AN INTRODUCTION TO INTEGRAL PROJECTION MODELS (IPMS)

Cory Merow
REVIEW
Advancing population ecology with integral projection models: a practical guide

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IPMs

**Process-based demography:**

- Accurate stage structure
- Decompose life history to desired level of detail
- Link vital rates to covariates
- Heterogeneity among individuals
What is an IPM?

The Lefkovich matrix for a long-lived perennial shrub:

<table>
<thead>
<tr>
<th>Time t+1</th>
<th>Recruit</th>
<th>Juvenile</th>
<th>Non-flowering adult</th>
<th>Flowering adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recruit</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.56</td>
</tr>
<tr>
<td>Juvenile</td>
<td>0.79</td>
<td>0.23</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Non-flowering adult</td>
<td>0</td>
<td>0.54</td>
<td>0.41</td>
<td>0.29</td>
</tr>
<tr>
<td>Flowering adult</td>
<td>0</td>
<td>0.02</td>
<td>0.36</td>
<td>0.7</td>
</tr>
</tbody>
</table>

Transition Probability

0.0 to 0.6
What is an IPM?

Transition Probability

<table>
<thead>
<tr>
<th>Size (t)</th>
<th>2</th>
<th>4</th>
<th>6</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size (t+1)</td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>0</td>
<td>0.79</td>
<td>0.23</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
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<td>0.41</td>
<td>0.29</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0.02</td>
<td>0.36</td>
<td>0.7</td>
<td></td>
</tr>
</tbody>
</table>

At time t, the transition probability from Recruit to Flowering adult is 0.56.

Transition:

\[
\begin{bmatrix}
50 \\
23 \\
14 \\
23
\end{bmatrix}
= 
\begin{bmatrix}
18 \\
13 \\
14 \\
48
\end{bmatrix}
\]
What is an IPM?

Transition Probability

Size (t)

Size (t+1)

2 4 6 8

0 0 0 0.56

0.79 0.23 0 0

0 0.54 0.41 0.29

0 0.02 0.36 0.7
What is an IPM?

More stages = more heterogeneity among individuals
What is an IPM?

Matrix models and IPMs arrive at matrices for different reasons.
Workflow

Life History → Data → Vital Rate Regressions → IPM Kernel → Analysis

Analysis

IPM Kernel

Vital Rate Regressions

Data

Life History

Size (t+1)

Size (t)
Workflow

- **Life History**
- **Data**
- **Vital Rate Regressions**
- **IPM Kernel**
- **Analysis**
Life history

growth

flowering probability

survival

fecundity

germination

germinant survival
Workflow

1. Life History
2. Data
3. Vital Rate Regressions
4. IPM Kernel
5. Analysis

Heatmap with Size (t) on the x-axis and Size (t+1) on the y-axis.
Data: Growth
Data: Survival

Survival curves for each plot

probability of survival

size
Data: Fecundity

Germination probability
Workflow

Life History → Data → Vital Rate Regressions → IPM Kernel → Analysis

**Analysis**

**IPM Kernel**

**Vital Rate Regressions**

**Life History**

**Data**

**Size (t)**

**Size (t+1)**

Heatmap with values:

- 0.00
- 0.02
- 0.04
- 0.06

Values:

- 0.01
- 0.03
- 0.02
- 0.05
- 0.04
- 0.15
- 0.06
- 0.08
- 0.00
- 0.02
- 0.04
- 0.06
Vital Rate Regression: Growth

\[ \text{mean} = b_0 + b_1 \text{size} + b_2 \text{size}^2 \]
Vital Rate Regression: Growth

\[
\text{mean} = b_0 + b_1 \text{size} + b_2 \text{size}^2
\]
\[
\text{variance} = b_3 + b_4 \text{size}
\]
Vital Rate Regression: Growth

\[ \text{mean} = b_0 + b_1 \text{size} + b_2 \text{size}^2 \]

\[ \text{variance} = b_3 + b_4 \text{size} \]
Vital Rate Regression: Growth

\[ g(x, y) = \frac{1}{\sqrt{2\pi}\sigma(x)^2} \exp\left(\frac{(y - \mu(x))^2}{2\sigma(x)^2}\right) \]
Workflow

1. Life History
2. Data
3. Vital Rate Regressions
4. IPM Kernel
5. Analysis

![Heatmap Image]
The model

- $t = \text{time}$
- $x = \text{size at } t$
- $y = \text{size at } t+1$
- $n_t(x) = \text{size distribution at } t$
- $n_{t+1}(y) = \text{size distribution at } t+1$
- $K(x,y) = \text{full kernel}$
- $P(x,y) = \text{growth/survival kernel}$
- $F(x,y) = \text{fecundity kernel}$

Number of individuals of each size
The model

- \( t = \text{time} \)
- \( x = \text{size at } t \)
- \( y = \text{size at } t+1 \)
- \( n_t(x) = \text{size distribution at } t \)
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The model

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- $n_{t+1}(y) = \text{size distribution at } t+1$

\[ n_{t+1} = An_t \]  
\[ n_{t+1}(y) = \int_{\text{all sizes}} K(y, x) n_t(x) \, dx \]  

- $K(x, y) = \text{full kernel}$
- $P(x, y) = \text{growth/survival kernel}$
- $F(x, y) = \text{fecundity kernel}$
The model

\[
\begin{align*}
\mathbf{n}_{t+1} &= \mathbf{A} \mathbf{n}_t \\
\mathbf{n}_{t+1}(y) &= \int_{all\ sizes} K(y,x) \ n_t(x) \, dx
\end{align*}
\]

\[
\begin{pmatrix}
50 \\
23 \\
14 \\
23
\end{pmatrix}
\begin{pmatrix}
18 \\
13 \\
14 \\
48
\end{pmatrix}
\]

- \( K(x,y) \) = full kernel
- \( P(x,y) \) = growth/survival kernel
- \( F(x,y) \) = fecundity kernel

(Matrix)

(IPM)
The model

- $t = \text{time}$
- $x = \text{size at } t$
- $y = \text{size at } t+1$
- $n_t(x) = \text{size distribution at } t$
- $n_{t+1}(y) = \text{size distribution at } t+1$

\[ n_{t+1} = A \cdot n_t \]  \hspace{1cm} \text{(Matrix)}

\[ n_{t+1}(y) = \int_{\text{all sizes}} K(y,x) \ n_t(x) \, dx \]  \hspace{1cm} \text{(IPM)}

\[ n_{t+1}(y) = \int_{\text{all sizes}} \left[ P(x,y) + F(x,y) \right] n_t(x) \, dx \]

- $K(x,y) = \text{full kernel}$
- $P(x,y) = \text{growth/survival kernel}$
- $F(x,y) = \text{fecundity kernel}$
The model

- \( t = \text{time} \)
- \( x = \text{size at } t \)
- \( y = \text{size at } t+1 \)
- \( n_t(x) = \text{size distribution at } t \)
- \( n_{t+1}(y) = \text{size distribution at } t+1 \)

\[
\begin{align*}
n_{t+1} &= A \cdot n_t \\
n_{t+1}(y) &= \int_{\text{all sizes}} K(y, x) \ n_t(x) \ dx \\
n_{t+1}(y) &= \int_{\text{all sizes}} \left[ P(x, y) + F(x, y) \right] n_t(x) \ dx \\
\text{size}(y)_{t+1} &= \int_{\text{all sizes}} \left[ \text{growth(size } x \rightarrow y) + \text{offspring(size } x \rightarrow y) \right] \text{size}(x), dx
\end{align*}
\]

- \( K(x,y) = \text{full kernel} \)
- \( P(x,y) = \text{growth/survival kernel} \)
- \( F(x,y) = \text{fecundity kernel} \)
We need functions for...

- Growth
- Survival
- Reproduction

We have the option of splitting these in to finer detail if the data are available and the life history requires it.
Life History

\[ n(y, t + 1) = \int_{\Omega} \left[ P(x, y) + F(x, y) \right] n(x, t) \, dx \]

Example 1: Long-lived perennial plant

\[ P(x,y) = \text{(survival probability at size x)} \times \text{(growth from x to y)} \]
\[ = s(x) \times g(x,y) \]
Life History

\[ n(y, t + 1) = \int_{\Omega} \left[ P(x, y) + F(x, y) \right] n(x, t) \, dx \]

Example 1: Long-lived perennial plant

\[ P(x, y) = (\text{survival probability at size } x) \times (\text{growth from } x \text{ to } y) \]
\[ = s(x) \times g(x, y) \]

\[ F(x, y) = (\text{mean # seeds of size } x \text{ parent}) \times \]
\[ (\text{establishment probability}) \]
\[ (\text{probability of size } y \text{ offspring from size } x \text{ parent}) \]
\[ = f_{\text{seeds}}(x) \times p_{\text{estab}} \times f_{\text{recruit}}(y) \]
Life History

$$n(y, t + 1) = \int_{\Omega} \left[ P(x, y) + F(x, y) \right] n(x, t) \, dx$$

Example 1: Long-lived perennial plant

$$P(x, y) = \text{(survival probability at size } x) \ast \text{(growth from } x \text{ to } y)$$
$$= s(x) \ast g(x, y)$$

$$F(x, y) = \text{(mean } \# \text{ seeds of size } x \text{ parent)} \ast$$
$$\text{(establishment probability)}$$
$$\text{(probability of size } y \text{ offspring from size } x \text{ parent)}$$
$$= f_{\text{seeds}}(x) \ast p_{\text{estab}} \ast f_{\text{recruit}}(y)$$
Life History

\[ n(y, t + 1) = \int_{\Omega} \left[ P(x, y) + F(x, y) \right] n(x, t) \, dx \]

Example 1: Long-lived perennial plant

\( P(x, y) = (\text{survival probability at size } x) \times (\text{growth from } x \text{ to } y) \)

\[ = s(x) \times g(x, y) \]

\( F(x, y) = (\text{mean # seeds of size } x \text{ parent}) \times \text{(establishment probability)} \times \text{(probability of size } y \text{ offspring from size } x \text{ parent}) \)

\[ = f_{\text{seeds}}(x) \times p_{\text{estab}} \times f_{\text{recruit}}(y) \]
Workflow

1. Life History
2. Data
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[Heatmap image showing size (t+1) to size (t)]
Vital Rate Regression: Growth – $g(x, y)$

Jongejans et al. 2011

Metcalf et al. 2008

Ferrer-Cervantes et al. 2012

Hegland et al. 2010

Merow et al. 2014

Ozgul et al. 2010
Vital Rate Regression: Survival – \( s(x) \)

- Dahlgren et al. 2011
- Salguero-Gomez et al. 2012
- Metcalf et al. 2009
- Jongejans et al. 2011
- Merow et al. 2014
- Metcalf et al. 2008
Vital Rate Regression: Flowering – $p_{\text{flower}}(x)$

Metcalf et al. 2008
Salguero-Gomez et al. 2012
Hegland et al. 2010

Jongejans et al. 2011
Dahlgren et al. 2011
Rose et al. 2005

Flowering Probability
Size
Vital Rate Regression: Fecundity – $f_{\text{seeds}}(x)$

- Easterling et al. 2000
- Metcalf et al. 2009
- Ferrer-Cervantes et al. 2012
- Jongejans et al. 2011
- Rose et al. 2005
- Dahlgren et al. 2011
Vital Rate Regression: Fecundity – $f_{\text{recruit}}(x,y)$

Usually...

$$f_{\text{recruit}}(y) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(\frac{(y - \mu)^2}{2\sigma^2}\right)$$
Vital Rate Regression: Fecundity – $f_{\text{recruit}}(x,y)$

Usually...

$$f_{\text{recruit}}(y) = \frac{1}{\sqrt{2\pi}\sigma^2} \exp\left(\frac{(y - \mu)^2}{2\sigma^2}\right)$$

but sometimes...

$$\mu(x) = ax + b$$

$$f_{\text{recruit}}(x, y) = \frac{1}{\sqrt{2\pi}\sigma^2} \exp\left(\frac{(y - (ax + b))^2}{2\sigma^2}\right)$$

Easterling et al. 2000
Workflow

Life History → Data → Vital Rate Regressions → IPM Kernel → Analysis
Analysis

• Want the same things from IPMs as from matrix models
  • Eigenvalues
  • Eigenfunction (vectors)
• Can do all the same analyses with IPMs as matrix models
  • Elasticity/sensitivity
  • Forward projections
  • Stochastic dynamics
  • Life table response experiments
  • Passage time, Life expectancy
  • Etc…
Full kernel function

\[
size(y)_{t+1} = \int_{all\ sizes} \left[ \text{growth}(\text{size } x \rightarrow y) + \text{offspring}(\text{size } x \rightarrow y) \right] \size(x)_t \, dx
\]

\[
n_{t+1}(y) = \int_{\Omega} \left[ \frac{\logit(a_s x + b_s)}{1} \frac{1}{\sqrt{2\pi(a_g x + b_g)^2}} \exp \left( \frac{(x - (a_{g\mu} x + b_{g\mu}))}{2(a_{g\sigma x} + b_{g\sigma})^2} \right) + \frac{\exp(a_f x + b_f)}{1} \frac{1}{\sqrt{2\pi\sigma^2}} \exp \left( \frac{(x - (a_f x + b_f))^2}{2\sigma^2} \right) \right] n_t(x) \, dx
\]
Numerical integration

Midpoint rule

IPMs discretize for numerical integration
Numerical integration

Evaluate kernel at midpoint of each cell to obtain a large matrix.
Numerical integration

Evaluate kernel at midpoint of each cell to obtain a large matrix

\[ n_{t+1}(y) = \int_{\Omega} K(y, x) \ n_t(x) \ dx \]

\[ n_t = K \ n_{t+1} \]
Full kernel function

- ~Nicolé et al. 2011
- Easterling et al. 2000
- Dalgliesh et al. 2011
- Rees et al. 2002
- Godfray et al. 2002
- Merow et al. 2014

~Nicolé et al. 2011

Easterling et al. 2000

Dalgliesh et al. 2011

Rees et al. 2002

Godfray et al. 2002

Merow et al. 2014
Analysis

Stable size distribution

Reproductive values

Elasticity

Sensitivity
Summary - Why IPMs?

**Process-based demography**

- Continuous stages
- Heterogeneity among individuals
- Decompose life history to desired level of detail
- Built on regressions and matrices
Summary - Why IPMs?

**Process-based demography**

- Continuous stages
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Questions?