Linking complex demographic transitions with population behavior: An integral projection approach

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[Ellner & Rees 200?, "tentatively" accepted @Am Nat]
What do these have in common?

(hint: not earrings)
1. Can track marked individuals for life, measuring attributes: size, weight, disease state, etc. fates: growth, survival, fecundity

2. Fates strongly affected by multiple attributes, continuous and discrete
   - Size and age (many plants, Soay sheep)
   - Size, age, disease state (seafan corals)

3. You can't measure everything: latent variability seen in mixed-effects/hierarchical models.
   - *Onopordum*: survival variability unrelated to size or age
   - Kittiwake *Rissa tridactyla*: correlated latent variability in survival and fecundity (Cam et al. 2002).

Ignoring latent variability ➔ overestimate extinction risk (Fox & Kendall), underestimate forecast uncertainty (J. Clark), badly biased parameter estimates (J. Clark), mis-predict response to perturbations (T. Benton et al.)
Modeling complex demography: 
*Onopordum illyricum*

- Monocarpic perennial, reproduces by seed
- 6-year field study (n=1144) in southern France, sheep-grazed semiarid steppe.
- Census 4 yearly to monitor growth, survival, seed production of marked plants.
- Plant fates affected by multiple traits, continuous & discrete, measured & latent.
- How does flowering probability depend on age & size?
- How *should it* depend on age & size?

Previously (Rees, Mangel et al. 1999) via individual-based simulation of competition & natural selection. Now…
Seedling size distribution: Gaussian truncated at 0

$$x \sim N(x|\mu = 1.06, \sigma^2 = 3.4), \quad x > 0$$

Annual size changes: linear model with size-dependent variance

$$\bar{y} = 3.24 + 0.56x$$

$$\sigma_y^2 = 42.5\exp(-0.7\bar{y})$$
Survival probability: logistic regression on size $x$, age $a$

\[
\logit(\text{survival}) = q + 1.08x - 1.09a
\]

\[
\logit(p_{\text{flower}}) = -24.0 + 2.91x + 0.84a
\]

Seeds/flowering plant: allometric with size

\[
\log(\text{seeds}) = -11.8 + 2.3x
\]
Latent survival variability for *Onopordum* (age=3) median size, --- (5,95) percentiles

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LARGE variability unrelated to size or age: microsites?

(GLMM: intercept $q$ in logistic regression varies among individuals, $P<0.02$)
Typical population model: **matrix projection** based on "stage" transitions, $n_i(t) = \sum_j A_{ij} n_j(t)$,

\[ j = \text{size class, age class} \]

Statistical analysis of size-, age-, quality-dependent demography implies **integral projection model (IPM)**

- **Individual state** $x$, in "state space" $X$ consisting of discrete stages (points) and stages with continuous variation in 1 or more traits (intervals, rectangles etc.)
  
  Size and age: $[L_0,U_0], [L_1,U_1], \ldots, [L_M,U_M]$  
  
  With seedbank: add $\{s\}$ or $\{s_1,s_2,\ldots,s_m\}$

- **Population state**: distribution function $n(x,t)$,
  
  "# of state - $x$ individuals at time $t$".
Population dynamics = aggregate of individual behaviors

Fecundity (parent $x \rightarrow$ offspring $y$)  Survival & "growth" (state transition) $x \rightarrow y$

$$n(y,t+1) = \int \left[ F(y,x) + P(y,x) \right] n(x,t) dx$$

$$= \int K(y,x) n(x,t) dx$$

$K(y,x,n(t)), K(y,x,\theta(t))$: density-dependent, stochastic, etc.

Onopordum survival/growth kernel: to reach size $y$ must:

Survive  Not flower  Grow $x \rightarrow y$.

$$P_{a,k}(y,x) = s(x,a,q_k) \times (1 - p_f(x,a)) \times g(y|x)$$

$Logit(s) = q + 1.08x - 1.09a$

$Logit(p_f) = -24.0 + 2.91x + 0.84a$

$g(y|x) \sim Normal(\bar{y} = 3.24 + 0.56x, \sigma^2_y = 42.5 \exp(-0.7\bar{y}) )$
Why not use a matrix model?

Conventional matrix model:

• Suppose ages 0-4, 4 size classes, Q quality classes
• 4Q size-transition matrices of size 4 x 4
• Fecundities for ages 2 - 4 (many offspring types!)
  \[= 65Q+14 \text{ parameters (209 for Q=3).}\]

Integral Projection Model (IPM) fully specified by standard regression models: 17 parameters total.

• Linear OK here, nonlinear or nonparametric easy if needed.
• Model complexity by well-established stats methods
Everything you know is right: general theory for matrix models all carries over to IPM:

**Deterministic** (Easterling 1998, Ellner & Rees 200x):
- Stable growth rate $\lambda$, state distribution $w$
- Sensitivity/elasticity $s(y,x) = v(y)w(x)/\langle v,w \rangle$ etc.
- Local stability analysis for density-dependent models
- Evolutionary optimization criteria ($\lambda$, $R_0$)

**Stochastic** (Ellner & Rees *in prep*):
- long-run growth rate $\lambda$
- Asymptotic lognormal distribution
- Small-variance approx. for $\lambda$, sensitivities, etc.

**Numerical methods**: mostly=really big matrix model (not always: Ellner & Rees 200x)
Back to *Onopordum*... integral model works well.

<table>
<thead>
<tr>
<th></th>
<th>Model</th>
<th>Data</th>
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<tbody>
<tr>
<td>Mean age</td>
<td>2.1</td>
<td>1.9 - 2.4</td>
</tr>
<tr>
<td>Mean age@flower</td>
<td>4.1</td>
<td>3.6</td>
</tr>
<tr>
<td>Mean size</td>
<td>350</td>
<td>325</td>
</tr>
<tr>
<td>Mean size@flower</td>
<td>1722</td>
<td>1736</td>
</tr>
<tr>
<td>Density (plants/m²)</td>
<td>4.8</td>
<td>4.4</td>
</tr>
</tbody>
</table>
Total reproductive value vs age

Total elasticity versus age & survival intercept
Elasticity for different size transitions

Survival & growth (75%)

Fecundity (25%)
"Quality" (survival intercept) stays with individual through life \(\Rightarrow\) small changes can have large effects.

\[
\begin{align*}
\text{Mean Offspring Quality} & \quad \lambda \\
-3.0 & \quad -2.0 & \quad -1.0 & \quad 0.0 & \quad 0.8 & \quad 1.0 & \quad 1.2 \\
\text{Finite rate of increase, } \lambda & \quad \\
\text{Mean Offspring Quality} & \quad \text{Equilibrium density, plants } m^{-2}
\end{align*}
\]
Detailed testable evolutionary predictions, by
maximize $\lambda$ (density-independent)
maximize $R_0$ (density-dependent)
as function of parameters determining life history
[e.g., age & size coefficients in flowering probability]

• Easy to impose gradual responses (vs. abrupt thresholds in SDP).

• Temporal variability: optimize geometric mean fitness or invasion exponent (vs. SDP)

• Speed is power: optimization vs. individual-based simulations $\Rightarrow$ confidence limits by bootstrap, etc.
*Onopordum* flowering strategy is a response to temporal variability in growth rate:

- Matches stochastic model ESS
- Significantly different from deterministic model ESS ($P < 0.01$ based on 1000 bootstrap reps).
Carduus nutans, persistent seed bank (3-13+ yr).

Carlina vulgaris, no seed bank.

Joint evolution of germination & flowering (Rees et al. *in prep*)

a) ESS germination probability, $g$

b) ESS flowering intercept, $\beta_0$

95% CI  predicted ESS
Forecasting a size-structured population

Artificial data: 10 yrs $\times$ 125 individuals/year

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<tr>
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<th>True</th>
<th>Integral</th>
<th>Matrix</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E[\log \lambda(t)]$</td>
<td>-0.02</td>
<td>-0.03</td>
<td>-0.03</td>
</tr>
<tr>
<td>$SD[\log \lambda(t)]$</td>
<td>0.30</td>
<td>0.32</td>
<td>0.23</td>
</tr>
</tbody>
</table>
Conclusions

IPM is a *practical* alternative to matrix population models for forecasting, demographic and evolutionary analysis when traits affecting demography vary continuously.

IPM ↔ statistical analysis of continuous trait-fate relationships

- Often easier to parameterize, better use of sparse data
- Eliminates artifacts from lumping into "stages"
- Brings the theoretical toolkit for matrix & other structured population models to situations that have required individual-based simulations (multi-trait, complex life cycles)

IPM is **not** a complete replacement for matrix models

- Discrete happens, too.
- The simplest structured model for addressing *theoretical* questions will often be a matrix model.
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