

Challenges in Modeling Biological
Invasions and Population Distributions
in a Changing Climate

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Some possible effects of climate change on invasions

(Hellman et al. (2008), Conservation Biology 22, 534-543)

Invasion process: transport → survival in new range → population growth / new populations → spread across landscape

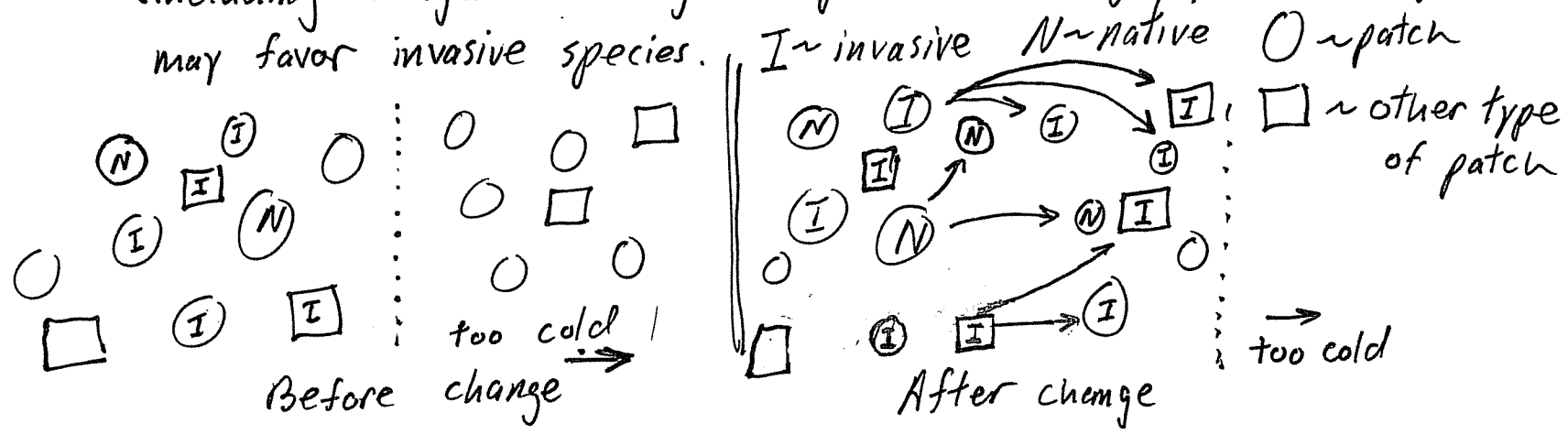
Possible effects of climate change:

- Changes in commerce and human movement (transport) ★
- Changes in abiotic environment (survival)
- Changes in native species / communities (survival, population growth)
- Changes in landscape structure (population growth, spread) ★
(e.g. forest vs. grassland, degree of fragmentation)

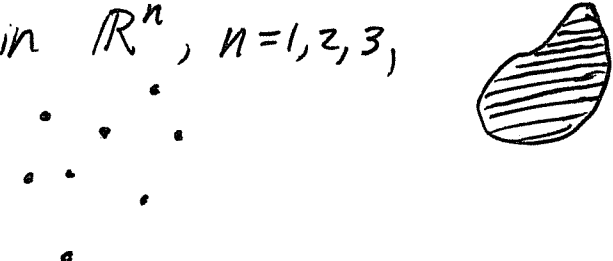
★ Transport and landscape structure are affected by global change not directly related to climate change, e.g. political / economic / social changes, human population growth

A bit more detail:

- Change could eliminate or create dispersal barriers, changing the rate at which possible invaders arrive at any location
- Change could cause niches to open by eliminating native populations via changes in abiotic conditions, as well as allowing invaders to survive
- Invasive species may tend to be good at long distance dispersal and tolerant of a broad range of habitats - so change itself (including changes that might expand the range of native species) may favor invasive species.



"Classical" modeling of dispersal and invasion

- Space is either a domain in \mathbb{R}^n , $n=1,2,3$,
or a collection of patches,  with fixed size (or number of patches) and shape (or connectivity)
 - For invasions, space is usually 1-dimensional;
 - if continuous it is uniform or perhaps periodic or a gradient
 - if discrete it is usually a lattice
- Dispersal is by diffusion, discrete diffusion, or simple (e.g. Laplace kernel) integro-difference operators
- There are only one or two species, with simple interactions, and the species have fixed properties
- Parameters describing movement and population dynamics are constant or possibly periodic in time

Some fairly recent directions in modeling space and dispersal:

(using PDEs)

- Advective environments (Lewis, Lutscher, Jin, ...)
- Anisotropic diffusion (Lewis, Hillen, et al.)
- Directed movement (Lou, Cantrell and C., ...)
- Propagation of wave-like solutions in general environments in n dimensions, with heterogeneity and advection (Berestycki, Hamel, et al.)

$$\star \frac{\partial u}{\partial t} = \nabla \cdot A(x, t) \nabla u + \vec{q}(x, t) \cdot \nabla u = f(x, t, u)$$

$$A = ((a_{ij}))$$

- Moving habitat: Potapov and Lewis 2004, Berestycki et al. 2008, BMB

$$\star \star \frac{\partial u}{\partial t} = D u_{xx} + f(u, x - ct) \quad (\text{or competition models of similar structure})$$

$$f(u, x) = \begin{cases} -\tilde{r}, & |x| > L \\ r(1 - \frac{u}{K}), & |x| < L \end{cases}$$

(Analysis giving biological details involves 1-d matching at $|x|=L$, phase plane methods, etc.)

Mathematical question/challenge:

Can we get any biological insight from models that combine

features of $\star \frac{\partial u}{\partial t} = \nabla \cdot A(x, t) \nabla u + \vec{q}(x, t) \cdot \nabla u = f(x, t, u)$

and $\star \star \frac{\partial u}{\partial t} = D u_{xx} + f(u, x - ct)$

as in $\star \star \star \frac{\partial u}{\partial t} = \nabla \cdot A(x, t) \nabla u + \vec{q}(x, t) \cdot \nabla u = f(x - ct, t, u) ?$

Observation: Some results for $u_t = D u_{xx} + (r - u)u$ on $(-L, L) \times (0, \infty)$
(+ boundary condition)

can be extended (at least qualitatively) to

$u_t = \nabla \cdot [D(x) \nabla u - u \vec{Q}(x)] + (r(x) - u)u$ on $\Omega \times (0, \infty)$

But that often requires detailed eigenvalue estimates.

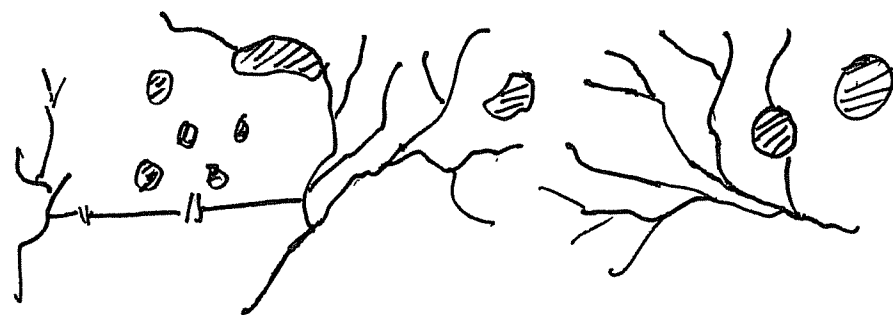
Are those feasible for interesting invasion models with somewhat general heterogeneity?

Note however: Actual space and dispersal are more complicated

A case study: Zebra Mussels

(Johnson and Carlton (1996), Ecology 77 1686-1690)

- Space consists of streams, lakes connected to streams, and "isolated" lakes.
- Networks of streams may be "isolated" from each other
- Dispersal is multimodal:
 - Larvae diffuse in lakes, advect downstream in streams
 - Commercial shipping can move adults upstream*
 - Recreational boaters can move mussels over land*
 - Aquatic organisms can transport mussels*



(etc.....)

* movement patterns may change over time

A different kind of "invasion" model:

(Fagan, Cantrell, C., Ramakrishnan *AmNat* 173 (2009), 363-375)

- o 1-d Environment consists of patches and gaps, alternating, with size drawn from some distributions:

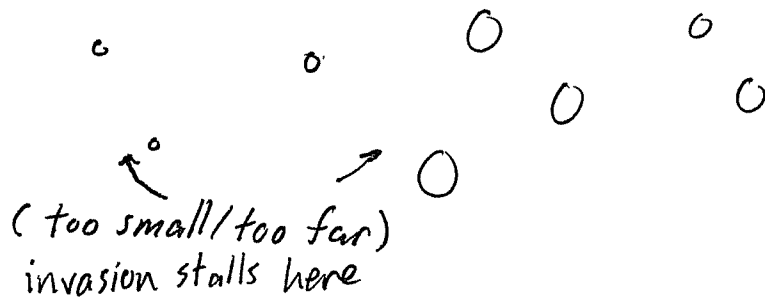
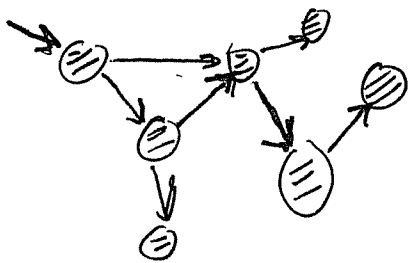


- o A population has a minimum patch size to survive and a maximum gap size it can cross. (Connected to mechanisms by diffusion

theory - minimum patch size for $u_t = du_{xx} + (r - u/k)u$ is $l = \pi\sqrt{d/r}$)

- o Population expands range until it hits too big a gap or too small a patch. This sets up a distribution for expected range size (Computable in some cases)

Can this be done in 2-d? (Is it worth trying?)



How about with patch and gap distributions that change over time?

Abiotic environment vs. population interactions

Change can directly influence habitat suitability for an invader — typically species distribution (niche) models are based on abiotic factors

However:

- Change can in principle make invasion more likely by making habitat unsuitable for competitors (creating empty niches)
- Change can in principle make invasion less likely by allowing invasion by generalist predators, pathogens, or other enemies of an invasive species

Bigger picture questions: To what extent do species interactions influence geographic distributions?
What effects could be expected?

(Current NIMBioS working group)

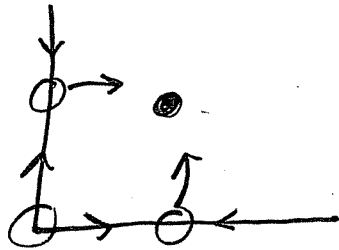
Example: Mutualism

$$\frac{dN_1}{dt} = N_1 \left[g_1(x) + \frac{c_1 N_2}{1+b_2 N_2} - d_1 N_1 \right] \quad \frac{dN_2}{dt} = N_2 \left[g_2(x) + \frac{c_2 N_1}{1+b_1 N_1} - d_2 N_2 \right]$$

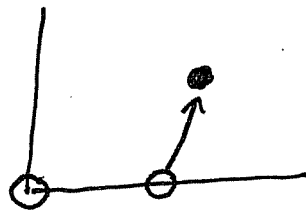
$g_1, g_2 \sim$ environmental gradients. $\{x: g_i(x) > 0\} =$ natural range of species i by itself

Phase portraits (○ unstable, ● stable)

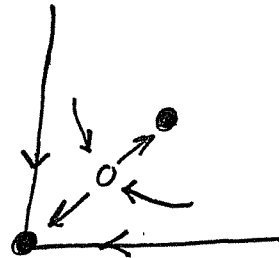
$g_1, g_2 > 0$



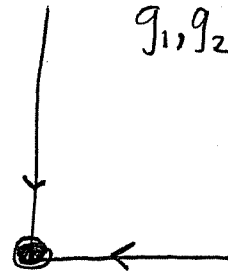
(for some parameters)
 $g_1 > 0, g_2 < 0$



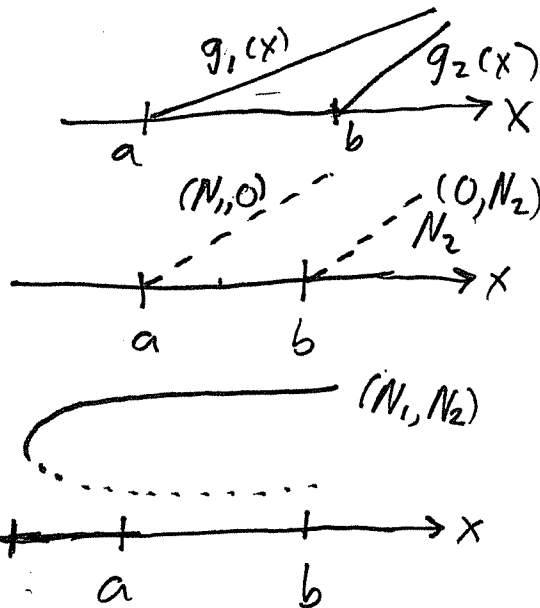
$g_1 < 0, g_2 < 0$



$g_1, g_2 \ll 0$



Bifurcation diagrams



Mutualism extends natural ranges - but leads to "Allee" effect

Connection to invasions and climate change:

Suppose $g_i = g_i(x-ct)$
Once $x-ct = x^*$ there will be a sudden collapse of populations, opening an interval of length $a-x^*$ for possible invasion

More on species interactions:

- The presence of a generalist predator could stop an invasion by prey
- Loss of the predator due to climate change could open new regions to prey invasion. Possible model:

$$\frac{\partial u}{\partial t} = D u_{xx} + (a(x-ct) - u - bv)u \quad (\text{prey})$$

$$\frac{\partial v}{\partial t} = D v_{xx} + (f(x-ct) + ebu - v)v \quad (\text{predator})$$

(Possible challenge - spreading speed in predator-prey models)

More generally: To what extent can single species modeling in changing environments be extended to systems of interacting species?

(2x2 competition and any mutualism are monotone systems; predator-prey are not; they embed in 4x4 monotone systems but it's messy)

A different view of climate change vs. species interactions: phenology matching.

- In temperate zones, many plants and insects are dormant (possibly as seeds, or eggs or pupae) over winter, emerge in spring, develop and experience mortality over summer, and reproduce during summer or fall to generate next year's emerging populations
- To interact with each other, species have to be present at the same time in the same place
- Timing may depend on different factors - photoperiod, temperature, ... that could be affected differently by climate change, leading to loss of interaction.

A crude consumer-resource phenology matching model

$T \sim$ year $t \sim$ time during summer; $0 \leq t \leq 1$.
 $R(T, t) \sim$ resource density
 $C(T, t) \sim$ consumer density
 (in summer)

$$R(T, 0) = 0 \quad C(T, 0) = 0$$

$$\frac{dR}{dt} = \underbrace{r_R R(T-1, 1)}_{\text{Survival / Reproduction from previous year}} \underbrace{g_R(T, t)}_{\text{emergence rate (has parameters)}} - \underbrace{d_R R(T, t)}_{\text{mortality}} - \frac{fR(T, t)C(T, t)}{1 + hR(T, t)}$$

Survival / Reproduction from previous year
 emergence rate (has parameters)

(r_R may depend on $R(T-1, 1)$)

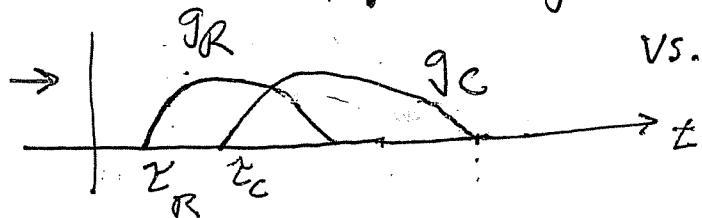
(Model could easily be "spatialized")

$$\frac{dC}{dt} = r_C C(T-1, 1) g_C(T, t) - \left[d_C - \frac{efR(T, t)}{1 + hR(T, t)} \right] C(T, t)$$

($ef < d_C$ so that resource reduces consumer mortality, but does not cause population growth.)

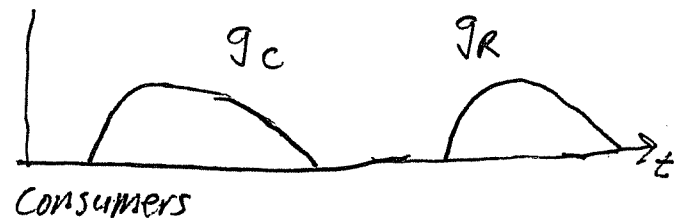
(Possible effect of climate change)

OK for consumers



vs.

Not OK for consumers



Evolution of dispersal in invasions

- "Evolutionarily accelerated invasions: the rate of dispersal evolves upward during the range expansion of cane toads"
(empirical) Phillips et al. (2010), *J. Evolutionary Biology* 23, 2595-2601
- "Accelerating invasion rates result from the evolution of density-dependent dispersal"
(simulations) Travis et al. (2009), *J. Theoretical Biology* 259, 151-158
- "Dispersal polymorphism and the speed of biological invasions";
Elliot and Cornell. (2012), *PLoS ONE* 7 (7): e40496
doi:10.1371/journal.pone.0040496
(Analytic models, but no true evolution - phenotypic or behavioral plasticity)

Elliot and Cornell:

$e \sim$ establisher (slower disperser, faster reproducer) $n_e \sim$ density
 $d \sim$ disperser (faster disperser, slower reproducer) $n_d \sim$ density

$$\frac{\partial n_e}{\partial t} = D_e \frac{\partial^2 n_e}{\partial x^2} + r_e n_e (1 - m_{ee} n_e - m_{ed} n_d) + \mu_d n_d - \mu_e n_e$$

$$\frac{\partial n_d}{\partial t} = D_d \frac{\partial^2 n_d}{\partial x^2} + r_d n_d (1 - m_{de} n_e - m_{dd} n_d) + \mu_e n_e - \mu_d n_d$$

Results - linearized analysis of wavespeed
(But the system is not monotone - is that valid?)
numerical calculations

Conclusion: polymorphism increases invasion speed.
(Challenge - additional rigorous mathematical analysis)
(Harder challenge - can we build true evolutionary processes into invasion models we can actually analyze?)

- Large literature (starting with Fisher!) on the movement of alleles through a population whose density is uniform in space. For two alleles -

$p \sim$ fraction of population with the first allele

$$\frac{\partial p}{\partial t} = d\Delta p + g(x)p(1-p) \quad (\text{etc.})$$

But: In the context of climate change and invasions, population densities are not uniform in space.

Some specific issues:

- To what extent can native populations evolve dispersal strategies and/or mechanisms for coping with new abiotic condition to keep pace with a shifting climate or survive change? How fast would they need to evolve?
- How does evolution influence invasions?
 - adaptation to new environments after introduction
 - evolution of dispersal during spread

Possible model types:

1. Models that track both the population density u and the proportion with some allele (say A , from $A \times a$):

$$\frac{\partial u}{\partial t} = D \Delta u + f(x, t, u, p) u \quad \frac{\partial p}{\partial t} = D \Delta p + g(x, t, u, p)$$

$$(D = D(u, p)?)$$

$$(g(x, t, u, 0) = g(x, t, u, 1) = 0)$$

or models that track population densities of individuals

$$u_{AA} \sim AA, u_{Aa} \sim Aa, u_{aa} \sim aa$$

$$\frac{\partial u_{AA}}{\partial t} = D_{AA} u_{AA} + f_{AA}(x, t, u_{AA}, u_{Aa}, u_{aa}), \quad \frac{\partial u_{Aa}}{\partial t} = \dots$$

(some ideas in work by Nagylaki (1975-1980))

2. Quantitative genetics approaches (already used for range limits)

(Kirkpatrick and Barton (1997) *Am. Nat.* 150, 1-23)

(Holt et al. (2011) *Am. Nat.* 178, 488-500)

$N \sim$ population density

$\bar{z} \sim$ mean phenotype

$z_0 \sim$ optimal phenotype

$$\frac{\partial N}{\partial t} = \frac{\partial^2 N}{\partial x^2} + \left[f(N) - \frac{1}{2} (\bar{z} - z_0)^2 \right] N \quad (\mathbb{R}_+ \times (0, \infty))$$

$$\frac{\partial \bar{z}}{\partial t} = \frac{\partial^2 N}{\partial x^2} + 2 \frac{\partial (\ln N)}{\partial x} \frac{\partial \bar{z}}{\partial x} - A(\bar{z} - z_0)$$