# Environmental stochasticity in IPMs

Vital rate functions can readily accommodate covariates, such as environmental conditions, that help to predict individuals' vital rates above and beyond the state variable. For example, plant growth may be determined both by its previous size, and the nutrient conditions in its habitat.

In the case, the growth kernal G is then a function fof the state variable of size and nutrients as: $G(z'|z, nutrients)$.

If these nutrients vary through time we could then state that time dependence as $G(z'|z, nutrients_t)$

# Example: Temperature dependent growth of gilthead seabream

Heather et al. (2018) used this approach to explore how temperatures in the Mediterranean might affect growth rates of gilthead seabream, an important aquaculture species

# Example: Temperature dependent growth of gilthead seabream

- obtained 11 years of growth increments by examining the otoliths of wild juvenile and adult fish caught between 2008–2011
- fitted a series of mixed effects models to account for intrinsic (e.g. random individual effects) and extrinsic (e.g. water temperature, random year effects) effects on the rate of otolith growth
- water temperature records for the Gulf of Lions (NW Mediterranean)
- best model (selected by AIC) included random effects of fish and year, and fixed effects of otolith size at previous year and mean Mediterranean summer temperature
- used otolith annual increment width as a proxy for individual-level growth within specified years, which was then coupled with an allometry model to estimate fish body growth, to project under climate warming

# General stochastic IPM

- of course any of the kernels, or even multiple components of the same kernel could be dependent on environmental covariates that fluctuate through time. More generally, we can note that the kernel is dependent on time varying parameters in the vector, $\theta$, as:

$$n(z', t+1) = \int_L^U K(z', z; \theta(t))n(z, t)dz$$

# Two methods for IPM stochasticity

There are two basic approaches to building an IPM with environmental stochasticity: 1. Kernel selection, or 2. Parameter selection

These methods are analogous to those used for matrix population models, where one either chooses from a set of transition matrices at random, or one chooses life history parameters from some relevant distribution. However, for IPMs parameter selection must be followed by constructing the relevant kernel

# Two methods for IPM stochasticity: Kernel Selection

**Kernel Selection**. If we are starting from data: for each year in the study, a fitted fixed-effects model gives us a vector of year-specific values for each parameter, and a fitted mixed-effects model gives us a vector of fitted values or posterior modes for each parameter. In either case, we construct a set of kernels using each of the year-specific sets of parameters, and then simulate the model by selecting from the set of kernels at random.

**Kernel selection process**

1) Construct set of yearly kernels $\rightarrow$ 2) Select a kernel at random $\rightarrow$ 3) Project the population forward one time step, and then repeat from 2).

# Two methods for IPM stochasticity: Parameter Selection

**Parameter Selection** If you have characterized the between-year variation in the parameters using mixed-effects models, then you can sample from the fitted distributions and build a unique kernel for each year that you simulate.

**Parameter selection process** 1) Simulate a parameter vector from fitted distributions $\rightarrow$ 2) Construct kernel $\rightarrow$ 3) Project the population forward one time step, then repeat from 1).

# Advantages and disadvantages

**Kernel selection:** - An IPM using kernel selection runs much faster than one using parameter selection, as all the kernels can be constructed before iterating the model. - Parameter estimation is easier for kernel selection as you don't have to worry about correlations between different demographic processes. These correlations are already "built in" to the year-specific parameter estimates.

**Parameter selection:** - this method is a little slower, since for every year simulated we need to both randomly select the kernel parameters, and then construct the kernel - it is unusual to have sufficiently long datasets to characterize some times of important environmental stochasticity, or we may wish to estimate the impacts of future climate conditions, and parameter selection is important in these cases - if we have functions that describe how parameters vary with environmental variation we can take advantage of long term climate datasets or climate projections

# Examples

Models in which demographic rates are functions of environmental covariates are an important example of parameter selection (e.g., Dalgleish et al. (2011) and Simmonds and Coulson (2015))

- Dalgleish et al. (2011) modeled effects of precipitation and temperature on all vital rates of three sage-brush steppe plants, including effects of climate in previous years
- Simmonds and Coulson (2015) linked vital rates of Soay sheep on St. Kilda to the NAO (North Atlantic Oscillation) index, based on previous studies of NAO effects.

# Analysis of stochastic IPMS

- much of the same analysis that we completed for stochastic matrix models can be completed for stochastic IPMS
- we can:

1. estimate the long run stochastic growth rate
2. determine how variance or covariance in various model components impacts the growth rate
3. calculate stochasticity sensitivity

# Long run stochastic growth rate, $\lambda_S$

There are four main things to know about $\lambda_S$: - it exists, - it can be computed by simulation - it can be approximated - and there is a perturbation theory

Overall, just about any analysis you could do for a density-independent deterministic IPM or matrix model can also be done for a density-independent stochastic IPM.

# $\lambda_S$ does exist

$\lambda_S$ is the long-term growth rate of total population size N(t), exactly as in stochastic matrix models:

$$\lim_{t\to\infty} \frac{1}{t} log(\frac{N(t+1)}{N(t)}) = log\lambda_S$$

which exists, if the following assumptions hold: 1. the parameter vectors $\theta(t)$ in equation must be stationary, ergodic random variables (e.g. finite-order autoregressive processes) 2. the kernel $K(z', z, \theta)$ is a positive, continuous function of its three arguments (piecewise functions are also okay) 3. the distributions of all model parameters are bounded. (e.g., we may need to truncate Gaussian distributions at 99.99% percentiles)

# We can compute $\lambda_S$

$\lambda_S$ is equal to the average annual growth rate,

$log(\lambda_S) = E[log(\frac{N(t+1)}{N(t)})]$ where N(t) is total population size at time t.

# Reproductive value approximation???

In most cases, it will be better to use the reproductive value to calculate this quantity as : $log(\lambda_S) = E[log(\frac{V(t+1)}{V(t)})]$

where V (t) = mean kernel $K(z', z) = E[K(z', z; \theta(t))]$ (or instead of v use v0, the dominant left eigenvector for the average-environment kernel $K(z', z; \theta)$). V (t) is an approximation to the total reproductive value in year t. The advantage of V is that values of r(t) = log(V (t + 1)/V (t)) are nearly uncorrelated. So if you have computed the r(t) values from a simulation of the model, you can compute a confidence interval on their mean as if they were an independent random samples

# We can approximate $\lambda_S$ using Tuljapurkar's small fluctuations approximation

- the small fluctuation approximation is not only useful on its own, it provides some insight into the impact of environmental stochasticity
- It can be approximated using the IPM version of Tuljapurkar's small fluctuations approximation, which is analogous to the approximation for matrix models:

$$log \lambda_S \approx log \lambda_1 - \frac{Var\langle v, K_t w\rangle}{2\lambda_1^2} + \sum_{j=1}^{\infty} c_j,$$

where the first term, $\lambda_1$, is the dominant eigenvalue of the mean kernel $\overline{K}$, in the second term, $K_t$ is equal to $K(z', z; \theta(t))$, $v$ and $w$ are the left and right eigenvectors of $\overline{K}$ scaled so that $\langle v, w\rangle = 1$, and $K_t w = \int_Z K_t(z', z) w(z) dz$.

# Covariance in life history components

- Some recent studies have shown, for stochastic matrix models, that both the between-year and within-year correlations among matrix entries can have a significant impact on model predictions—it is not enough to correctly specify the marginal distribution of each matrix entry
- the same issue occurs for stochastic IPM models

# Covariance in life history components

- the second term in our approximation $-\frac{Var\langle v, K_t w\rangle}{2\lambda_1^2}$ indicates that variance in the life history parameters is always going to decrease our growth rates
- we can write this term as:

$$-\frac{1}{2\lambda_1^2}\int\int\int\int \boldsymbol{s}(z_2', z_2)\boldsymbol{s}(z_1', z_1)Cov(K_t(z_2', z_2)K_t(z_1', z_1))dz_1 dz_2 dz_1' dz_2',$$

- so analogous to our work in stochastic matrix models, we can see that the impact of stochasticity in an IPM will be determined both by covariance in the model elements and the sensitivity, $\boldsymbol{s}$ of the mean kernel, to these variance elements, where we need to integrate over all Z

# Correlation in environmental fluctuations

- the third term of our approximation $c_j$ is the effect of environmental correlations at time-lag j (i.e., between $\theta(t)$ and $\theta(t-j)$)
- the formula for this term is

$$c_j = E\langle v, M_j D^{l-1} M_0 w\rangle$$

where $M_t = (K_t - \overline{K})/\lambda_1$ and $D^m = (\overline{K}/\lambda_1)^m - P_0$ where $P_0(z', z) = v(z')w(z)$ for $v, w$ scaled so that $\langle v, w\rangle = 1$

(see Rees and Ellner (2009, Appendix C), which is a translation from Tuljapurkar (1990) and Tuljapurkar and Haridas (2006) into IPM notation.

# Material on stochastic sensitivity???

- to calculate time-varying sensitivity we can use:

$$\frac{\partial log \lambda_S}{\partial \epsilon} = \frac{1}{\lambda_S} \frac{\partial log \lambda_S}{\partial \epsilon} = E\left[\frac{\langle v_{t+1}, C_t w_t \rangle}{\langle v_{t+1}, K_t w_t \rangle}\right]$$

-which is an IPM version of the matrix formula from Tuljapurkar (1990)

- the formula describes a general perturbation of $K_t$ to $K_t + \epsilon C_t$ where $C_t = C(z', z; \theta_t)$ is a sequence of kernels such that the perturbed IPM satisfies the small perturbation requirements

# Material on stochastic sensitivity???

- to calculate sensitivity we first need to generate $v_t, w_t$ from $t = 0$ to large time as:

$$\tilde{w}_{t+1} = K_t w_t, w_{t+1} = \tilde{w}_{t+1} / \int_Z \tilde{w}_{t+1}(z)dz$$

$$\tilde{v}_{t-1} = v_t K_t = \int_Z v_{z'} K_{t-1}(z', z)dz',$$

$$v_{t-1} = \tilde{v}_{t-1} / \int_Z \tilde{v}_z(z)dz$$

# Material on stochastic sensitivity???

- for IPMs every possible perturbation to a deterministic model is now tripled:
  1. change in mean
  2. only the standard deviation,
  3. or do a fractional perturbation (e.g., a 5% higher value each year) that changes both the mean and the standard deviation (Tuljapurkar et al. 2003, 2004)
- therefore our stochasticity sensitivity equations can be used to generate a giant list of perturbation formulas for changes to kernel entries, demographic functions, and parameter values (see Table 7.2 in Ellne, Rees and Ellner (2009; Appendices E and F))

# Material on stochastic sensitivity???

- in addition, the equation for sensitivity isn't informative when the right-hand side is 0, which will be true whenever the fluctuations $C_t$ have zero mean and are independent of the unperturbed kernel.
- we need to carry the expansion out to second order in $\epsilon$ for these cases

# References


Dalgleish, H. J., Koons, D. N., Hooten, M. B., Moffet, C. A., & Adler, P. B. (2011). Climate influences the demography of three dominant sagebrush steppe plants. *Ecology*, *92*(1), 75-85.

Ellner, S. P., & Rees, M. (2007). Stochastic stable population growth in integral projection models: theory and application. *Journal of mathematical biology*, *54*(2), 227-256. https://link.springer.com/content/pdf/10.1007/s00285-006-0044-8.pdf

Heather, F. J., Childs, D. Z., Darnaude, A. M., & Blanchard, J. L. (2018). Using an integral projection model to assess the effect of temperature on the growth of gilthead seabream Sparus aurata. PloS one, 13(5), e0196092.

Levin, S. C., Childs, D. Z., Compagnoni, A., Evers, S., Knight, T. M., & Salguero-Gómez, R. (2021). ipmr: Flexible implementation of Integral Projection Models in R. *Methods in Ecology and Evolution*, *12*(10), 1826-1834.