Course Title :
Population Dynamics [Environmental Sciences]
Environmental Management and Policy III

(Advanced course of)

The Theory in Bio-Demography

Kinya Nishimura & Takenori Takada

Basic population metrics II

Oct. 10 and 17

Chapter 6

Basic population metrics of *Trillium apetalon*

We use computer programming language (R, Mathematica, Matlab etc.) to obtain them because it's too difficult to obtain them using pen and paper.

Life history of a perennial

<u>*Trillium apetalon*</u>

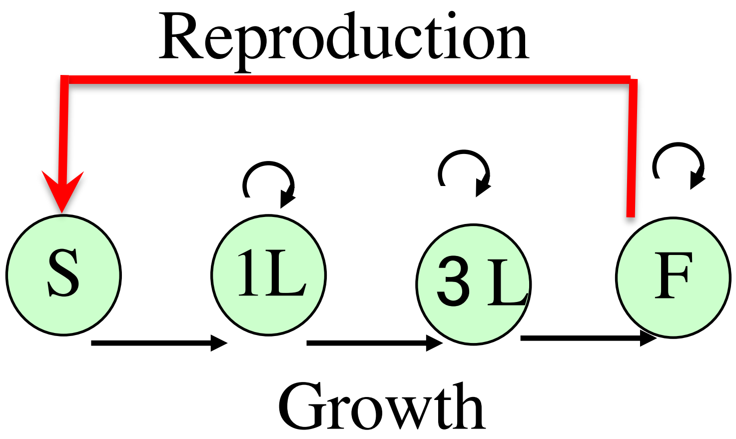
One of Trillium species

- Perennial herb in understory of cool temperate forest (liliaceous)
- Flowering a single flower on April to May
- At least 6 years until flowering
- Tracing the fate of each individual during 12 years

Seedling (S)   One-leaf (1L)   3-leaf (3L)   Flowerling (F)

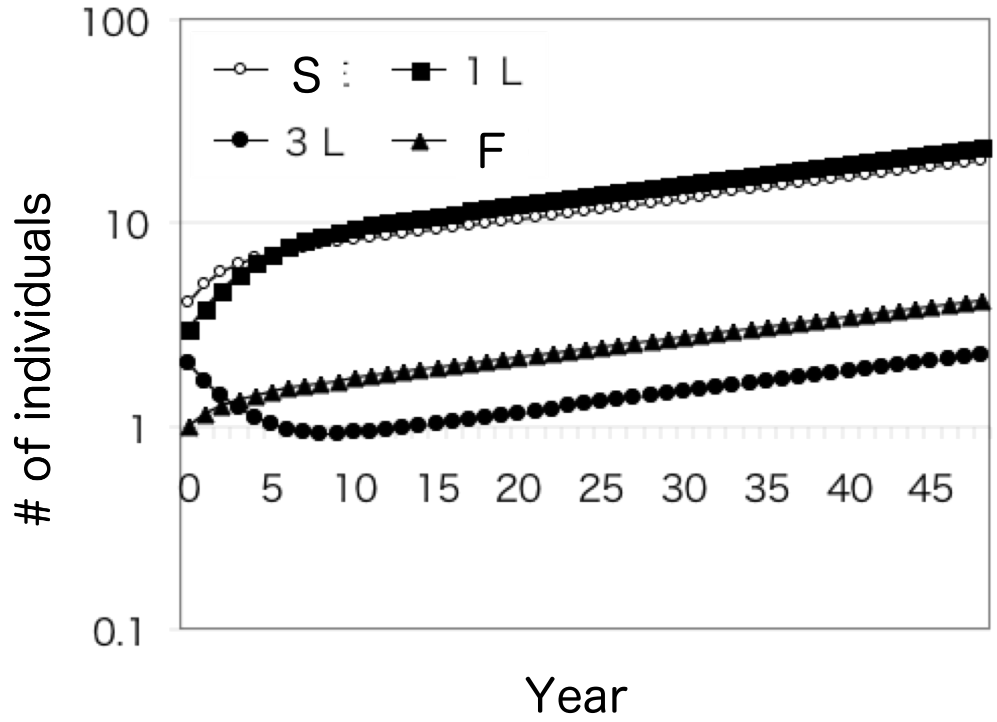
Stages

Flow chart and population matrix



$$\vec{x}_{t+1} = A\vec{x}_t$$

	S	1L	3L	F
S	0	0	0	5.13
1L	0.451	0.643	0	0
3L	0	0.021	0.8	0
F	0	0	0.08	0.981



Basic population metrics in *T. apetalon*

Population growth rate — 1.0252 (dominant eigenvalue; λ)

Stable stage distribution

Stages	Frequensies
Seedling	0.402
1L	0.474
3L	0.044
Flowering	0.08

Right eigenvector (**u**) (the sum of the elements = 1)

Reproductive value

Stages	Frequensies
Seedling	1
1L	2.27
3L	41.72
Flowering	117.44

Left eigenvector (**v**) (the first element = 1)

(See file "mathema2")

Mathematica program code

```
m={{0, 0,0, 5.12963}, {0.4508671, 0.6428571, 0,0},{0, 0.0208333, 0.8,0},{0,0,0.08,0.981

{{0, 0, 0, 5.12963}, {0.450867, 0.642857, 0, 0},
 {0, 0.0208333, 0.8, 0}, {0, 0, 0.08, 0.981482}}

N[m,4]//MatrixForm
```

$$\begin{pmatrix} 0 & 0 & 0 & 5.12963 \\ 0.450867 & 0.642857 & 0 & 0 \\ 0 & 0.0208333 & 0.8 & 0 \\ 0 & 0 & 0.08 & 0.981482 \end{pmatrix}$$

```
Eigenvalues[m]
```

Population growth rate

```
{1.02516 + 0. i, 0.7033 + 0.108865 i, 0.7033 - 0.108865 i, -0.00742379 + 0. i}

Eigenvectors[m]

{{0.639832 + 0. i, 0.754579 + 0. i, 0.0698181 + 0. i, 0.127871 + 0. i},
 {0.127925 + 0.230408 i, 0.954238 + 0. i, -0.0906679 - 0.102075 i,
  0.0126493 + 0.0343051 i}, {0.127925 - 0.230408 i, 0.954238 + 0. i,
  -0.0906679 + 0.102075 i, 0.0126493 - 0.0343051 i},
 {-0.821705 + 0. i, 0.569723 + 0. i, -0.0147001 + 0. i, 0.0011892 + 0. i}}
```

Right eigenvector

```
u=%[[1]]

{0.639832 + 0. i, 0.754579 + 0. i, 0.0698181 + 0. i, 0.127871 + 0. i}

totalu=Sum[u[[i]],{i,1,4}]

1.5921 + 0. i

frequency=u/totalu
```

Stable stage distribution

(To be continued)

```
{0.401879 + 0. i, 0.473952 + 0. i, 0.0438528 + 0. i, 0.080316 + 0. i}
```

Summary

Again

∗ Normalized left eigenvector (i. e. the first element = 1) is "Reproductive value" in matrix population model.

$$\mathbf{v} = \begin{pmatrix} 1 \\ v_2 \\ \vdots \end{pmatrix}$$

∗ Fisher's reproductive value proposed in 1930 is proportional to the left eigenvector.

∗ Goodman (1968) mathematically proved the above statement.

∗ Reproductive value in stage-structured population is obtained by this method.

∗ How to obtain the left eigenvalue numerically:

$$\mathbf{v}^T \mathbf{A} = \mathbf{v}^T \lambda \Longleftrightarrow \mathbf{A}^T \mathbf{v} = \lambda \mathbf{v}$$

Focus!!

Left eigenvector **v** is the right eigenvector of transposed matrix of **A**

Mathematica program code

Left eigenvector **v** is the right eigenvector of transposed matrix of **A**

```
lm=Transpose[m]
```

Transposing the matrix

```
{{0, 0.450867, 0, 0}, {0, 0.642857, 0.0208333, 0},
 {0, 0, 0.8, 0.08}, {5.12963, 0, 0, 0.981482}}
```

```
Eigenvectors[lm]
```

```
{{-0.00802229 + 0. i, -0.0182407 + 0. i, -0.334729 + 0. i, -0.942104 + 0.
 {-0.0473146 + 0.0185164 i, -0.0782761 + 0.017459 i,
  -0.318333 - 0.358382 i, 0.872475 + 0. i}, {-0.0473146 - 0.0185164 i,
  -0.0782761 - 0.017459 i, -0.318333 + 0.358382 i, 0.872475 + 0. i},
 {0.188407 + 0. i, -0.00310223 + 0. i, 0.0968315 + 0. i, -0.977301 + 0. i
```

```
v=%[[1]]
```

Left eigenvector

```
{-0.00802229 + 0. i, -0.0182407 + 0. i, -0.334729 + 0. i, -0.942104 + 0. i
```

```
% / -0.008022
```

Normalized reporoductive value

```
{1.00004 + 0. i, 2.27384 + 0. i, 41.7264 + 0. i, 117.44 + 0. i}
```

Remaining lifetime in *T. apetalon*

Stages		Remaining(Yr)
Seedling	S	2.0
1-leaf stage	1 L	3.3
3-leaf stage	3 L	25.1
Flowering	F	51.6

Comment on population dynamics of *Trillium apetalon*

- Population growth rate is 1.025 (good).
- 10% mature plants support the population growth rate.
- The death of mature plants is very rare (never die?)
- Remaining lifetime of mature plants is about 50 years.

↓

Non-stationary events such as natural disturbance or forest clear-cut affects the population dynamics. Otherwise, it is O.K.

Chapter 7

Basic population metrics II

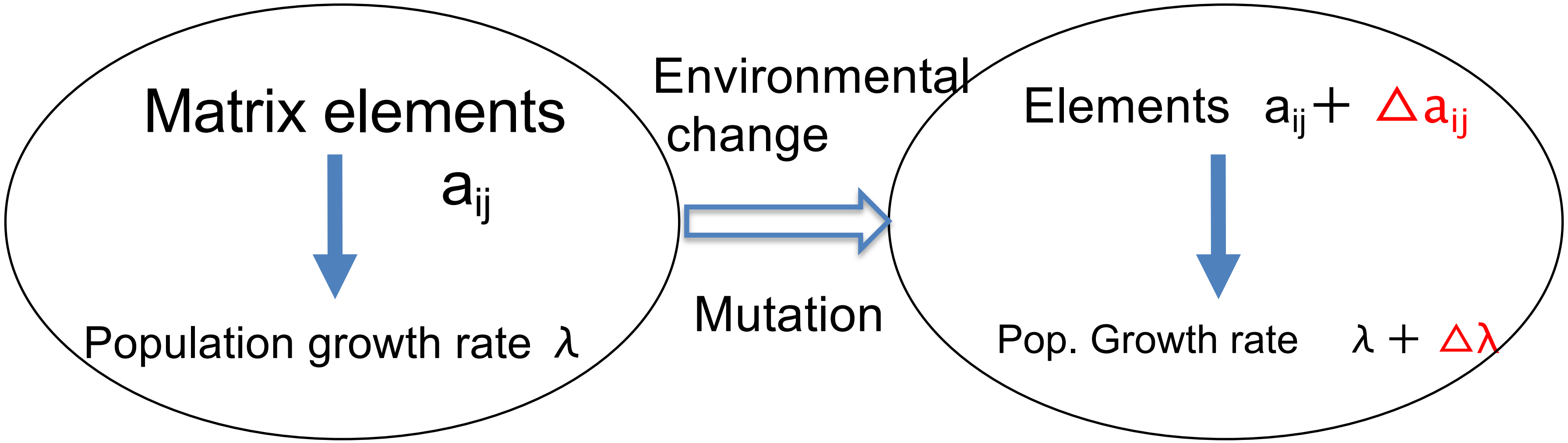
Again

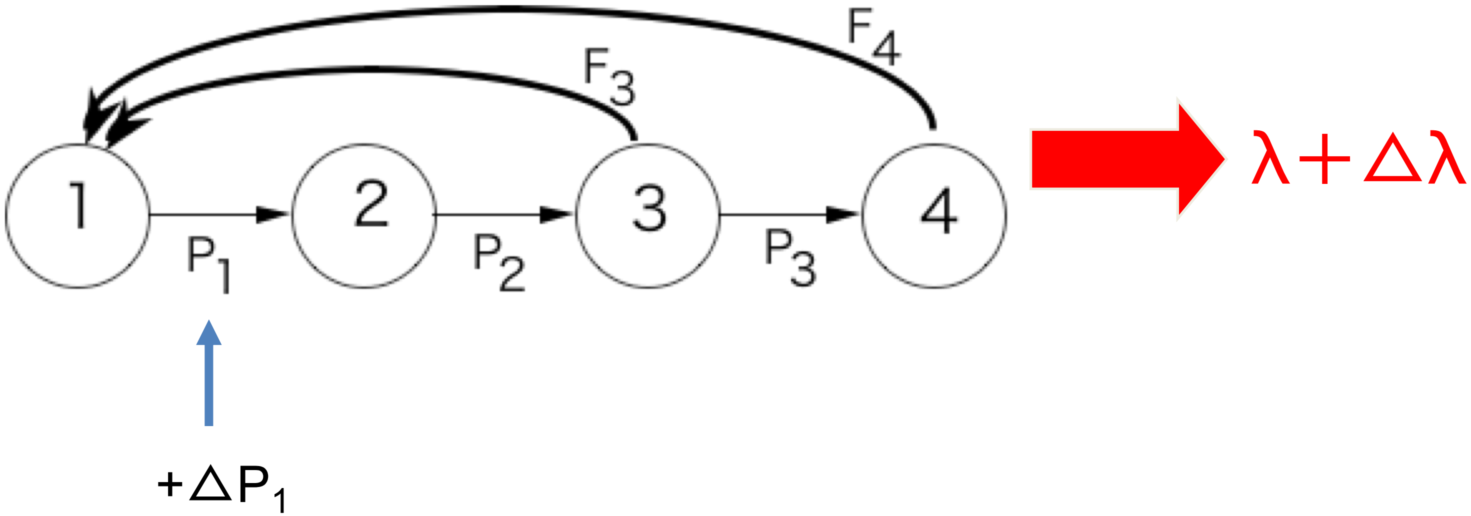
Population metrics from matrix models

1. Population growth rate (previously covered) λ
2. Stable stage distribution (previously covered) $\mathbf{u}$
3. Reproductive value
4. Life expectancy & remaining lifetime
5. Sensitivity of population growth rate accompanied with environmental change
6. Elasticity of population growth rate accompanied with environmental change
7. ・・・・

Perturbing a matrix

sensitivity analysis





Increment at each transition must be different. Which is the best?

Sensitivity matrix (Caswell, 1978)

* Formula

$$s_{ij} = \frac{v_i u_j}{\sum_k v_k u_k}$$

u_j: j-th element of the right eigenvector
v_i: i-th element of the left eigenvector

* The biological meaning of sensitivity: the change in population growth rate (PGR) responding to the change in matrix elements (life history parameters). $\lim_{\Delta a_{ij} \to 0} \frac{\Delta\lambda}{\Delta a_{ij}}$

* Each element of sensitivity matrix is defined by the first partial derivative $\lim_{\Delta a_{ij} \to 0} \frac{\Delta\lambda}{\Delta a_{ij}} = \frac{\partial\lambda}{\partial a_{ij}}$

* To examine the response to environmental change or to analyze life history evolution (tool of evolutionary analysis).

Derivation of sensitivity formula

Assumption : change is small $\Delta\mathbf{A}$

$$\begin{cases} \mathbf{Au}=\lambda\mathbf{u} & \text{right eigenvector} \\ \mathbf{v}^T\mathbf{A}=\lambda\mathbf{v}^T & \text{leftt eigenvector} \end{cases}$$

Matrix $\mathbf{A} \rightarrow \mathbf{A} + \Delta\,\mathbf{A}$

Eigenvalue and eigenvector, too.
$\lambda + \Delta\lambda, \mathbf{u} + \Delta\mathbf{u}$

Vector eq.

$$\begin{cases} (\lambda + \Delta\lambda)(\mathbf{u} + \Delta\mathbf{u}) = (\mathbf{A} + \Delta\mathbf{A})(\mathbf{u} + \Delta\mathbf{u}) \\ \lambda\mathbf{u} + \Delta\lambda\mathbf{u} + \lambda\Delta\mathbf{u} \approx \mathbf{Au} + \Delta\mathbf{Au} + \mathbf{A}\Delta\mathbf{u} \\ \Delta\lambda\mathbf{u} + \lambda\Delta\mathbf{u} \approx \Delta\mathbf{Au} + \mathbf{A}\Delta\mathbf{u} \end{cases}$$

Neglecting 2nd order term,
Using $\mathbf{Au}=\lambda\mathbf{u}$,

T $\mathbf{v}$

Multiplying $\mathbf{v}^T$ from left

$$\begin{cases} (\Delta\lambda)\mathbf{v}^T\mathbf{u} + \lambda\mathbf{v}^T(\Delta\mathbf{u}) = \mathbf{v}^T(\Delta\mathbf{A})\mathbf{u} + \mathbf{v}^T\mathbf{A}\,(\Delta\mathbf{u}) \\ (\Delta\lambda)\mathbf{v}^T\mathbf{u} = \mathbf{v}^T(\Delta\mathbf{A})\mathbf{u} \\ \Delta\lambda = \dfrac{\mathbf{v}^T(\Delta\mathbf{A})\mathbf{u}}{\mathbf{v}^T\mathbf{u}} \end{cases}$$

Using $\mathbf{v}^T\mathbf{A}=\lambda\mathbf{v}^T$

Scalar eq.

(to be continued)

(continued) $$\Delta\lambda = \frac{\mathbf{v}^T(\Delta\mathbf{A})\mathbf{u}}{\mathbf{v}^T\mathbf{u}}$$

If $$\Delta\mathbf{A} = \begin{array}{cc} \begin{pmatrix} 0 & 0 & \cdots & \cdots & 0 \\ 0 & 0 & \cdots & \cdots & 0 \\ 0 & \cdots & \Delta a_{ij} & \cdots & 0 \\ 0 & 0 & \cdots & \cdots & 0 \\ 0 & 0 & \cdots & \cdots & 0 \end{pmatrix} & \begin{matrix} \\ \\ i\ \text{行} \\ \\ \\ \end{matrix} \\ \begin{matrix} \qquad\qquad j\ \text{列} \end{matrix} & \end{array}$$

$$\Delta\lambda = \frac{v_i u_j}{\sum_k v_k u_k} \Delta a_{ij}$$

$$s_{ij} = \lim_{\Delta a_{ij} \to 0} \frac{\Delta\lambda}{\Delta a_{ij}} = \frac{v_i u_j}{\sum_k v_k u_k} = \frac{\partial\lambda}{\partial a_{ij}}$$

Biological meaning:
The change in population growth rate under the change in the elements of population matrix.

Sensitivity in *Trillium apetalon*

(See file ”mathma2”)

Population matrix

$$
\begin{array}{c c}
 & \begin{array}{cccc} \mathrm{S} & \mathrm{1L} & \mathrm{3L} & \mathrm{F} \end{array} \\
\begin{array}{c} \mathrm{S} \\ \mathrm{1L} \\ \mathrm{3L} \\ \mathrm{F} \end{array} &
\begin{pmatrix}
0 & 0 & 0 & 5.13 \\
0.451 & 0.643 & 0 & 0 \\
0 & 0.021 & 0.8 & 0 \\
0 & 0 & 0.08 & 0.981
\end{pmatrix}
\end{array}
$$

The sensitivity matrix

$$
\begin{array}{c c}
 & \begin{array}{cccc} \mathrm{S} & \mathrm{1L} & \mathrm{3L} & \mathrm{F} \end{array} \\
\begin{array}{c} \mathrm{S} \\ \mathrm{1L} \\ \mathrm{3L} \\ \mathrm{F} \end{array} &
\begin{pmatrix}
- & - & - & \color{red}{0.006} \\
0.072 & 0.085 & - & - \\
- & \color{red}{1.550} & 0.145 & - \\
- & - & 0.407 & \color{red}{0.738}
\end{pmatrix}
\end{array}
$$

Minimum

Maximum

2^{nd} maximum

Large sensitivity ---> Good change leads to the big benefit
Bad change leads to the big damage

Small sensitivity ---> Not effective, small benefit or damage

Population metrics from matrix models

1. Population growth rate (previously covered) λ
2. Stable stage distribution (previously covered) $\mathbf{u}$
3. Reproductive value
4. Life expectancy & remaining lifetime
5. Sensitivity of population growth rate accompanied with environmental change
6. Elasticity of population growth rate accompanied with environmental change
7. ・・・・

Elasticity matrix (Hans de Kroon, 1986) many citations!!

∗ Formula

Sensitivity

$$e_{ij} = \frac{a_{ij}}{\lambda} s_{ij} = \frac{a_{ij}}{\lambda} \frac{v_i u_j}{\sum_k v_k u_k}$$

u_j: j-th element of the right eigenvector
v_i: i-th element of the left eigenvector

∗ Meaning:

"proportional sensitivity".

Relative change of λ

$$e_{ij} = \lim_{\Delta a_{ij} \to 0} \frac{\frac{\Delta \lambda}{\lambda}}{\frac{\Delta a_{ij}}{a_{ij}}}$$

Relative change of a_{ij}

Sensitivity

$$= \frac{a_{ij}}{\lambda} \lim_{\Delta a_{ij} \to 0} \frac{\Delta \lambda}{\Delta a_{ij}} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = \frac{a_{ij}}{\lambda} s_{ij}$$

Elasticity matrix (Hans de Kroon, 1986) many citations!!

$$\mathbf{Au}=\lambda\mathbf{u}$$

$$\sum_j a_{ij}u_j = \lambda u_i$$

＊The sum of all the elasticities is equal to 1 (Elasticity was very popular from 1990 because the quantity means the proportion.)

$$\sum_i \sum_j e_{ij} = \sum_i \sum_j \frac{a_{ij}}{\lambda} s_{ij} = \sum_i \sum_j \frac{a_{ij}}{\lambda} \frac{v_i u_j}{\sum_i v_i u_i} = \frac{1}{\sum_i v_i u_i} \sum_i \sum_j \frac{a_{ij}}{\lambda} v_i u_j$$

$$= \frac{1}{\sum_i v_i u_i} \sum_i \frac{v_i}{\lambda} \sum_j a_{ij} u_j = \frac{1}{\sum_i v_i u_j} \sum_i \frac{v_i}{\lambda} \lambda u_i = 1$$

＊ Easy to understand which life history process contributes more proportionally.

Elasticity in *Trillium apetalon*

(See file "mathma2")

Population matrix

$$
\begin{array}{c|c}
 & \begin{array}{cccc} \mathrm{S} & \mathrm{1L} & \mathrm{3L} & \mathrm{F} \end{array} \\
\begin{array}{c} \mathrm{S} \\ \mathrm{1L} \\ \mathrm{3L} \\ \mathrm{F} \end{array} & \begin{pmatrix} 0 & 0 & 0 & 5.13 \\ 0.451 & 0.643 & 0 & 0 \\ 0 & 0.021 & 0.8 & 0 \\ 0 & 0 & 0.08 & 0.981 \end{pmatrix}
\end{array}
\Rightarrow
$$

The elasticity matrix

$$
\begin{array}{c|c}
 & \begin{array}{cccc} \mathrm{S} & \mathrm{1L} & \mathrm{3L} & \mathrm{F} \end{array} \\
\begin{array}{c} \mathrm{S} \\ \mathrm{1L} \\ \mathrm{3L} \\ \mathrm{F} \end{array} & \begin{pmatrix} 0 & 0 & 0 & 0.032 \\ 0.032 & 0.053 & 0 & 0 \\ 0 & 0.032 & 0.113 & 0 \\ 0 & 0 & 0.032 & 0.707 \end{pmatrix}
\end{array}
$$

Maximum

Survival of adult is important in the population dynamics of *Trillium apetalon*.

Summary

Again

- Population growth rate is 1.025 (good).
- 10% mature plants support the population growth rate.
- Transition from 1L to 3L (juveniles) and survival of mature plants are important

  （from sensitivity analysis）
- The death of mature plants is very rare.
- Remaining lifetime of mature plants is about 50 years.
- Generally, survival of mature plants is a key factor in long-lived species.

↓

Non-stationary events such as natural disturbance or forest clear-cut affects the population dynamics. Otherwise, it is safe.

Chronological table

Again

Nishimura Part

1826 Babbage — Life table

A Comparative View of the various Institutions for the Assurance of Lives.

1910 Sharpe & Lotka — Euler-Lotka equation

1912 Frobenius — Peron–Frobenius theorem

1930 Fisher — Basic theory, Defining “Reproductive value”

1941 Bernardelli — Age-structured “Leslie model”

1945 Leslie — Leslie matrix

1963, 1965 Lefkovitch — Stage-structured “Matrix population model”

1978 Caswell — Sensitivity analysis (New metrics)

1986 De Kroon et al. — Elasticity analysis (New metrics)

2015 Salguero-Gomez et al. — COMPADRE Plant Database

Significance of constructing models

- It allows quantitative analysis from field data.
- Established method (linear algebra) can be applied.
- To grasp which parameter is a key factor.
- To estimate the change of result when the assumption is changed.

（Using simulation model of environmental change or change in life history traits ）

My study on elasticity matrix

(Takada et al. 2018, Takada & Kawai 2000)

$$e_{ij} = \lim_{\Delta a_{ij} \to 0} \frac{\Delta\lambda}{\lambda} \Bigg/ \frac{\Delta a_{ij}}{a_{ij}} = \frac{a_{ij}}{\lambda} \frac{\partial\lambda}{\partial a_{ij}}$$

proportional change in population growth rate under proportional change in matrix elements

Used to evaluate which demographic process affects the population growth rate much.

The sum of all the elements of elasticity matrix is equal to 1.

What Silvertown group did for comparative study (1996)

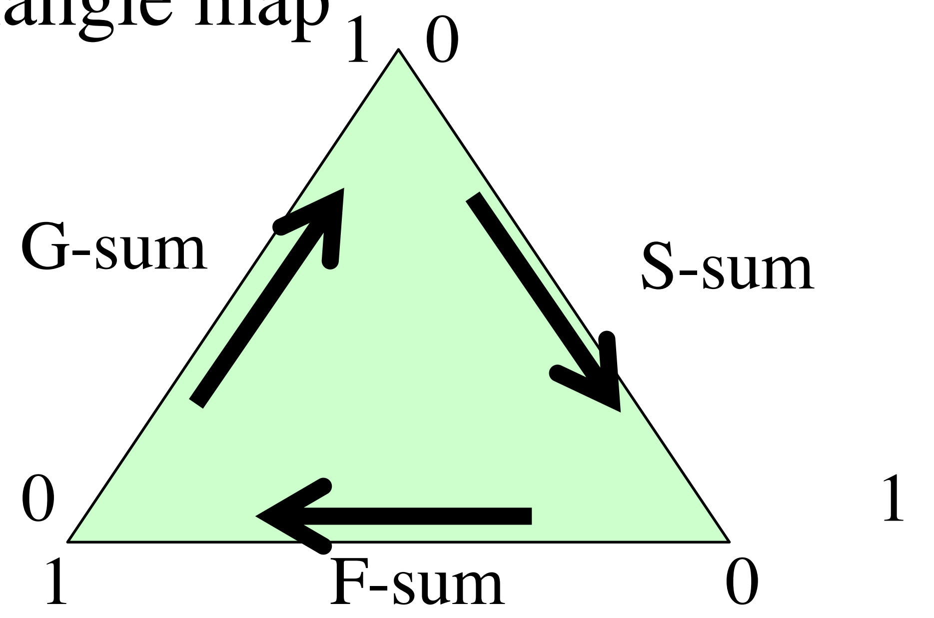
Dividing elas into
3 categories

$$\mathbf{E} = \{e_{ij}\} = \begin{pmatrix} S & F & F & F \\ G & S & S & S \\ G & G & S & S \\ G & G & G & S \end{pmatrix}$$

F: Fecundity
G: Growth
S: Stasis

Sum in F + sum in G + sum in S = 1

Triangle map

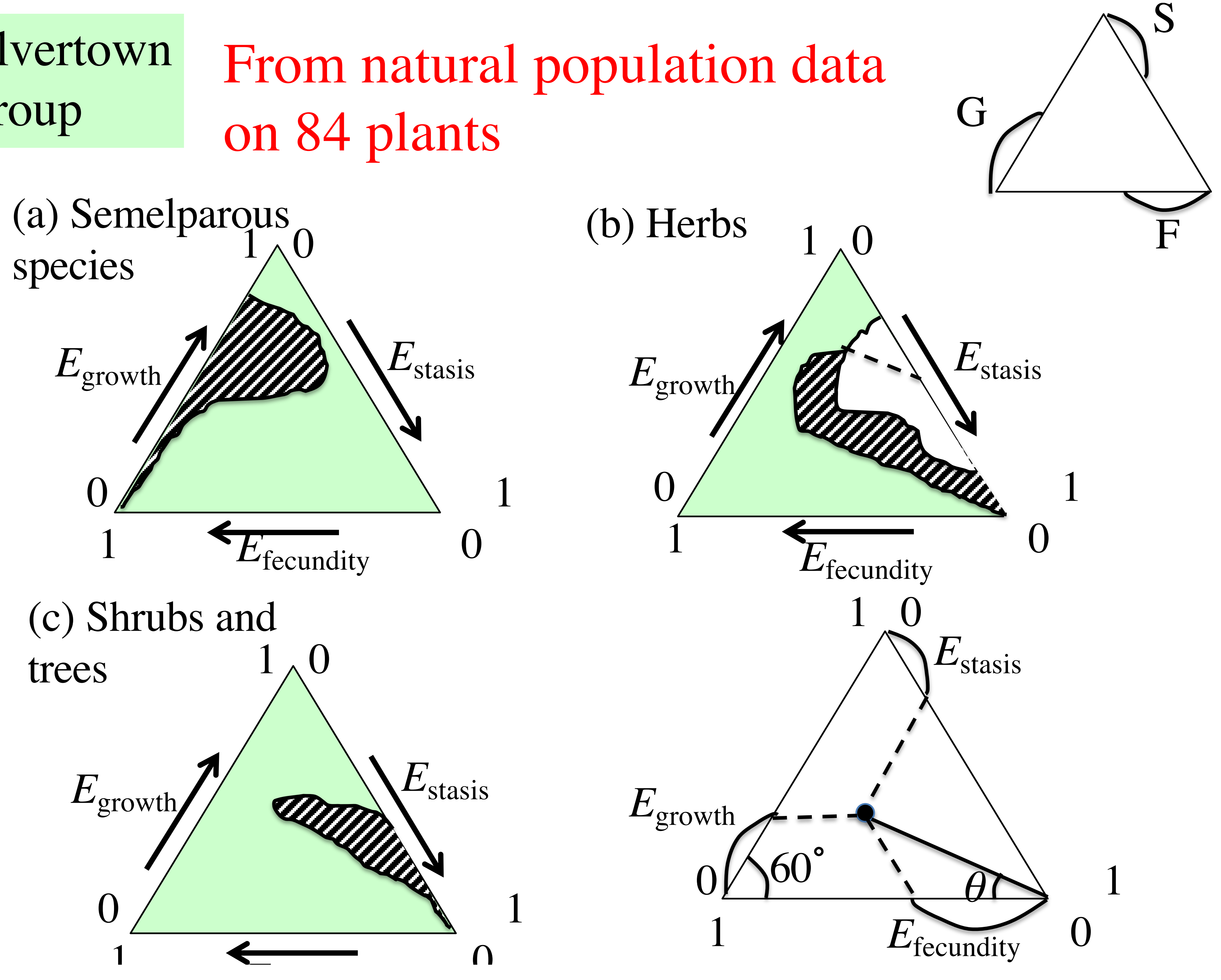


Elasticity vector
(F-sum, G-sum , S-sum)

Plot the elasticity vector on triangle map.

Silvertown group

From natural population data on 84 plants



Trillium apetalon (Iteroparous perennial)

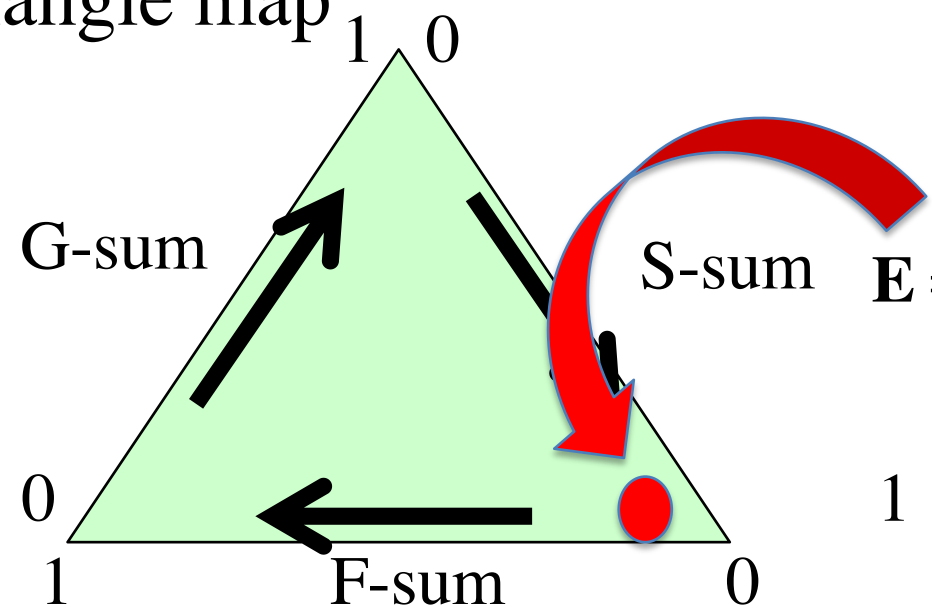
Dividing into 3 categories

$$\mathbf{E} = \{e_{ij}\} = \begin{pmatrix} S & F & F & F \\ G & S & G & G \\ G & G & S & G \\ G & G & G & S \end{pmatrix}$$

F: Fecundity
G: Growth
S: Stasis

Sum of F + sum of G + sum of S = 1

Triangle map



$$\mathbf{E} = \begin{pmatrix} 0 & 0 & 0 & 0.032 \\ 0.032 & 0.053 & 0 & 0 \\ 0 & 0.032 & 0.113 & 0 \\ 0 & 0 & 0.032 & 0.707 \end{pmatrix}$$

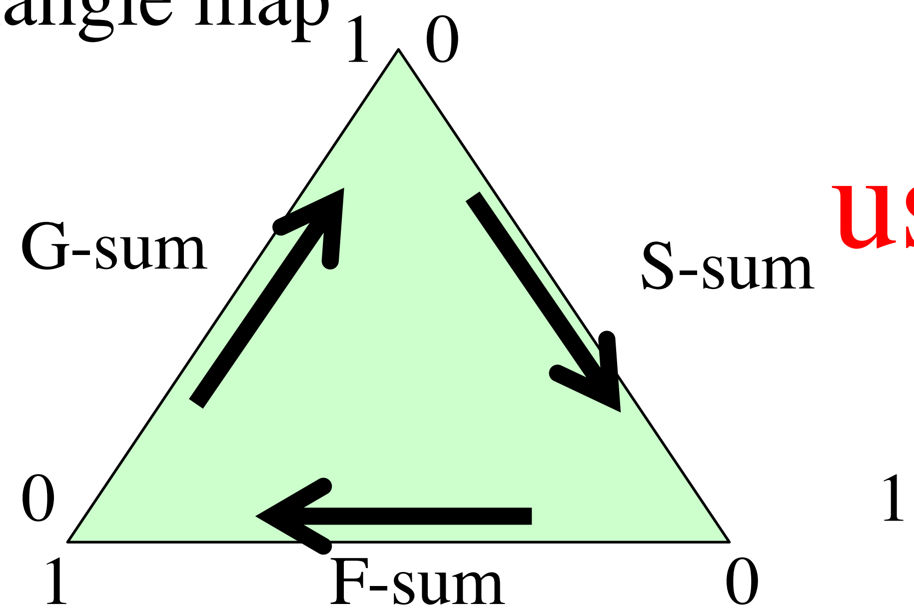
What I did

Divide into
3 categories

$$\mathbf{E} = \{e_{ij}\} = \begin{pmatrix} S & F & F & F \\ G & S & S & S \\ G & G & S & S \\ G & G & G & S \end{pmatrix}$$

F: Fecundity
S: Stasis
G: Growth

Triangle map



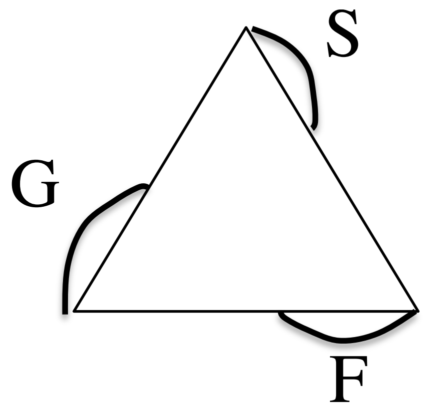
Except for
using 3000 random
matrices

My questions

1）What is the potential range of space occupied by elasticity vectors of random matrices (RPMs) in the triangle?

2）Is there any special elasticity distribution in matrices with high population growth rates (because of natural selection)?

Assumption 1 : Column-sum < 1



3000 random matrices $\begin{cases} f\text{: Poisson dist. with average p} \\ \text{tij: Random number} \end{cases}$

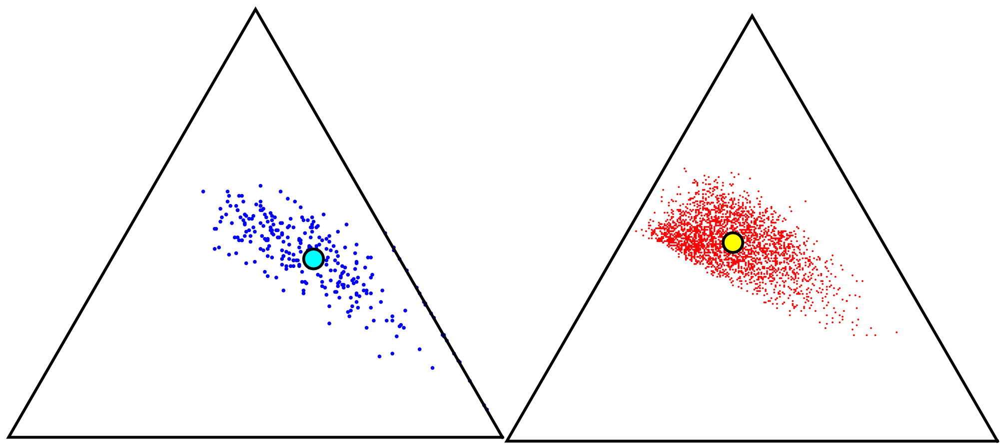
Assumption 1 $\boxed{0 < \sum_i t_{ij} < 1}$

Blue : $\lambda < 1$

Red : $\lambda > 1$

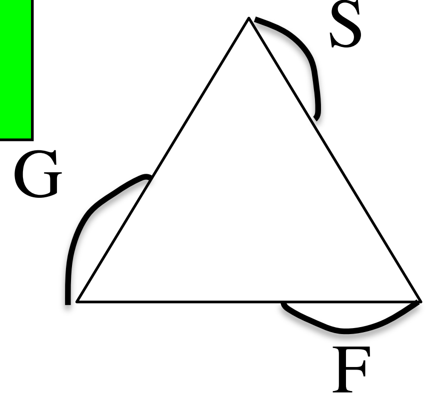
$$\mathbf{A} = \begin{pmatrix} t_{11} & t_{12} & t_{13} & f \\ t_{21} & t_{22} & t_{23} & t_{24} \\ t_{31} & t_{32} & t_{33} & t_{34} \\ t_{41} & t_{42} & t_{43} & t_{44} \end{pmatrix}$$

Survival prob.



The elasticity distribution is in the center.
The distributions with low and high PGR are not so different.

Assum. 2: Big one has greater survival

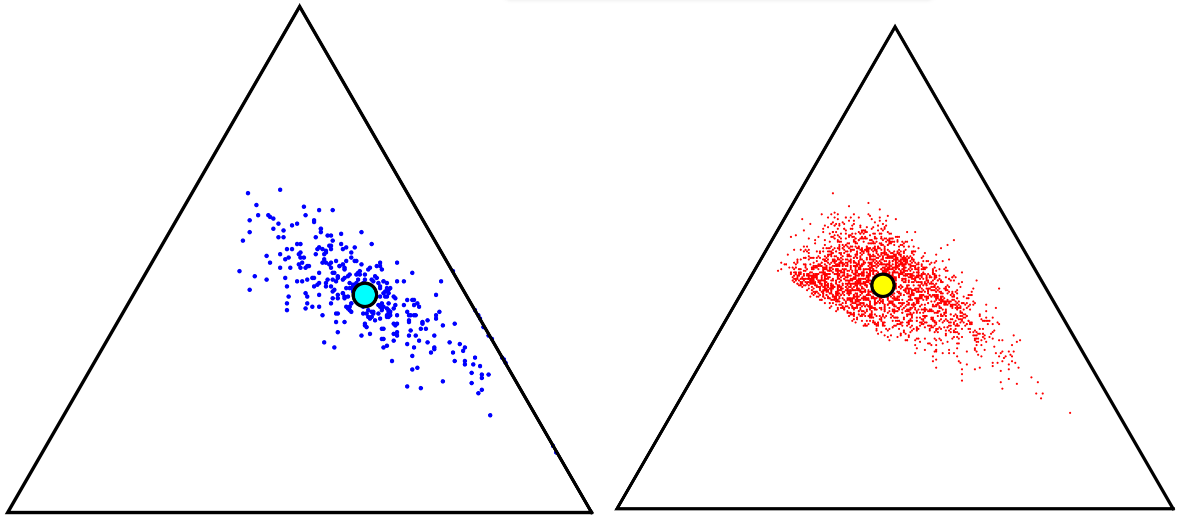


$$\mathbf{B} = \begin{pmatrix} t_{11} & t_{12} & t_{13} & f \\ t_{21} & t_{22} & t_{23} & t_{24} \\ t_{31} & t_{32} & t_{33} & t_{34} \\ t_{41} & t_{42} & t_{43} & t_{44} \end{pmatrix}$$

f: Poisson dist. with average p

tij: Random number

$$\boxed{\sum_i t_{ij} < \sum_i t_{i,j+1}}$$



Blue : $\lambda < 1$

Red : $\lambda > 1$

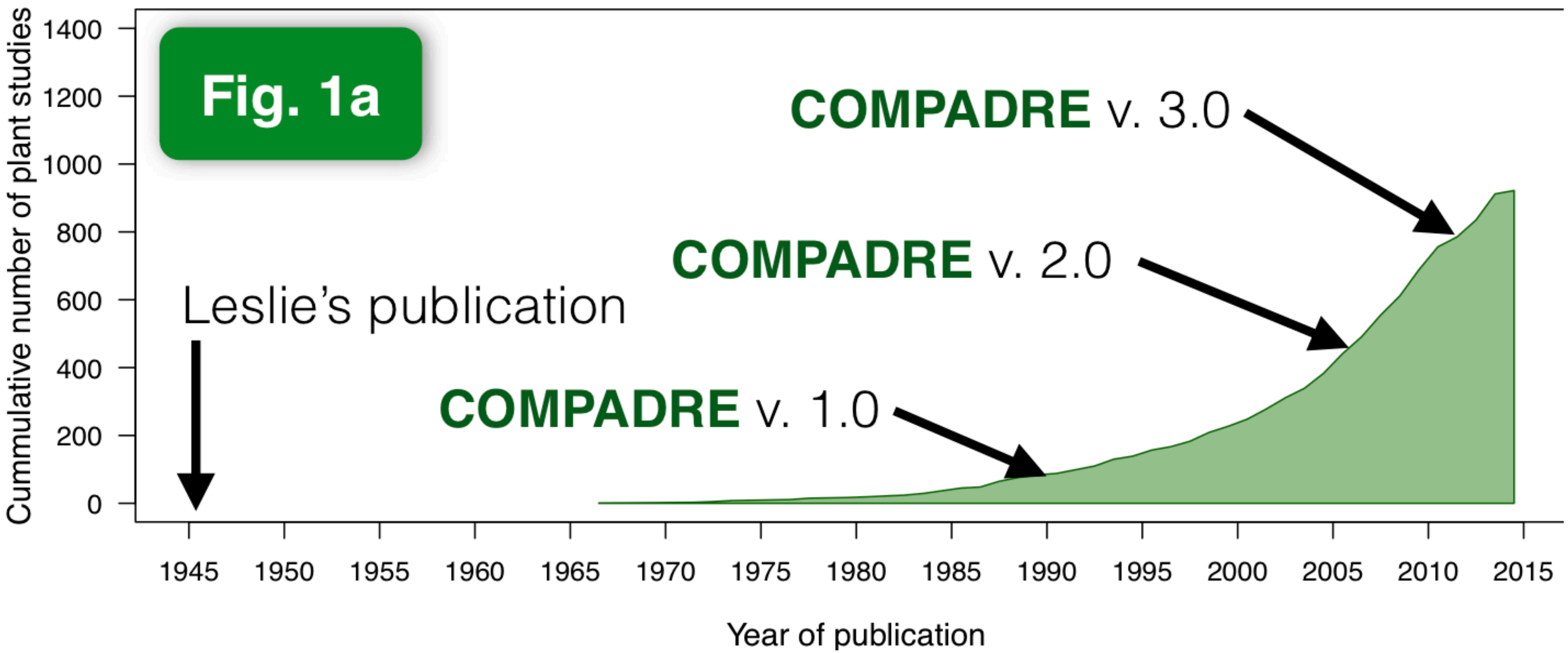
Assumptions 1 & 2 do not explain the distribution in natural plants

History of Matrix Population Model

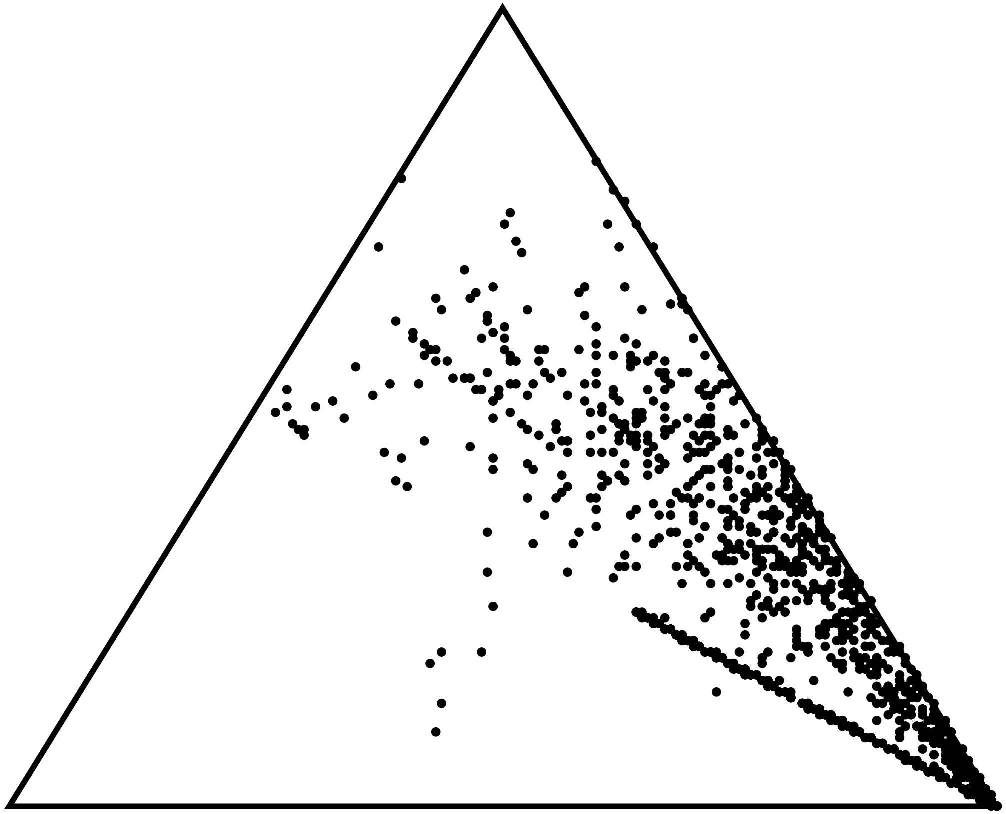
Bernardelli (1941), Lewis (1942), Leslie (1945)　Age-structured model
Lefkovitch (1965) and Keyfitz (1964)　　Stage-structured model
１９７０年代から様々な動植物に応用がなされ、理論的研究も進

データベースの歴史

Version 1: Silvertown & Franco (1989) 105種
Version 2: Salguero-Gomez & Hodgson(2008) 500種
Version 3: Max Plank Institute (2011–)



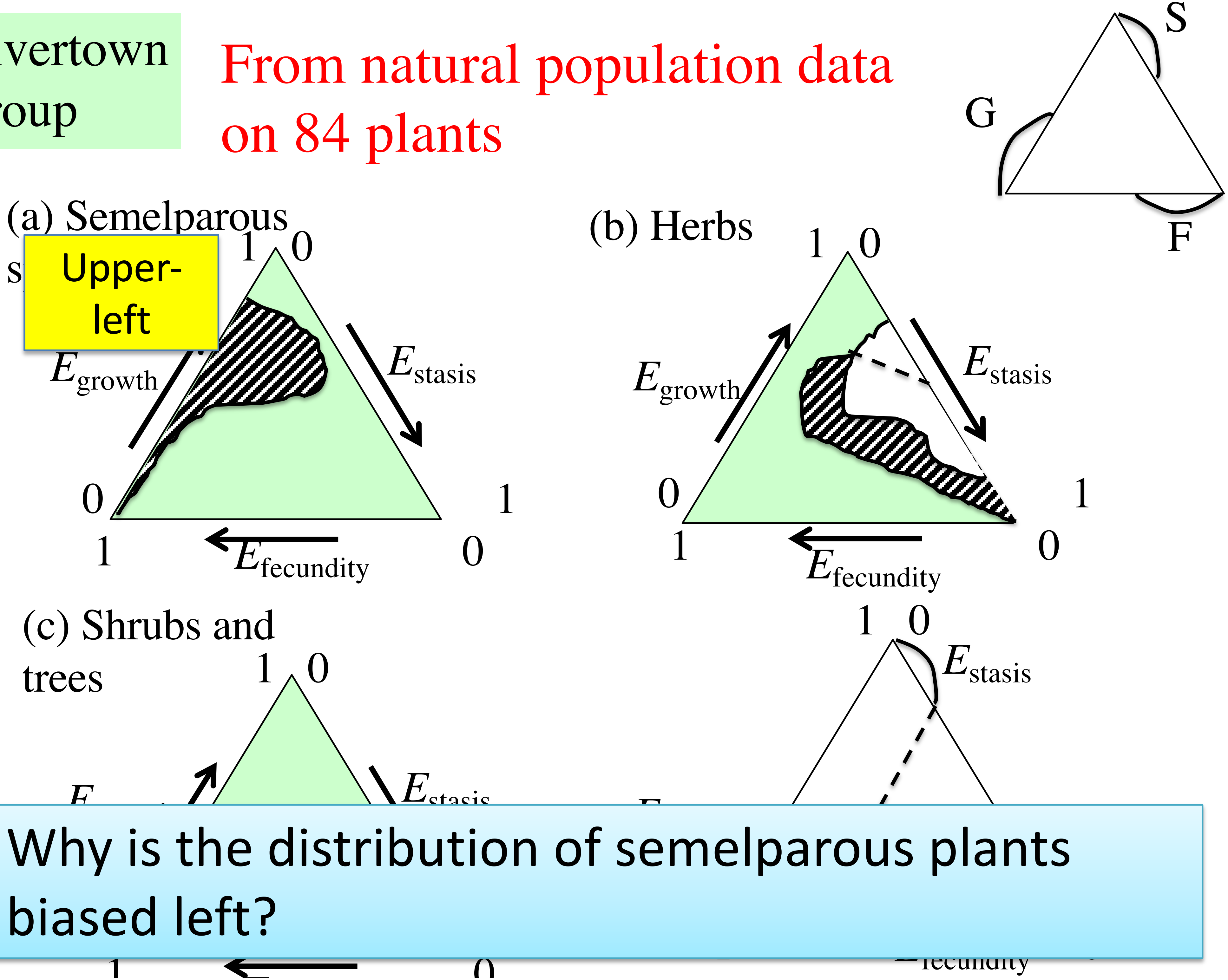
COMPADRE Plant Matrix Database (selected 1230 matrices)



Why is the distribution of real plants biased right than that of randomly-generated matrix?

Silvertown group

From natural population data on 84 plants



Why is the distribution of semelparous plants biased left?

Randomly-generated population matrices of semelparous species

$$\left\{ \begin{array}{l} f\text{: Poisson dist. with average p} \\ \text{tij: Random number } (0 < .. < 1) \end{array} \right.$$

Big-bang reproduction

$$\mathbf{A} = \begin{pmatrix} t_{11} & t_{12} & t_{13} & f \\ t_{21} & t_{22} & t_{23} & 0 \\ t_{31} & t_{32} & t_{33} & 0 \\ t_{41} & t_{42} & t_{43} & 0 \end{pmatrix}$$

Mature individuals die after reproduction
(Semelparity)

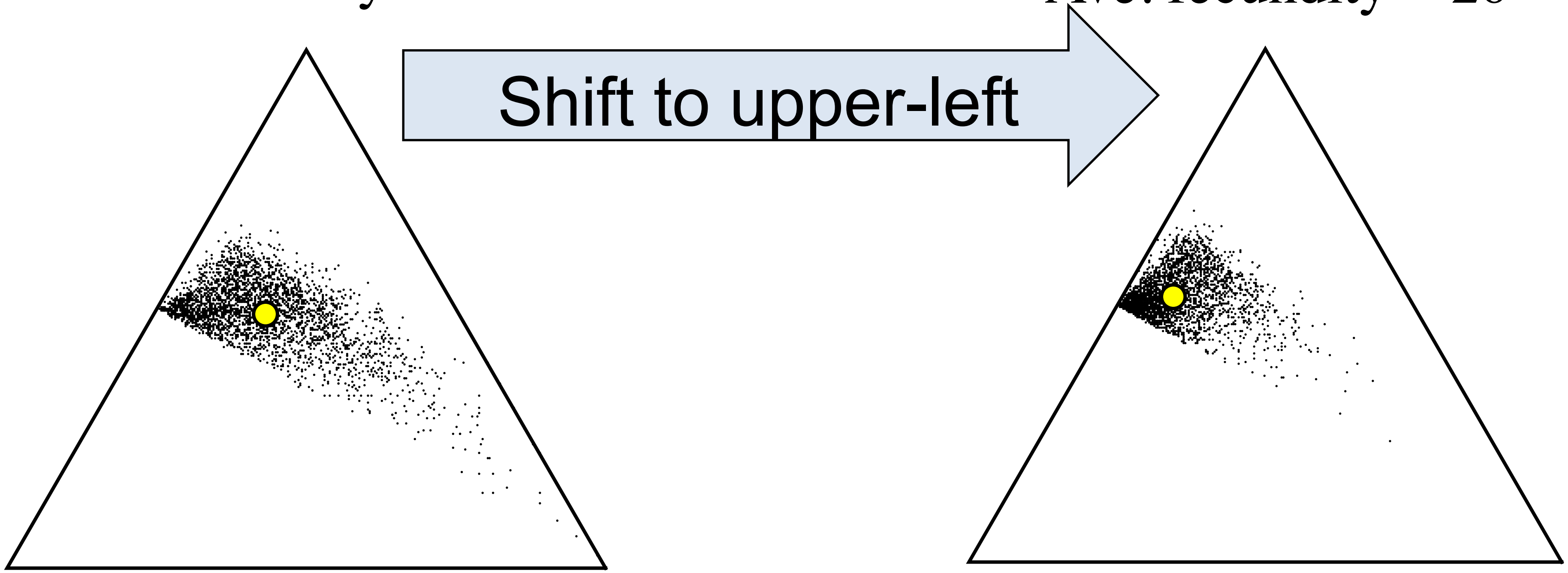
Hurry up

Effect of big-bang reproduction

$$0 < \sum_{i} t_{ij} < 1$$

Ave. fecundity = 5

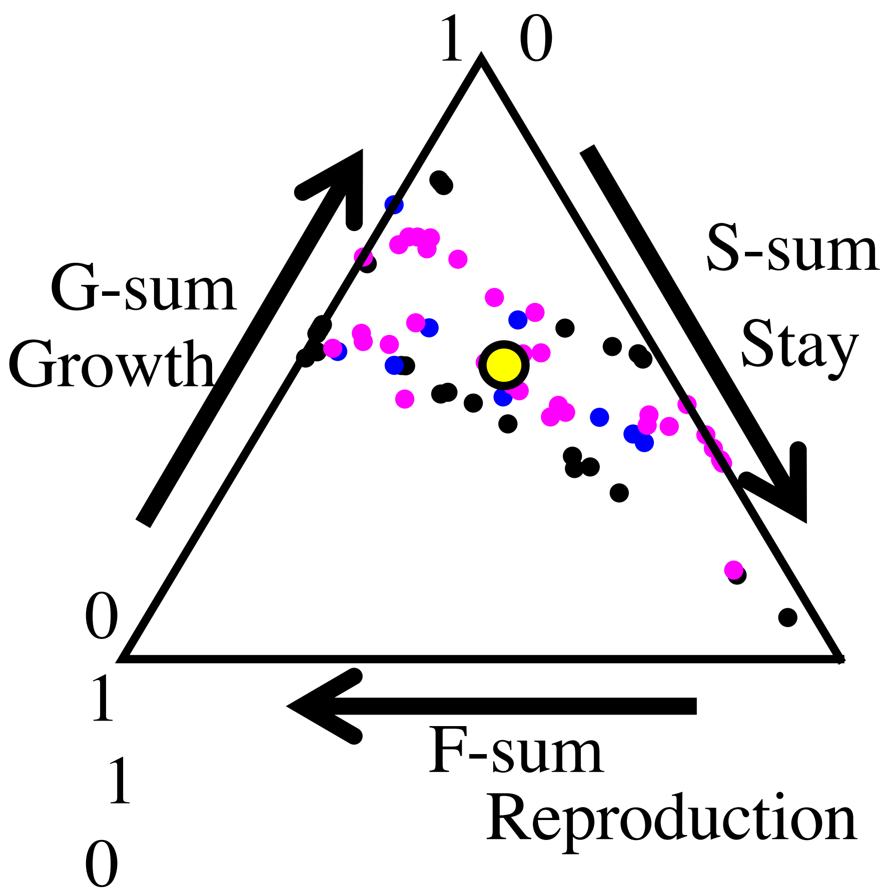
Ave. fecundity = 20



Distributed in upper-left when fecundity is large.
Big-bang reproduction could be the reason.

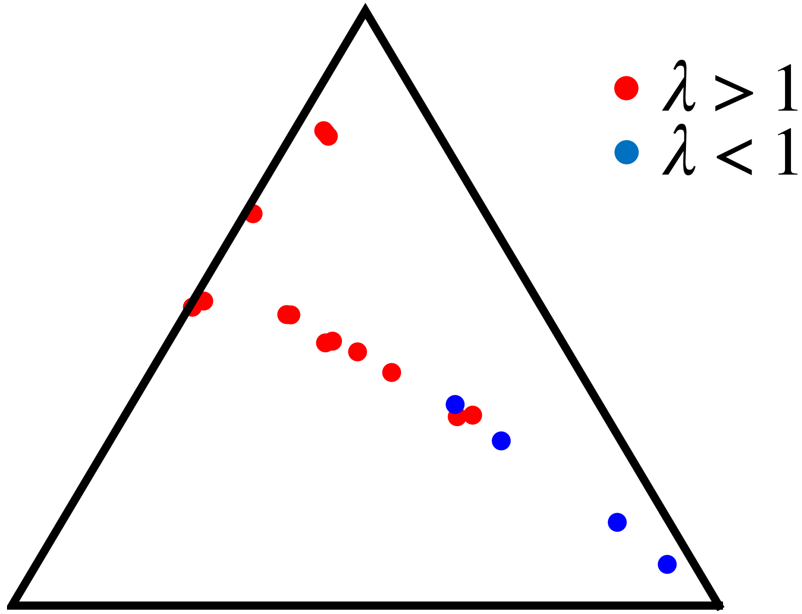
Semelparous herbs in COMPADRE database

68populations (17 species)



The distribution is not biased

Alliaria petiolata
(14 populations)



Located on the upper-left when population growth rate > 1.

Summary

∗ The elasticity distribution in iteroparous plants (herbs, shrubs and trees) is biased right in triangle map of elasticity vectors.

∗ The right-biased distribution is different from the elasticity distribution of randomly-generated matrices. There must be some reason in the discrepancy; natural selection.

∗ The elasticity distribution in semelparous plants is biased left in triangle map of elasticity vectors.

∗ Big-bang reproduction and natural selection could be the reason of the left-biased distribution.