Discussions on “Chapter 6: General Deterministic IPM”

Book: Data-driven Modelling of Structured Populations by S.Ellner, D. Childs, M. Rees

UTK Math Bio Seminar

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Overview

Main Idea: Extend theory for basic IPM to framework for populations with complex demography

Examples:

1. Demographic rates are affected by multiple attributes
   - age and size, size and disease state, age and sex, etc.
2. Use different attributes at different life cycle stages
   - above-ground plants classified by size while buried seeds are classified by depth of burial
3. Future depends on past as well as present (time delays)

Commonality: Individual state is not specified by just one number!

Soay Sheep Population Recap

Chapter 2 considered a size-structured model. Now we want to incorporate both size and age.

Recall:

- Size is log body mass
- Still use post-reproductive census
- Only consider dynamics of females
- Density-independence

Structure of an age-size IPM

General form of deterministic age-size IPM:

$$n_0(z', t+1) = \sum_{a=0}^{M} \int_L^U F_a(z', z) n_a(z, t) dz$$

$$n_a(z', t+1) = \int_L^U P_{a-1}(z', z) n_{a-1}(z, t) dz \quad a = 1, 2, \ldots, M$$

where M is the age past which no individual can survive

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If no max age of survival, add "greybeard" age-class:

$$n_{M+1}(z', t+1) = \int_{\mathbf{Z}} [P_M(z', z) n_M(z, t) + P_{M+1}(z', z) n_{M+1}(z, t)] dz$$

Soay Sheep Model

- Based on dataset constructed from IBM
- Set of linear and generalized linear models fitted to dataset as in previous chapters
  - Models for survival, growth, and reproduction include both log body mass and female age
  - Lamb recruitment and birth size only depend on maternal age and size, respectively
- Reproductive and Survival kernels:

$$F_a(z', z) = s(z, a)p_b(z, a)p_r(a)C_0(z', z)/2$$
$$P_a(z', z) = s(z, a)G(z', z, a)$$

- Model will converge to stable age-distribution, $w_a(z)$, with growth rate λ (provided conditions in Section 6.5 hold)
- Can compute size-dependent reproductive value for age a, $v_a(z)$

Soay Sheep Model

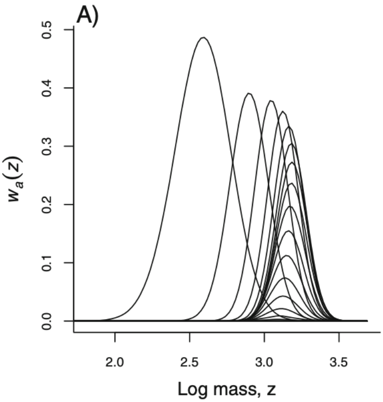


Fig. 6.1: A) Stable age-size structure. B) Reproductive value functions for each age class.

Is this worth the effort?

- If statistical analysis of data implies a state variable influences vital rates... might as well include
- But, this may increase complexity in constructing and analyzing the model
- Does it matter if some state variables are ignored?

Soay Sheep Comparison - λ and $\mathcal{R}_0$

- Size-only IPM
  - $\lambda = 1.025$ and $\mathcal{R}_0 = 1.337$.
- Age-size IPM
  - $\lambda = 1.013$ and $\mathcal{R}_0 = 1.083$.

Note: Size-only IPM over-estimates average lifespan - poorly estimates $\mathcal{R}_0$

Soay Sheep Comparison

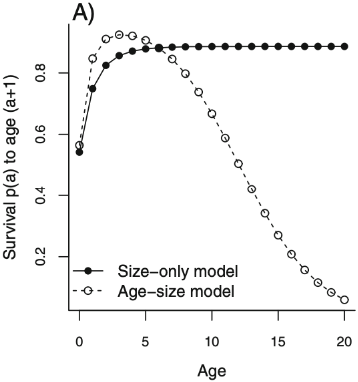


Fig. 6.4: Comparison of age-size and size-only ungulate models

Soay Sheep Comparison

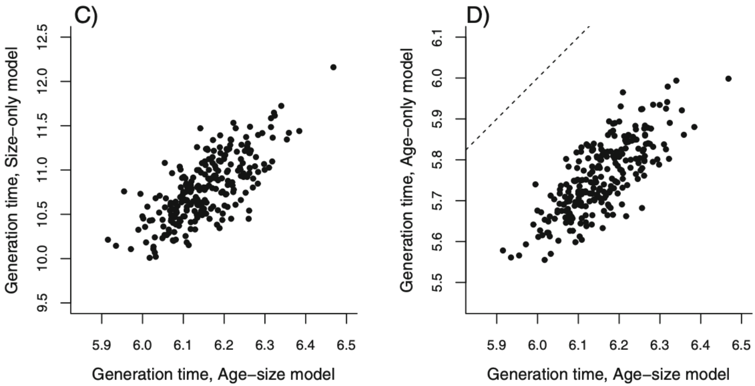


Fig. 6.4: Comparison of age-size and size-only ungulate models

Seeds and Plants

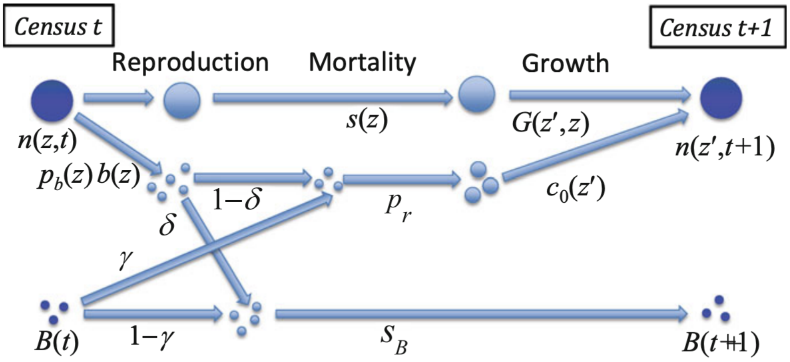
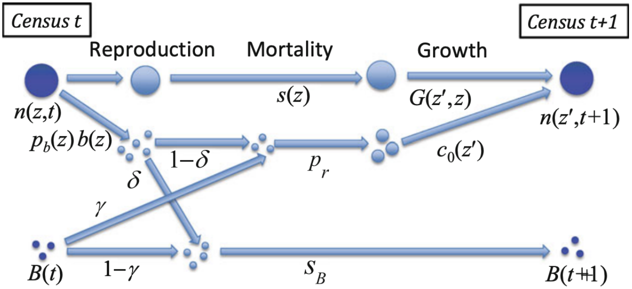


Fig. 6.2: Life cycle diagram for the monocarpic perennial model with a persistent seed bank and pre-reproductive census.



$$B(t+1) = s_B\left[(1-\gamma)B(t) + \delta \int_L^U p_b(z)b(z)n(z,t)dz\right]$$

$$n(z', t+1) = \int_L^U G(z'z)s(z)n(z,t)dz$$

$$+ c_0(z')p_r\left[(1-\delta)\int_L^U p_b(z)b(z)n(z,t)dz + \gamma B(t)\right]$$

Susceptible and Infected

- IPM for sea fan coral *Gorgonia ventalina* (Bruno et al. 2011)
- Fungal pathogen *Aspergillus sydowii*
- Observed $\sim$ 750 sea fans at 3 sites on Belizean Barrier Reef, Mexico
- Future fates affected by disease state (infected or uninfected) and by area of uninfected tissue
- size measure $z =$ cube root of healthy tissue area

Susceptible and Infected

$$n_H(z', t+1) = \int_0^{20} P_{HH}(z', z) n_H(z, t) dz + \int_0^{20} P_{HI}(z' z) n_I(z, t) dz + \mathcal{R} c_0(z')$$

$$n_I(z', t+1) = \int_0^{20} P_{IH}(z', z) n_H(z, t) dz + \int_0^{20} P_{II}(z', z) n_I(z, t) dz$$

Ex. (Healthy to Infected Transitions):

$$P_{IH}(z', z) = \tau(z)(1 - m_H(z)) g_H(z'|z)$$

Time Delays

- IPM for Alpine monocarpic perennial (Kuss et al. 2008)
- $$n(z', t+1) = \int_L^U P(z', z)n(z, t)dz + \int_L^U F(z', z)n(z, t-1)dz$$
- Leaves wither during winter, bolting occurs after snowmelt
- Size in year $t-1$ is better predictor of flowering than size in year of flowering t

Integration Techniques (Midpoint Rule)

- Simple, robust, *usually* efficient
  - Ex. Inverting a 250x250 matrix takes < 0.1 seconds in R
- Midpoint rule can lead to very large iteration matrices for some models
  - Ex. Add continuous variable with 50 mesh points to size-structured IPM
    - Inverting this matrix takes about 50^3 times longer in R.

Integration Techniques (Gauss Legendre Quadrature)

- If kernel is smooth, using higher-order methods can be beneficial
- Gauss-Legendre uses unevenly spaced mesh points z_i and unequal weights W_i
- z_i and W_i are chosen so

$$\int_a^b f(x)dx \approx \sum_{i=1}^{N} W_i f(z_i)$$

  is exact when f has degree $< 2N + 1$
- Problem: Mesh points are densest near endpoints of integration range
  - Endpoints might not be where IPM kernel is most nonlinear

Integration Techniques (Sub-interval Gauss Legendre)

- Divide range of integration into sub-intervals
- On each sub-interval, use medium-order quadrature
- More evenly spaced mesh points

Integration Techniques Comparison

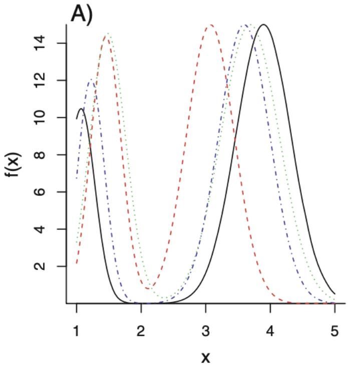


Fig. 6.5: Comparing the accuracy of quadrature methods

Integration Techniques Comparison

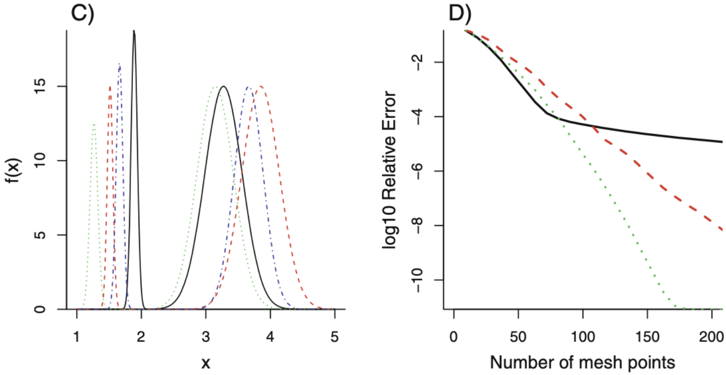


Fig. 6.5: Comparing the accuracy of quadrature methods

Integration Techniques (General Advice)

- Default is Midpoint Rule
- If iteration matrix size is problematic, try Gauss-Legendre or sub-interval Gauss-Legendre if kernel is smooth
- If kernel has sharp spikes, try bin-to-bin
    - Similar to midpoint rule
    - Every kernel value is replaced by its average over the grid rectangle

Stable Population Growth (Power-positivity)

The main results regarding stable population growth still apply to all models in Chapter 6.

- For MPM, the only assumption for stable pop. growth is: $\exists m > 0$ s.t. all entries of A^m are positive (i.e. power-positive/primitive)
- For IPM, kernel K must be power-positive: $\exists m > 0$ s.t. $K^m(z', z) > 0 \; \forall z', z, \in \mathbf{Z}$.
  - $K^1 = K$ and $K^{m+1}(z', z) = \int_{\mathbf{Z}} K(z', y) K^m(y, z) dy$
- Most published IPMs satisfy this condition
- What if power-positivity does not hold or is difficult to prove?

Stable Population Growth (u-boundedness)

Stable population growth occurs for kernels that are not power-positive provided K^m is u-bounded.

u-boundedness: K^m is u-bounded if there exists a probability distribution $u(z)$ on **Z** s.t. for any $n(z,0)$, $\exists\ \alpha, \beta > 0$ (depending on $n(z,0)$) s.t. $\alpha u(z) \leq n(z,m) \leq \beta u(z)$.

The kernel is often u-bounded due to mixing at birth

Compactness

- Section 6.9 gives detailed assumptions for the theory of general deterministic IPMs
- Assume K is a compact operator - ensures dominant eigenvalue is "isolated"
- Question: Does the theory for IPMs extend when the integral projection operator is not compact?

New Result: (2021)

Reichenbach M, Rebarber R, Tenhumberg B. Spectral properties of a non-compact operator in ecology. J Math Biol. 2021 Apr 13;82(6):50. doi: 10.1007/s00285-021-01600-7. PMID: 33847821.

- Motivating Example: Consider population of Northern Pike where the structure variable is length
- If individuals can decrease in size, the IPM operator will be compact
  - Plants that shrink over time in poor growing conditions
  - Biomass of sheep can decrease in poor conditions
  - Proportion of coral covered with fungal infection can decrease with time
- But, length of fish can't decrease with time

New Result: (2021)

- If structure variables can't decrease with time they prove:
  - The growth subkernel G is unbounded -> so K will be unbounded
  - Also, the operator will not be compact

- Main Questions: Do IPMs with non-compact operators have an asymptotic growth rate? What about a stable-stage distribution?
  - Yes!

Discussion

Any questions/comments?