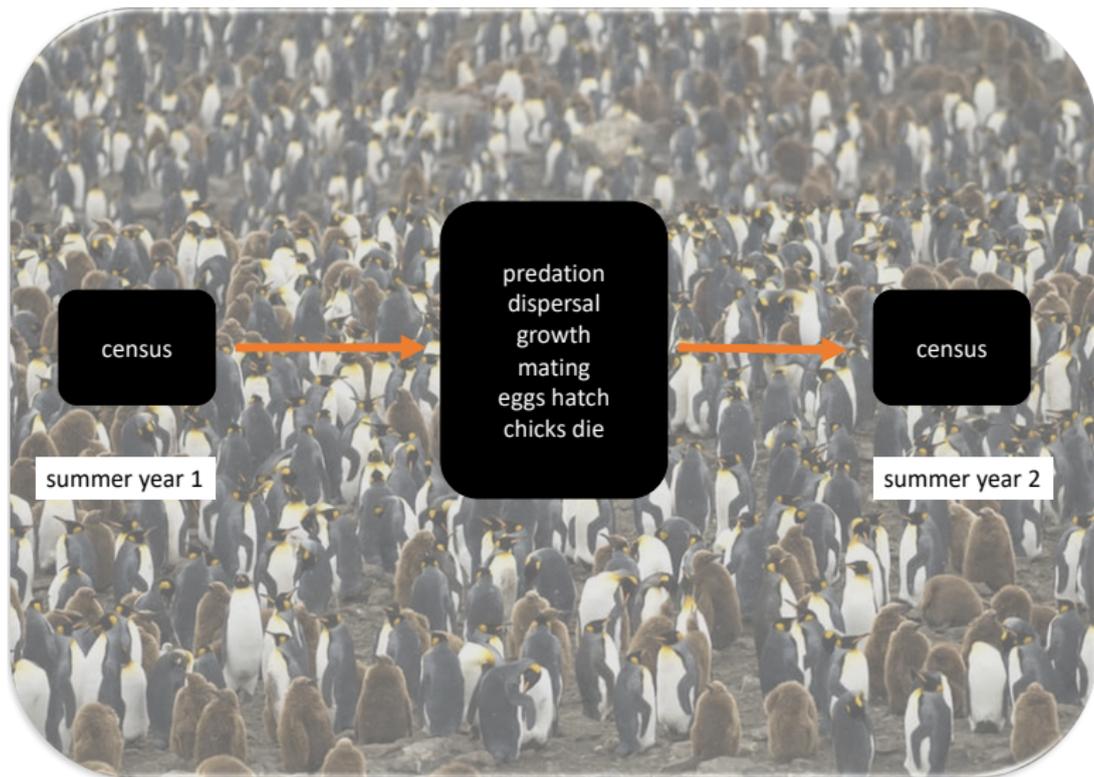


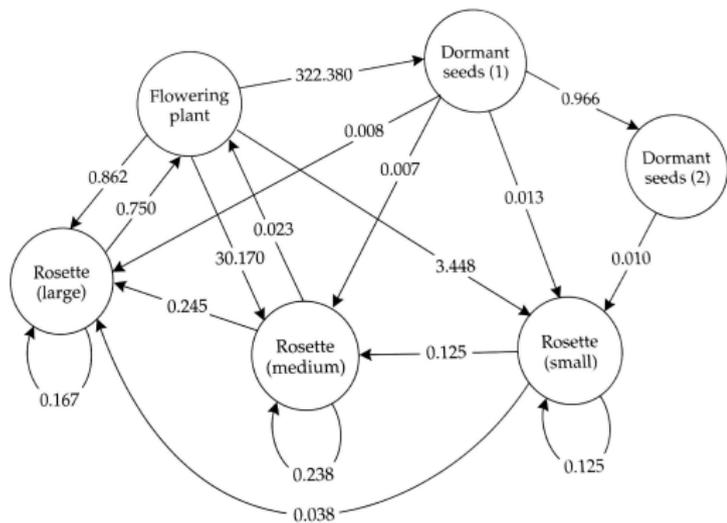
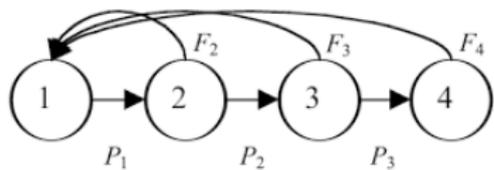
Comparing populations to investigate  
how vital rates drive population dynamics:  
Exact analysis of  
Life Table Response Experiments (LTRE)  
and an R package that does it for you

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

# Matrix models connect census data to population dynamics

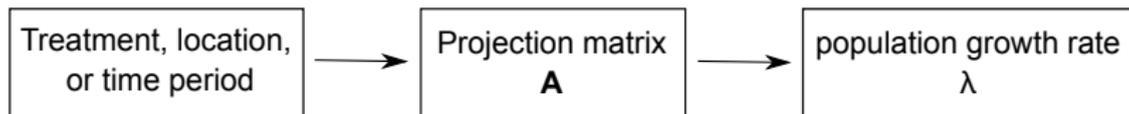


# Matrix models include population structure.



## From these models, we can estimate:

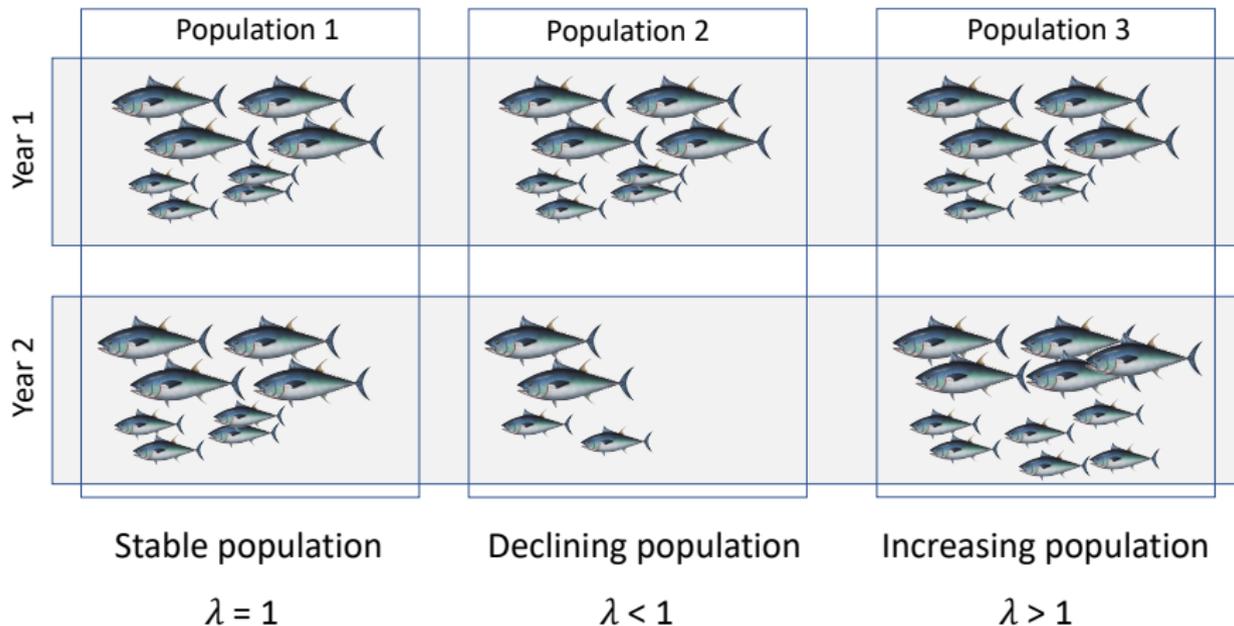
- population growth rate ( $\lambda$ )
- stable population structure
- expected lifetime reproductive output ( $R_0$ )
- expected lifespan
- generation time
- LOTS of other things
- sensitivity of any of these to changes in the vital rates



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.

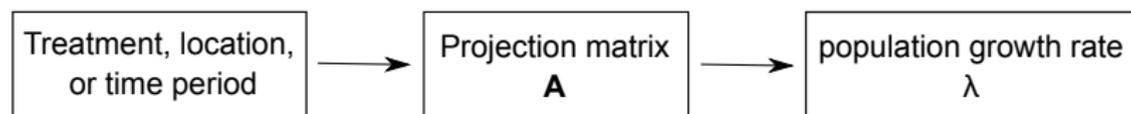
Most of what we'll talk about today is at the level of *matrix elements* but the analyses can also be carried out on underlying *vital rates*.

# Population variation



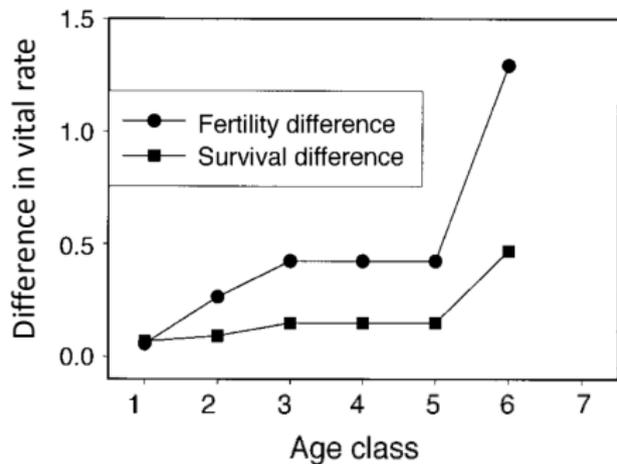
52

# Life Table Response Experiments

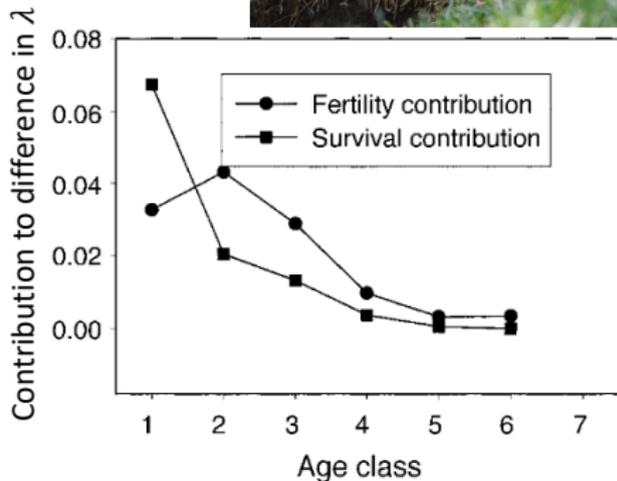


An LTRE decomposes the difference or variance in  $\lambda$  amongst multiple populations into the contributions from the matrix elements and their interactions.

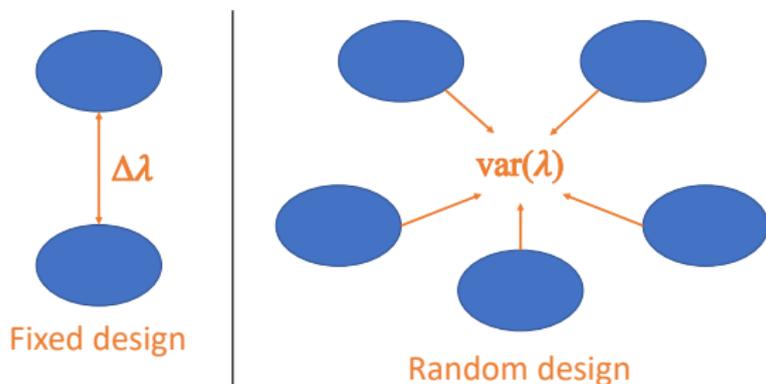
# LTRE example



Adapted from Oli et al. 2001



## We will focus on two types of LTRE:



- Fixed Design LTRE: **difference** in  $\lambda$  between two populations.
- Random Design LTRE: **variance** in  $\lambda$  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

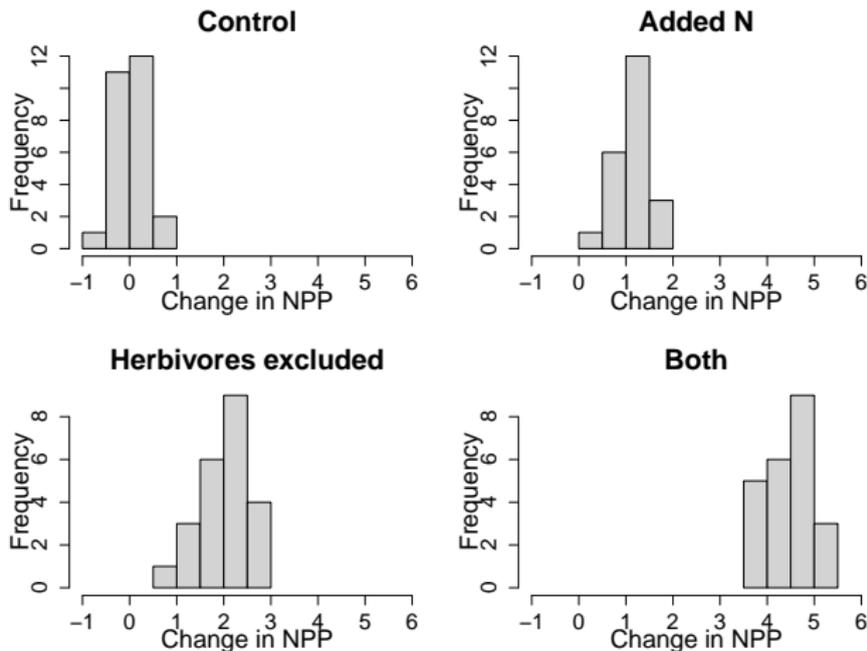
$$\text{Var}(\lambda) \approx \sum_{i,j} \sum_{k,l} C(ij, kl) s_{ij} s_{kl}$$

$C(ij, kl)$  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”

$\Delta$ NPP of individual plants after added N and/or Herbivore exclusion.



Goal:  $\Delta$ 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,

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

“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.

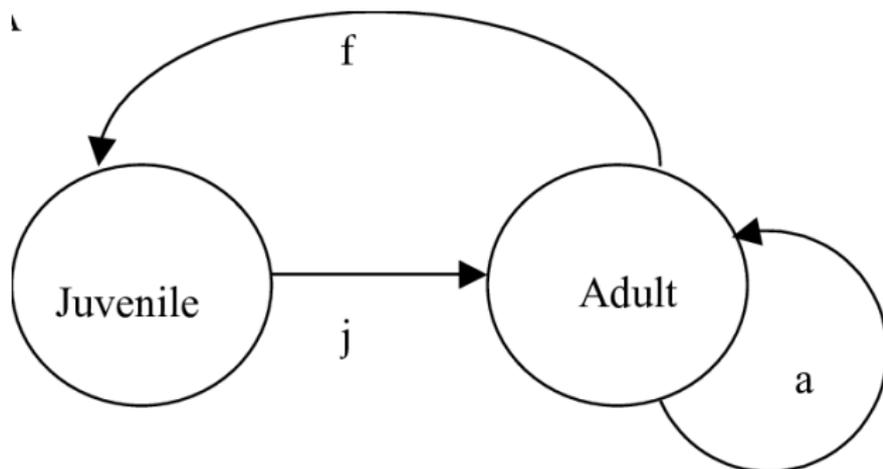
# Why do we need exact LTRE?

- 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  $\lambda$ .

# 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:

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

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  $\lambda$  between a Control and a Treatment population?



Use a Directional Fixed Design LTRE.

Do you want to understand the naturally occurring difference in  $\lambda$  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  $\lambda$ ?



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>