We always neglect prefactors.
- Guesses for the best strategy:
  - Exclude the poor that live elsewhere.
    Avoid the bad tree – select $\mu=0$.
  - Share the wealth.
    Migrate to share the risk -select μ very large.
- Our result: *Neither strategy is optimum:*
  The best migration rate is small, but not zero.



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Model

- Dynamics: m=# on good site, n=# on bad site
  Birth: X→X+X, (rate 1, sets time unit).
  Death: X+X→0, (rate $1/K_i$)
  Migration: m, n←→ m-1, n+1 (rate μ)
- Mean field model: $x=m/K$, $y=n/K$, $K_2=\kappa K$, $K_1=K$:
  - $dx/dt = x - x^2 - \mu(x-y)$
    $dy/dt = y - y^2/\kappa - \mu(y-x)$
- Fixed points: $[x^*(\kappa,\mu), y^*(\kappa,\mu)]$; $[0,0]$.
  - $\mu=0$: $x^*=1$; $y^*=\kappa$.
  - $\mu=\infty$: $x^*= y^*=2\kappa/(1+\kappa)$; $1/x^* = 1/y^* = (1/2)(1+1/\kappa)$.
    - Effective carrying capacity per site is the *harmonic mean*
      $1/K_{eff} = (1/2)\ (1/K_1 + 1/K_2)$,
      dominated by smaller K. Total capacity is $4\kappa/(1+\kappa)$.

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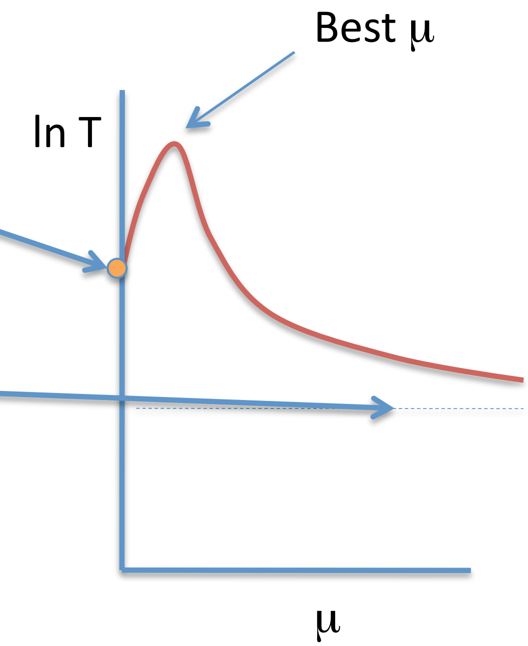
Best strategy (hand waving)

- For no migration at all, the bad site goes extinct quickly,
  $$T_2 \sim \exp(SK_2),$$
  and the extinction of the population is dominated by
  $$T_1 \sim \exp(SK_1).$$

- For very fast migration, both populations go to the harmonic mean, K_{eff}, which is *less* than K_1.
  $$T \sim \exp(2SK_{eff}).$$

- *However:* when the good site is going extinct, if there is a *very small* migration rate, the bad site can *serve as a refuge* and re-colonize the good site.
  - If you get into trouble, you may need help from your poor neighbors!
  - This turns out to give the maximum T.



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Maximum extinction time

- Recolonization and synchronization:

  When both sites go extinct, they must be *synchronized*: the time of extinction cannot differ by longer than the time to transfer one agent, $t_r=1/\mu K$, and rescue the empty site.

  We will assume $\mu K>1$, so t_r is a short time.

- If $\mu<<1$ the on-site dynamics is unaffected by migration.
- In order to have extinction we need both sites to go extinct together within time t_r. The probability for this is the *product of probabilities*:

$$t_r^2\ \omega_1 \exp(-K_1 S)\ \omega_2 \exp(-K_2 S)$$

- Thus the effective carrying capacity for $\mu \sim 1/K$ is the *sum*:

$$T(\mu=0^+) \sim \exp[S(K_1+K_2)] > T(\mu=0) > T(\mu=\infty)$$

- All of this will be checked in two ways: WKB and numerically.

Master equation

- Master equation for probability P(m,n):

$$\dot{P}_{m,n}(t) = \hat{H}P_{m,n} \equiv \quad (m-1)P_{m-1,n} + (n-1)P_{m,n-1} + \frac{(m+1)(m+2)}{2K}P_{m+2,n} + \frac{(n+1)(n+2)}{2\kappa K}P_{m,n+2}$$

$$+\mu(m+1)P_{m+1,n-1} \qquad +\mu(n+1)P_{m-1,n+1} - \left[(1+\mu)(m+n) + \frac{m(m-1)}{2K} + \frac{n(n-1)}{2\kappa K}\right]P_{m,n}.$$

- Extinction probability: $dP_{0,0}/dt = P_{2,0}/K + P_{0,2}/\kappa K$
- Quasi-stationary state: MFT, x*, y*.
- Master equation is linear: Expand in eigenvalues

  $\hat{H}P = - P/T_{i\,;} \quad P = \Sigma P_i \exp(-t/T_i)$.
- Large eigenvalues give fast relaxation to x*,y*.
- Smallest non-zero eigenvalue gives extinction time:
  - $P_{m,n} = \pi_{m,n} e^{(-t/T)}; \quad P_{0,0} \sim [1- e^{(-t/T)}]. \;\; T = T_1$
- T is large; $\hat{H}\, \pi_{m,n} = \pi_{m,n}/T \sim 0$.

  $1/T = [\pi_{2,0}/K + \pi_{0,2}/\kappa K]$

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WKB approximation

- We expect π to have an exponentially small tail in the region near 0,0.
  - WKB ansatz (Kubo, 73, …): $\pi_{m,n} = \exp(-KS(x,y))$; S is the action.
  - Set x=m/K; y=n/K; treat as continuous variables.
- Put ansatz in master equation: replace differences in m,n by derivatives in x,y.
- Equation for S to leading order in 1/K has the form of a Hamilton-Jacobi equation: we have a *classical mechanics problem.*

$$H(x, y, \partial_x S, \partial_y S) = 0; \quad p_x = \partial_x S; \quad p_y = \partial_y S$$

$$\begin{aligned} H(x, y, p_x, p_y) = x\left(e^{p_x} - 1\right) + \frac{x^2}{2}\left(e^{-2p_x} - 1\right) \\ + y\left(e^{p_y} - 1\right) + \frac{y^2}{2\kappa}\left(e^{-2p_y} - 1\right) \\ + \mu x\left(e^{-p_x+p_y} - 1\right) + \mu y\left(e^{p_x-p_y} - 1\right). \end{aligned}$$

HJ equations and classical mechanics

- The PDE $H(x,y,p_x,p_y)=0$ can be solved by characteristics, i.e. finding paths $x(t),y(t)$.
- In physics terms we have to find the path of a fictitious particle with E=0 whose equations of motion are:

$$\dot{x} = \partial_{p_x} H; \dot{p}_x = -\partial_x H$$
$$\dot{y} = \partial_{p_y} H; \dot{p}_y = -\partial_y H$$

- We need to find the *instanton*, the path (x,y,p_x,p_y) that goes from the quasi-stationary state, $(x^*,y^*,0,0)$ $(t=-\infty)$ to the exit point (0,0).
  - For technical reasons, for this type of extinction the momenta at the exit are infinite: the exit point is actually $(0,0,-\infty, -\infty)$.
- The instanton is the path with the least action:

$$S = \int (p_x dx + p_y dy)$$

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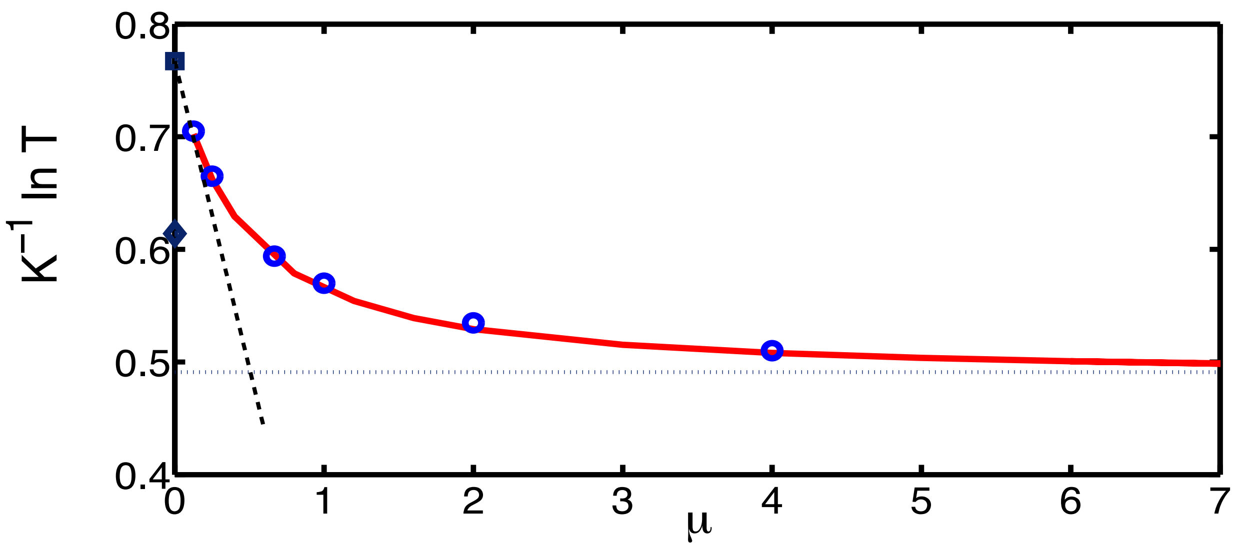
Solving the classical problem

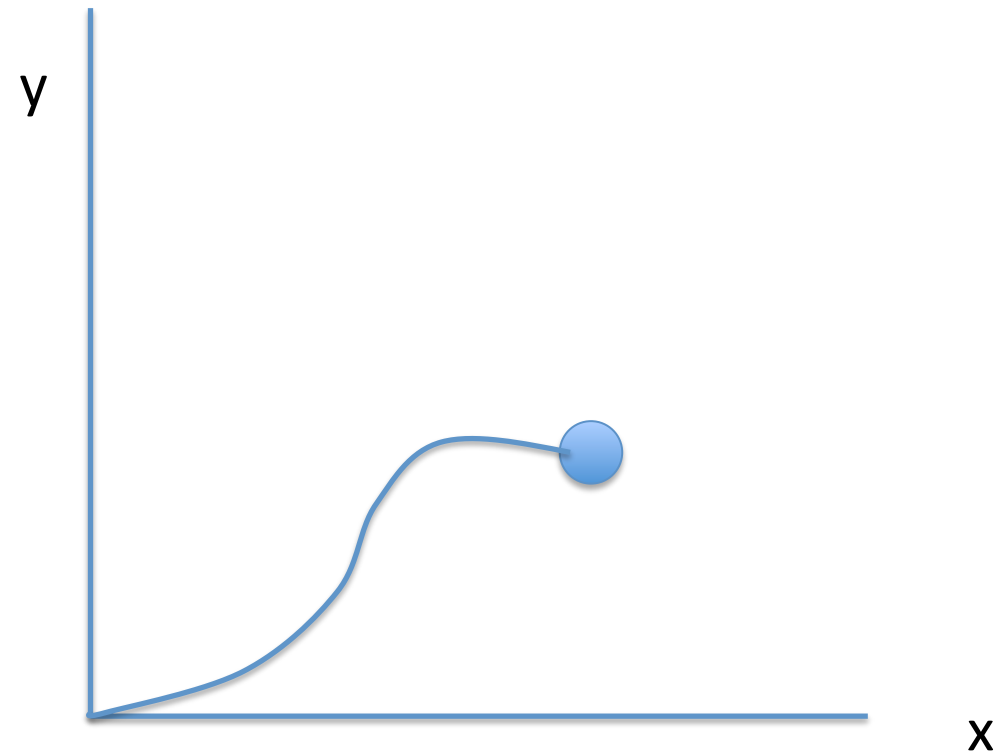
- Four dimensional phase space, one constraint, so 3d.
- In general must solve numerically by shooting.



κ=0.25,
Circles, WKB, numerical,
Red line, numerical solution of master equation,
Diamond, μ== 0,
Square, μ -> 0^+,
Dotted line, T~ $\exp(2K_{eff})$

Path to extinction

- For large K the extinction time is dominated by one path.
- There is no path for the dynamics that starts at (x*,y*,0,0) and stays in $p_x = p_y = 0$.
- We need the action along the path.



Analytics: limit of slow migration

- For $\mu \rightarrow 0^+$, the problem separates:

$$H(x,y,p_x,p_y) = x\left(e^{p_x}-1\right) + \frac{x^2}{2}\left(e^{-2p_x}-1\right)$$

$$+y\left(e^{p_y}-1\right) + \frac{y^2}{2\kappa}\left(e^{-2p_y}-1\right) = 0$$

- Solutions:

$$x(p_x) = \frac{2e^{2p_x}}{e^{p_x}+1}, \quad y(p_y) = \frac{2\kappa e^{2p_y}}{e^{p_y}+1}.$$

- For the action we add carrying capacities:

$$\mathcal{S}(\mu \to 0) = \int_{-\infty}^{0} x(p_x)dp_x + \int_{-\infty}^{0} y(p_y)dp_y$$

$$= 2(1-\ln 2)(1+\kappa) \simeq \ln T_{\mu\to 0}/K.$$

  – This is much larger than what we get if we start with $\mu==0$, i.e. just the first term.
  – We have argued that near $\mu=0^+$ the populations are synchronized – this leads to the different behavior.
    - We can also give a more formal proof.

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Limit of fast migration

- For μ >>1, make a change of variables:
  - Q = x+y (total population, slow variable)
  - q=x ,
  - and corresponding momenta, p, P.
- We find, for μ >>1, a Hamiltonian for the slow variables:

$$H_{slow}(Q,P) = = (1/\mu)\left[Q(e^P-1)+\frac{1+\kappa}{8\kappa}Q^2\left(e^{-2P}-1\right)\right].$$

- As we already guessed: $2/\kappa_{eff}=(1/2)(1/\kappa+1)$:

$$\frac{\ln T_{\mu\to\infty}}{K} = \frac{8(1-\ln 2)\kappa}{1+\kappa}$$

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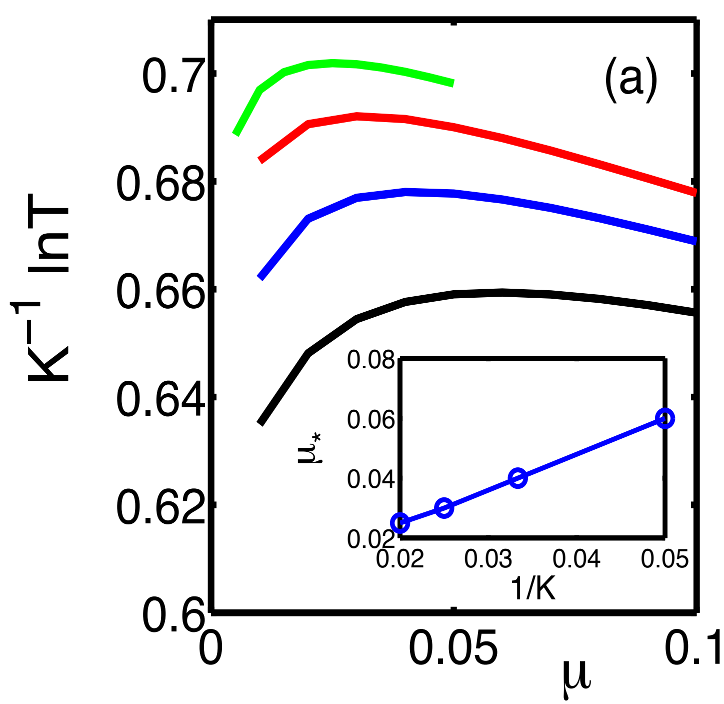
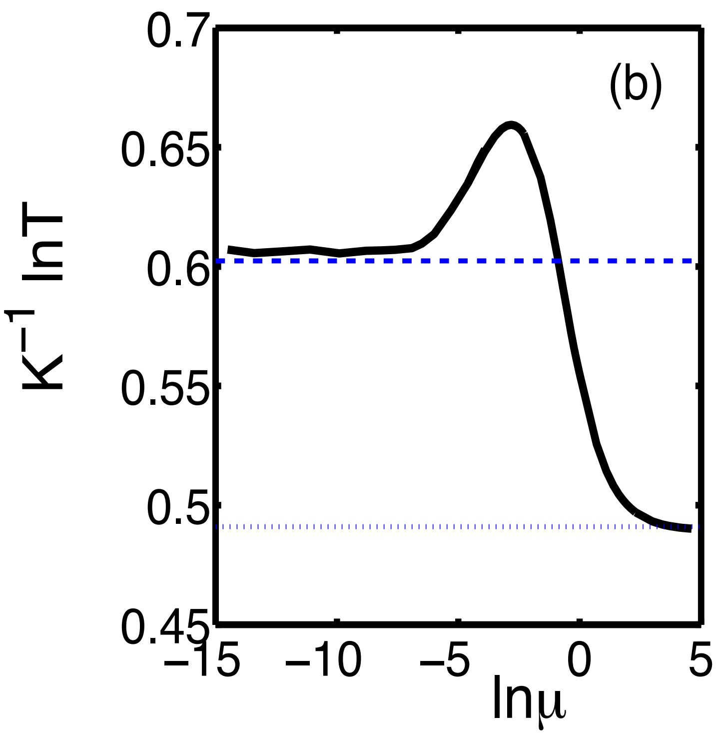
Numerics

- WKB *does not resolve the boundary layer* where T rises from the uncoupled value to the maximum.
  - This occurs for $\mu \sim 1/K$, where WKB is not valid.
  - This means one transfer per generation.
- We simulate the Markov process directly.



κ=0.25
K = 20, 30, 40, 50



κ=0.25, K=20

Many patches

- We can generalize the result to a network of patches with different carrying capacities.
  - We assume $K_i = \kappa_i K$, $\mu_{ij} = \theta_{ij}\,\mu$, κ_ι, θ_{ij} order unity.
- Large μ gives an effective carrying capacity for the whole population: $\kappa_{eff} = N^2/\Sigma\kappa_i^{-1}$.
- Small μ gives synchronization for
  $1/(nK) < \mu < 1/n$,
  n=typical number of bonds.
- We think that the maximum time for extinction is at $\mu \sim 1/(nK)$.

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Discussion

- WKB theory is valid for $\mu >> 1/K$, can't resolve smaller time scales.
  - Result is a finite jump at $\mu=0$.
  - We can show that for $1/K << \mu << 1$, T decreases.
- If the sites are identical, T is constant after the jump.
- Numerically we find $\mu_{selected} \sim 1/K$.
- For many patches the story is similar.
- This is a generic effect, not only for this dynamics. We have forthcoming work to show the class of models for which the same results hold.

Evolution of dispersion rates

- The standard lore in ecology is that organisms evolve non-zero dispersion rates only to be able to deal with *non-constant* resources.
  - Here, the habitats are constant, and evolution would favor $\mu > 0$. This is to deal with fluctuation-induced extinction.
- We have given another example where fluctuations favor $\mu > 0$, competition of a fast with a slow species:
  - D. Kessler and L. Sander, *Fluctuations and dispersal rates in population dynamics*, Physical Review E, **80**, 041907 (2009).
  - J. N. Waddell, L. M. Sander, and C. R. Doering, *Demographic Stochasticity versus Spatial Variation in the Competition between Fast and Slow Dispersers*, Theoretical Population Biology, **77**, 279 (2010).
  - Work in progress with M. Khasin to treat this in WKB.

Summary

- For populations distributed among patches, migration affects the extinction rate.
- The effect is large if the carrying capacity varies a good deal.
- The time to extinction is longest for a small migration rate so that the bad patches can serve as a refuge. They are quite important.
  - Moral:
    On a souvent besoin de un plus petit que soi.

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