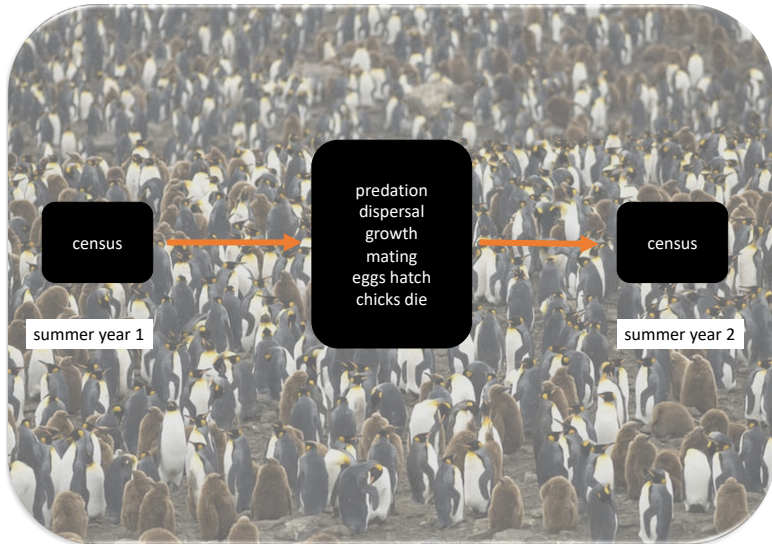


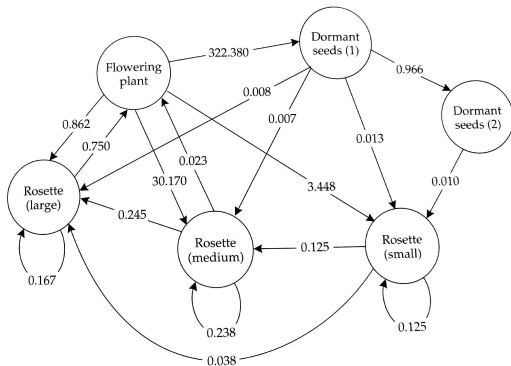
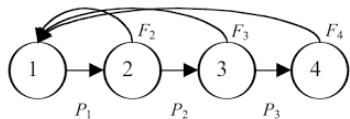
Comparing populations to investigate
how vital rates drive population dynamics:
Exact analysis of
Life Table Response Experiments (LTRE)
and an R package that does it for you

Chrissy Hernández, Steve Ellner, Robin Snyder,
Giles Hooker, and Peter Adler

Matrix models connect census data to population dynamics

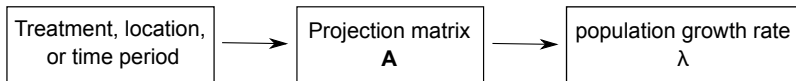


Matrix models include population structure.



From these models, we can estimate:

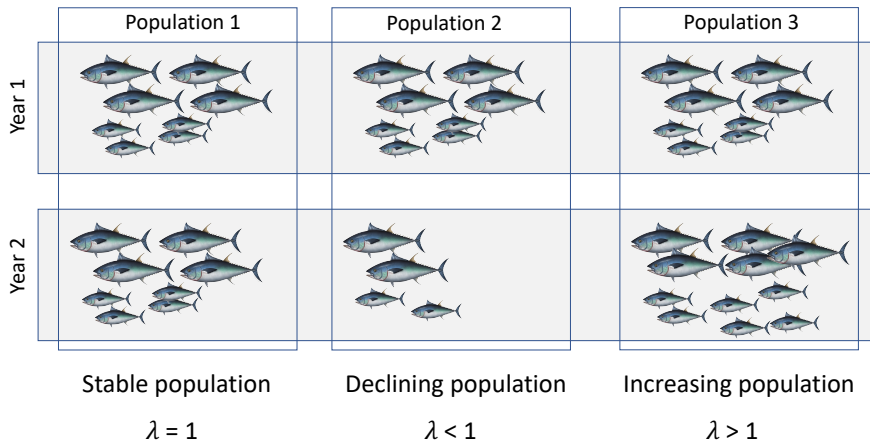
- population growth rate (λ)
- stable population structure
- expected lifetime reproductive output (R_0)
- expected lifespan
- generation time
- LOTS of other things
- sensitivity of any of these to changes in the vital rates



The conditions that a population experiences influences the elements of its density-independent projection matrix **A**. The entries of **A** determine the population growth rate.

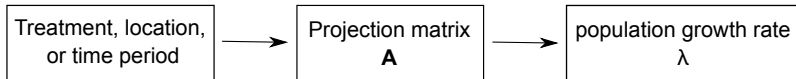
Most of what we'll talk about today is at the level of *matrix elements* but the analyses can also be carried out on underlying *vital rates*.

Population variation



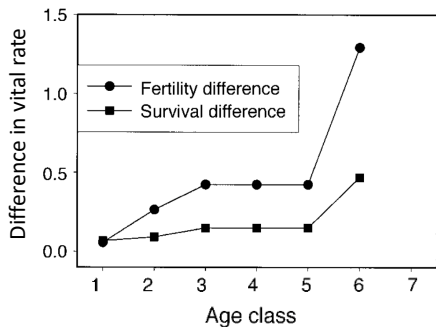
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Life Table Response Experiments

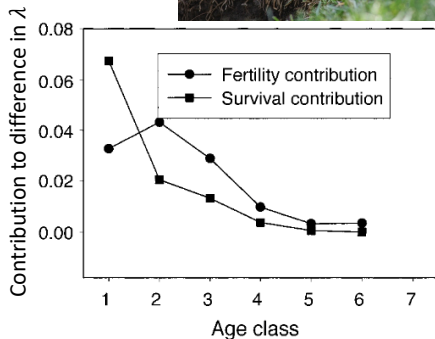


An LTRE decomposes the difference or variance in λ amongst multiple populations into the contributions from the matrix elements and their interactions.

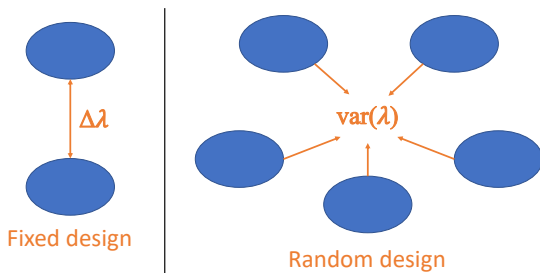
LTRE example



Adapted from Oli et al. 2001



We will focus on two types of LTRE:



- Fixed Design LTRE: **difference** in λ between two populations.
- Random Design LTRE: **variance** in λ across a set of populations.

Introduced into ecology by Hal Caswell in 1989 and 1996.

Approximate LTRE: Fixed design

$$\Delta\lambda = \lambda^{(m)} - \lambda^{(r)} \approx \sum_{i,j} \left(a_{ij}^{(m)} - a_{ij}^{(r)} \right) s_{ij}$$

where the a_{ij} are the entries of the projection matrices for treatment population m and reference population r , and

$$s_{ij} = \left. \frac{\partial \lambda}{\partial a_{ij}} \right|_{\bar{\mathbf{A}}}$$

is the sensitivity to a_{ij} evaluated at the mean matrix

$$\bar{\mathbf{A}} = (\mathbf{A}^{(m)} + \mathbf{A}^{(r)})/2.$$

Each term in the sum is the main effect of one matrix entry. *No interaction terms are computed.*

Approximate LTRE: Random design

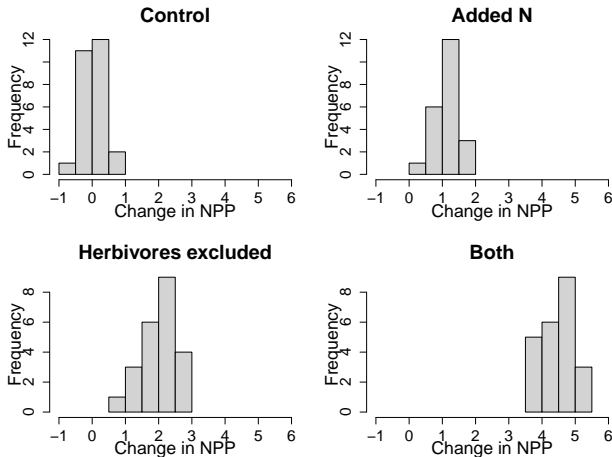
$$\text{Var}(\lambda) \approx \sum_{i,j} \sum_{k,l} C(ij, kl) s_{ij} s_{kl}$$

$C(ij, kl)$ is the covariance of a_{ij} and a_{kl} across all matrices in the set being analyzed (multiple years, multiple sites, etc.)

This approximation includes main effects (terms with $(i, j) = (k, l)$) and second-order interactions.

Background: a simple “experiment”

Δ NPP of individual plants after added N and/or Herbivore exclusion.



Goal: Δ NPP = main effect of N + main effect of H + interaction

Create data frame with DeltaNPP, N(0/1), H(0/1).

```
fit=lm(DeltaNPP ~ N + H + I(N*H), data=X);  
summary(fit);
```

	Estimate	Std.Error	t value	Pr(> t)
(Intercept)	-0.001259	0.080861	-0.016	0.988
N	1.131749	0.119439	9.476	3.52e-15 ***
H	1.985418	0.118024	16.822	< 2e-16 ***
I(N * H)	1.336704	0.170435	7.843	8.58e-12 ***

Multiple R-squared: 0.9437, Adj R-squared: 0.9419
F = 503.3 on 3 and 90 DF, p < 2.2e-16

Estimated coefficients quantify main effects and interaction.

Background: fANOVA

What can we do if the response of interest is a nonlinear function of many variables?

Given $f(x_1, x_2, \dots, x_d)$ that we can evaluate: how can we express f as a sum of main effects and interactions? That is,

$$\begin{aligned} f(x_1, x_2, \dots, x_d) = & \\ & f_0 \leftarrow \text{baseline or overall mean} \\ & + \sum_i f_i(x_i) \leftarrow \text{main effects} \\ & + \sum_{i \neq j} f_{i,j}(x_i, x_j) \leftarrow \text{2-way interactions} \\ & + \text{3-way, 4-way, } \dots, d\text{-way interactions} \end{aligned}$$

“Functional Analysis of Variance” (fANOVA) is an umbrella term for several different ways of doing that, useful for several different purposes.

Least unfamiliar (in ecology): model sensitivity analysis using *Sobol' indices*. Assumes input variables are drawn independently from probability distributions. R package **sensitivity**.

Here: “sensitivity” of response f to presence/absence of some “feature” (a mechanism or process).

- Each input variable $x_i = 1$ or 0 : presence or absence of some “feature” (such as N addition, H exclusion).
- $f(x_1, x_2, \dots, x_d)$ = response to a particular combination of features being present/absent.
- Effects and interactions measure deviations from baseline with all features absent (“Control”).
- Terms evaluated by including adding more and more features.

The two-factor case

$$f_0 = f(x_1 = 0, x_2 = 0) \leftarrow \textit{baseline}$$

$$f_1 = f(x_1 = 1, x_2 = 0) - f_0 \leftarrow \textit{feature 1 effect}$$

$$f_2 = f(x_1 = 0, x_2 = 1) - f_0 \leftarrow \textit{feature 2 effect}$$

$$f_{1,2} = f(x_1 = 1, x_2 = 1) - f_0 - (f_1 + f_2) \leftarrow \textit{interaction}$$

Interaction: effect of both being present, above and beyond the sum of their main effects.

And so on...

The same idea works for more factors and higher-order interactions:

$$\begin{aligned} f_{1,2,3} &= f(x_1 = 1, x_2 = 1, x_3 = 1) \\ &\quad - (f_0 + f_1 + f_2 + f_3) \\ &\quad - (f_{1,2} + f_{2,3} + f_{1,3}) \end{aligned}$$

Note: when the response is noise-free, all main effects and interactions of all orders are computed exactly.

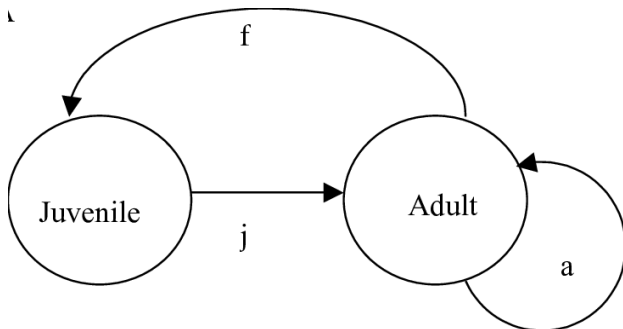
Why do we need exact LTRE?

- The approximate methods compute only main effects and (in Random design only) two-way interaction terms.
- The computed terms are approximations.

Meta-analysis of > 1500 LTREs using matrices from COMPADRE/COMADRE (Hernández et al., in review) shows that

- Usually those are not big problems, but sometimes they are.
- There's no easy way to know when the problem will be big or small.

A simple two-stage model



$$\begin{bmatrix} n_j(t+1) \\ n_a(t+1) \end{bmatrix} = \begin{bmatrix} 0 & f \\ j & a \end{bmatrix} \begin{bmatrix} n_j(t) \\ n_a(t) \end{bmatrix}$$

A simple two-stage model

Imagine we have a control population, and a population exposed to a pollutant.

$$\mathbf{A}^{(c)} = \begin{bmatrix} 0 & 3 \\ 0.6 & 0.9 \end{bmatrix}$$

$$\lambda = 1.87$$

$$\mathbf{A}^{(p)} = \begin{bmatrix} 0 & 1 \\ 0.35 & 0.5 \end{bmatrix}$$

$$\lambda = 0.89$$

$$\Delta\lambda = -0.98$$

How much of the difference $\Delta\lambda$ comes from

- Lower juvenile survival
- Lower adult fecundity
- Lower adult survival
- Interactions among those decreases?

To answer that question, we can do a Fixed Design LTRE.

We will do a “directional” analysis, using the Control population as the baseline in an fANOVA of λ .

Contribution of juvenile survival

We set all matrix elements to their **baseline** (control) values, and only **juvenile survival** varies from the baseline:

$$c^{(J)} = \Delta\lambda^{(J)} = \lambda \left(\begin{bmatrix} 0 & 3 \\ 0.35 & 0.9 \end{bmatrix} \right) - \lambda \left(\begin{bmatrix} 0 & 3 \\ 0.6 & 0.9 \end{bmatrix} \right) = -0.296.$$

The *contribution* to $\Delta\lambda$ of the effect of the pollutant on juvenile survival is -0.296— about 30% of $\Delta\lambda$.

Contribution of adult fertility

We set all matrix elements to their **baseline** (control) values, and only **adult fertility** varies from the baseline:

$$c^{(f)} = \Delta\lambda^{(f)} = \lambda \left(\begin{bmatrix} 0 & \textcolor{red}{1} \\ 0.6 & 0.9 \end{bmatrix} \right) - \lambda \left(\begin{bmatrix} 0 & 3 \\ 0.6 & 0.9 \end{bmatrix} \right) = -0.519.$$

The *contribution* to $\Delta\lambda$ of the effect of the pollutant on adult fertility is -0.519– about 50% of $\Delta\lambda$.

The interaction of juvenile survival and adult fertility

To evaluate the interaction between adult fertility and juvenile survival, we need to know the effect of changing both:

$$\Delta\lambda^{(s_J, f_a)} = \lambda \left(\begin{bmatrix} 0 & 1 \\ 0.35 & 0.9 \end{bmatrix} \right) - \lambda \left(\begin{bmatrix} 0 & 3 \\ 0.6 & 0.9 \end{bmatrix} \right) = -0.672.$$

But notice: $c^{(s_J, f_a)} \neq \Delta\lambda^{(s_J, f_a)}!!$

$$c^{s_J, f_a} = \Delta\lambda^{(s_J, f_a)} - (c^{(s_J)} + c^{(f_a)}) = 0.143.$$

The interaction of juvenile survival and adult fertility

$$c^{s_J, f_a} = \Delta\lambda^{(s_J, f_a)} - (c^{(s_J)} + c^{(f_a)}) = 0.143.$$

The contribution of this interaction is positive: it counteracts the negative effects of adult fertility and juvenile survival separately.

A decrease in adult fertility has a bigger effect with juvenile survival is high than when it is low.

When juvenile survival is low, the negative impact of low adult fertility is less severe.

Some advice for using exact LTRE methods

It is important to choose the LTRE analysis that best matches your question.

Do you want to understand the difference in λ between a Control and a Treatment population?



Use a Directional Fixed Design LTRE.

Do you want to understand the naturally occurring difference in λ between two populations?



Use a Symmetric Fixed Design LTRE.

Do you want to understand how variance in vital rates among populations (across time, space, or multiple unordered treatments) drives variance in λ ?



Then use a Random Design LTRE.

Choosing maximum interaction order to calculate

If m matrix entries differ among populations, there will be 2-way, 3-way, \dots , m -way interaction terms.

- That's a whole lot of terms. With 7 varying matrix entries, $\binom{7}{4} = 35$ 4-way interactions!
- For $m > 30$ the vector of terms would exceed the maximum object size in R ($m = 30$ is max in our package).
- Tell me again, what does a 4-way interaction mean?

We advise users to

- Calculate up to **three-way interaction terms**, and the sum of all higher-order contributions.
- Check that the high-order contribution sum is less than 5-10% of the observed $\Delta\lambda$ or $var(\lambda)$.

Let's pause for questions and general discussion about exact LTRE methods.

The R package exactLTRE

Install the package

If you don't already have the `devtools` package installed, install it first.

Then, to install `exactLTRE`:

```
devtools::install_github("chrissy3815/exactLTRE",  
force=TRUE)
```

If that doesn't work, try:

```
devtools::install_github("chrissy3815/exactLTRE",  
ref="main", force=TRUE)
```

The R package exactLTRE

We will now work through some tutorial code. You can find this code in a couple of places:

- I will share it here on Zoom.
- It gets installed with the package, look in the package library folder and find the directory called `ESA_workshop`
- You can download it directly from the Github:
<https://bit.ly/ESAexactLTRE>