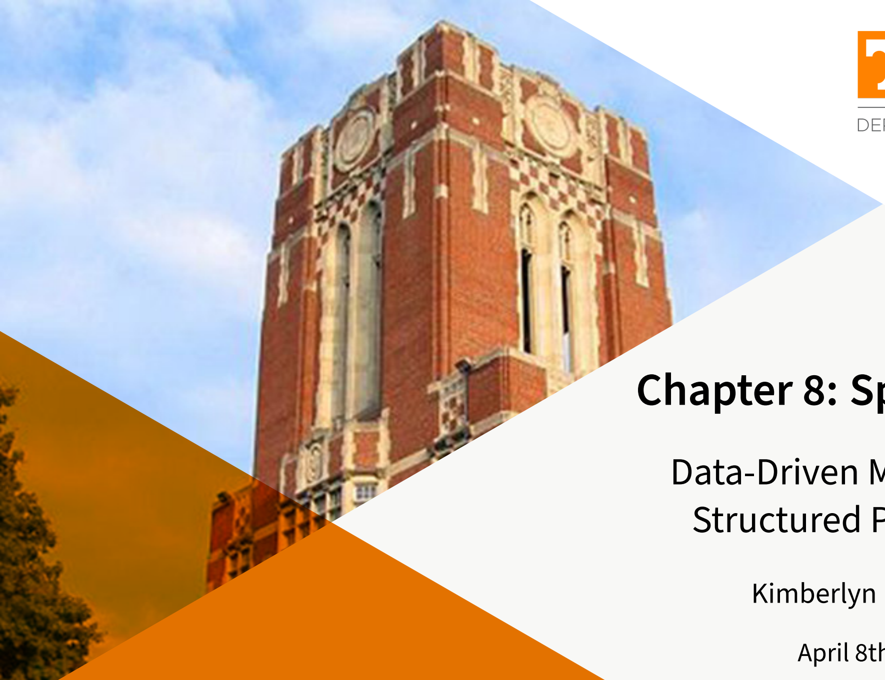

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DEPARTMENT OF MATHEMATICS

Chapter 8: Spatial Model

Data-Driven Modelleing of Structured Populations

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Overview of spatial IPMs

Overview of spatial IPMs

Spatial population structure is a natural application of IPMs because spatial location varies continuously.

First look at simpler situation where individuals differ only in spatial location:

- $n(x, t)$: population described by spatial distribution
  - x: spatial location
- z: bounded set of possible values

Let's also consider one-dimensional space first:

- so x is a point on the (infinite) line

Overview of spatial IPMs

Projection kernel K for a spatial IPM must include two parts:

- $k_d(x', x)$: the dispersal kernel
  - function describing the transport of individuals from an initial location x to a subsequent location x' within the spatial domain X
  - simplifying assumptions is that dispersal kernel only depends on distance: $k_d\left(|x' - x|\right)$
- model for population growth due to reproduction and mortality

Overview of spatial IPMs

Combining population growth and dispersal we have:

- In the absence of density dependence:

$$n(x', t+1) = \int_X R_0 k_d(x', x) n(x, t) dx$$

  - R_0: finite rate of population growth, a constant
- Density dependence in local population growth added by Kot and Schaffer (1986):

$$n(x', t+1) = \int_{-m}^{m} k_d(x' - x) f\left(n(x, t)\right) dx$$

  - $f(n)$: describes population growth
  - used to study combined effects of local interaction and dispersal
  - assumes the population's life cycle alternated between phases of local population growth and spatial redistribution with finite interval $[-m, m]$

Overview of spatial IPMs

- Density-independent with a general IPM to describe local population dynamics added by Jongejans et al. (2011):

$$n(x', z', t+1) = \int \int K(x' - x, z', z) n(x, z, t) dxdz$$

  - all other usual variations we have learned (density dependence, environmental stochasticity, demographic stochasticity) can also be added

Overview of spatial IPMs

Two-dimensional space:

- $k_R(r)$: probability density that describes two dimensional dispersal
  - r: dispersal distance
  - direction go movement uniformly distributed over $[0, 2\pi]$
- $k_R(r)dr$: probability of landing somewhere between the circles of radius r and $r + dr$ centered at the point of origin
- one- and two-dimensional models look the same, except x is a vector of two spatial coordinates

Building a dispersal kernel

Building a dispersal kernel

How do we come up with the dispersal kernel, $k_d(x', x)$?

Two main types of movement models:

- descriptive model: a probability distribution that represents the outcome of movement
  - fitted to data on the observed changes in location: where individuals started from and where they eventually got to
- mechanistic model: represents the process of movement
  - represents *how* they got there
  - fitted to data on the steps in the process of moving

Building a dispersal kernel

Descriptive movement modeling

Pons and Pausas (2007) studied acorn dispersal by jays:

- They put radio transmitters into acorns, and then recorded the final resting point of the uneaten acorns.

Turchin (1998) describes mark-recapture studies:

- Individuals or groups are given some distinct mark so they can be found again.

Bullock and Clarke (2000) studied wind dispersal of heather seeds:

- They counted the number of seeds that fell into pots of various distances.

Notice in all of these examples, the data tells us start and stop locations but not in between.

Building a dispersal kernel

Mechanistic movement modeling

Recall mechanistic models are built from the data on each step in the process of movement.

Classic example is Parlak's correlated random walk for animal movement:

- movement path in 2D consist of short linear segments
- for each segment, speed and time duration are chosen from probability distributions
    - independent of previous segment
- direction of motion is generated by randomly selecting a turning angle relative to the previous segment
    - movement is correlated with previous segment

Mechanistic models can rarely be solved analytically.

Building a dispersal kernel

Mechanistic movement modeling

- Morales et al. (2004) used high-precision data on movement of large animals (from GPS collars) to model a combination of several different random walks corresponding to different behavioral states of the individual.
  - Used Bayesian methods to fit a variety of models with multiple behavioral states to movement data on elk.
  - Model had two states: "encamped" and "exploratory", where the latter had longer step lengths and smaller turning radius
- Mechanistic models for animal-dispersed seeds have been developed by layering a probability distribution for seed retention time on top of a model for animal movement.

Theory: bounded spatial domain

Theory: bounded spatial domain

Now let's look at analysis and applications of spatial models.

Assume the spatial domain is bounded, $X = [-m, m]$.

Spatial location is just another "trait" that differs between individuals and changes over time, so all the general theory applies.
Thus density-independent spatially structured IPMs can predict:

- asymptotic spatial structure and space-dependent reproductive value (Chapter 2)
- the distribution of location at first reproduction (Chapter 3)
- how location-dependent demographic stochasticity affects population growth (Chapter 10)

Theory: bounded spatial domain

Now with density-dependence on growth, the interest becomes

- equilibria
- their stability
- oscillations around unstable equilibrium

The stability of the equilibrium can be studied by linear stability analysis.

Theory: unbounded spatial domain

Theory: unbounded spatial domain

Without spatial bounds, the populations range can expand without limits, so we no longer expect stationary or periodic spatial patterns as the long term behavior.

The only way to find constancy is though a moving frame of reference that moves with the spread of the population.

- Consider a frame of moving at constant rate c.
- An observer (in this frame) would move from location $x - c$ at time $t - 1$ to x at time t.
- The population will appear constant to the observer if

$$n(x, t) = n(x - c, t - 1).$$

  - i.e. one time unit ago, everything was the same except shifted c units of space

Theory: unbounded spatial domain

When the population appears constant to the observer, we then see that

$$n(x,t) = n(x-c,t-1) = n(x-2c,t-2) = \dots = n(x,0) =: n_0(x).$$

A population distribution with this property is called a traveling wave with speed c.

For the density-independent model with spatial domain $X = (-\infty, \infty)$, there are often infinitely many traveling waves solutions for different speeds c.

Theory: unbounded spatial domain

A straightforward calculation shows that

$$n(x,t) = N_0 e^{rt} e^{-sx}$$

is a traveling wave solution with $r = \log(R_0 M(s))$ and speed $c(s) = \log(r)/s$, where

$$M(s) = \int_{-\infty}^{\infty} e^{su} k_d(u) du$$

is called the moment generating function.

The number $s > 0$ is called the wave shape and determines how the traveling wave varies spatially at any one time t.

Theory: unbounded spatial domain

These traveling waves have the property that the population is present everywhere: $n(x,t) > 0$ for all x.

As a result, these waves spread faster than any population that was initially limited to a bounded region. Thus if a population that was initially limited to a bounded region settles into a traveling wave, its speed c^* must be no larger than the minimum of $c(s)$.

Fortunately, Hans Weinberger and Roger Lui showed that under general conditions, a population that is initially limited to a bounded region converges to a traveling wave speed

$$c^* = \min_s c(s).$$

Theory: unbounded spatial domain

Exactly the same is true for density-dependent spatial IPM in the absence of Allee effect in the local population growth function f, with $R_0 = f'(0)$.

From here on, we will assume that more complicated models act like the simpler one:
If you linearize an IPM at zero population density, and computer the minimum possible wave speed c^* for the linearized model, then solutions of the original model converge to a traveling wave with speed c^* so long as there are no Allee effects, and the original population was limited to a bounded region of space.

This is called the linearization conjecture.

Some applications of purely spatial IPMs

Some applications of purely spatial IPMs

Kot et al. (1996) explored the ecological implications of traveling waves in purely spatial IPMs.

- showed the speed of population spread could be drastically underestimated by classic reaction-diffusion models
- showed that dispersal kernels with fatter tails could lead to substantially faster predicted rates of population spread than a Gaussian dispersal kernel with the same variance (Fig. 8.4)

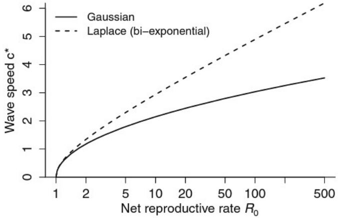


Fig. 8.4 Long-run traveling wave speed c^* for the Gaussian and Laplace (bi-exponential) dispersal kernels with variance=1, as a function of the low-density net reproductive rate $R_0 = f'(0)$. The moment-generating functions for these kernels are $M(s) = e^{\sigma^2 s^2/2}$ for the Gaussian with variance σ^2 and $M(s) = 1/(1 - b^2 s^2)$ for the Laplace with parameter b and variance $2b^2$; these lead to formulas for $c(s)$ that can be minimized to find c^*. The difference between c^* for Gaussian and Laplace kernels is less dramatic here than in Kot et al. (1996, fig.4) because they compared the Laplace kernel with a Gaussian fitted to the same data by least squares, while the comparison here (to a Gaussian with equal variance) corresponds to maximum likelihood fitting of the Gaussian. Source file: `GaussLaplaceWaves.R`

Some applications of purely spatial IPMs

- Kot et al. (1996) also suggested that highly fat-tailed kernels might explain cases such as the initial introduction of Japaneses beetles and European starlings in the USA, where the rate of the population spread initially increased over time, until the population started to encounter its geographical limits.
  - If the tails are so fat that $M(s)$, the moment generating function, is not finite for any s, then the purely spatial IPM predicts accelerating population spread rather than a wave with constant speed.

Combining space and demography: invasive species

Combining space and demography: invasive species

- If the spatial domain is bounded, then the spatial IPM,

$$n(x', z', t+1) = \int \int K(x' - x, z', z) n(x, z, t) dx dz,$$

  is just a general IPM with spatial location as one of the individual-level traits, and all the theory for those models, deterministic and stochastic, still applies.
- Beyond that, the above equation is too general for much more to be said.
- So we'll look instead at two empirical applications in which local demography and dispersal jointly determine the spread rate of an invading species.

Combining space and demography: invasive species

Jongejans et al. (2011) extended the analysis of traveling wave speed by Neubert and Caswell (2000).

- The kernel is assumed to have exponential or thinner tails so that $M(s)$ is finite in some interval containing 0.
- In one spatial dimension, the calculations are similar to those for the basic spatial IPM,

$$n(x', t+1) = \int_X R_0 k_d(x', x) n(x, t) dx.$$

Combining space and demography: invasive species

- A traveling wave is a model solution $n(x, z, t)$ such that $n(x, z, t) = n(x - c, z, t - 1)$.
  - We find them by considering solutions of the form $n(x, z, t) = n(z)e^{rt}e^{-sx}$.
- Subbing this into

$$n(x', z', t+1) = \int \int K(x' - x, z', z) n(x, z, t) dx dz,$$

we get a traveling wave where $n(z)$ is the dominant right eigenvector of the transformed kernel

$$H_s(z', z) = \int_{-\infty}^{\infty} e^{sx} K(x, z', z) dx$$

and

$$c(s) = \frac{1}{s} \log(\lambda(s)),$$

where $\lambda(s)$ is the dominant eigenvalue of H_s.

Combining space and demography: invasive species

- The wave speed
$$c(s) = \frac{1}{s}\log(\lambda(s))$$
is related to whether the total population grows or shirks.
- H_0 is the kernel for the total population, $\int n(x,z,t)dx$.
  - So the total population grows if $\lambda(0) > 1$.
  - Then $\lambda(s) > 1$ for s near 0.
  - $c(s)$ gives traveling wave solutions in which the population is expanding (moving with speed $c(s) > 0$ to the right).

Invasion speed in fluctuating environments

Invasion speed in fluctuating environments

Ellner and Schreiber (2012) took the final step by adding environmental stochasticity to a spatial IPM for invasive species spread.

- i.e. the demographic and dispersal kernels are allowed to vary randomly over time
- The calculations and results are again very similar to the pure spatial model.
- The transformed kernel is a stochastic IPM $H_{s,t}(z', z)$.
  - has a stochastic growth rate $\lambda_S(s)$ when the Chapter 7 assumptions are satisfied
- The predicted spread rate c^* is

$$c^* = \min_s \left(\frac{1}{s} \log \left(\lambda_S(s) \right) \right).$$

Invasion speed in fluctuating environments

Ellner and Schreiber (2012) showed that

- temporal variation in the demographic kernel slows down population spread
- variation in mean dispersal distance generally increases the rate of population spread
- when mean distance varies over time, demographic variation that is positively correlated with the variation in mean dispersal distance can also increase the rate of population spread

Invasion speed in fluctuating environments

Ellner and Schreiber (2012) developed an IPM for the spread of perennial pepperweed, Lepidium latifolium, a Eurasian crucifer that is now widely invasive in wetlands and riparian zones in the western USA to illustrate the potential importance of temporally variable dispersal.

- The model describes patches of pepperweed rather than individual plants.
  - $z =$log patch radius
- A density-independent IPM at the level of patches is valid (so long as patches are sparse enough that they don't collide with each other).
- According to the linearization hypothesis, this density-independent model will correctly predict the asymptotic spread rate of the population of patches.

Invasion speed in fluctuating environments

The Laplace-transformed kernel for the model is

$$H_{s,t} = \left(1 - s^2 L(t)^2\right)^{-1} F_t + P_t.$$

- P_t: represents survival and growth of established patches
- F_t: represents production of new patches
- $\left(1 - s^2 L(t)^2\right)^{-1}$: the Laplace transform of the dispersal kernel
  - Because established patches have dispersal distance of 0 with probability 1, the Laplace transform of their "dispersal distribution" is constant with value 1.

F_t and P_t are determined by

- $d(t)$: mortality
- $g(t)$: growth rate
- $f(t)$: fecundity

Invasion speed in fluctuating environments

Figure 8.6 shows how random variation in demography and dispersal affect the predicted population spread rate.

- variation in just the demographic parameters (solid gray curve) has much less effect
- demographic variation slows spread more substantially is it acts in opposition to dispersal variation (dotted curve)
  - So a good year for offspring dispersal (large $L(t)$) is a bad year for offspring production (small $L(t)$).

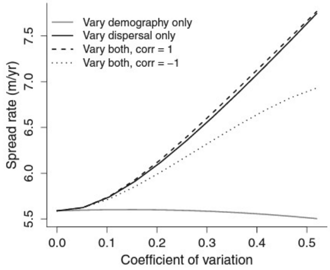
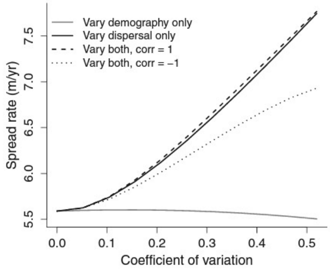


Fig. 8.6 Asymptotic one-dimensional spread rate c^* for the perennial pepperweed model. All time-varying parameters (d, f, g, L) had a uniform distribution centered on their estimated means ($\bar{d} = 0.06, \bar{f} = 0.04, \bar{g} = 0.5, \bar{L} = 15$). The local demography parameters (d, f and g) were perfectly correlated with each other, while mean displacement L was either perfectly correlated or perfectly anti-correlated with the local demography parameters (correlation coefficient= $+1$ or -1). Source files: `PepperweedIPMFunctions.R`, `PepperweedIPMRun=U.R`

Invasion speed in fluctuating environments

- Demographic variation that reinforces dispersal variation (large *f* with large *L*) has a positive effect, as predicted the the general analysis of Ellner and Schreiber (2012), but it is very small.

These results reinforce previous findings on population spread using integrodifference models.



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