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

(Advanced course of)

The Theory in Bio-Demography

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Biological meaning of matrix model

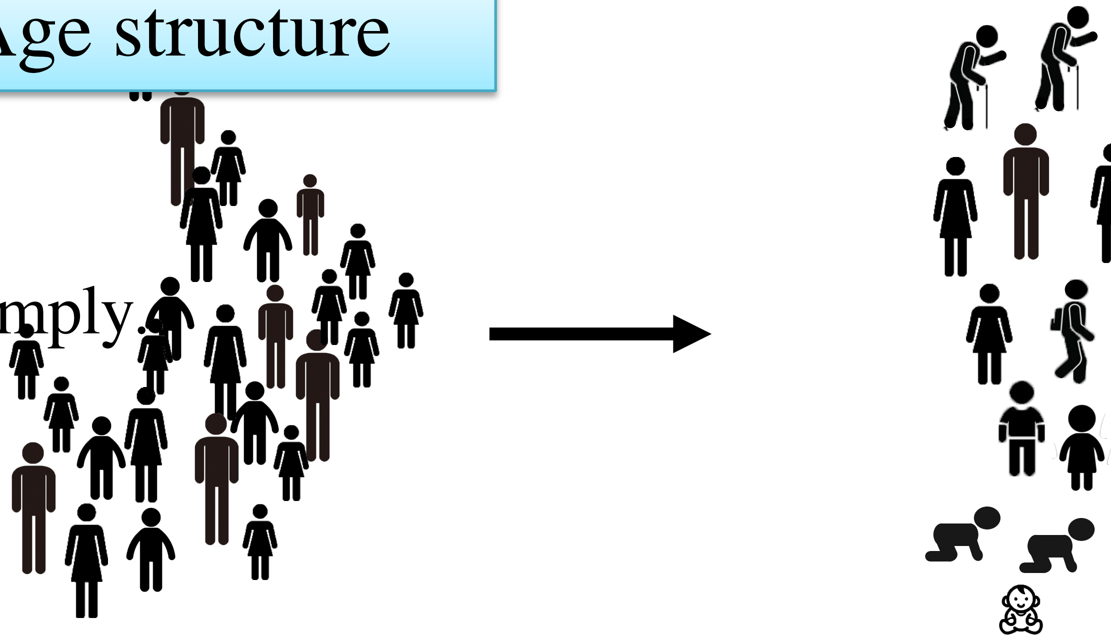
Oct. 10 and 17

Chapter 3

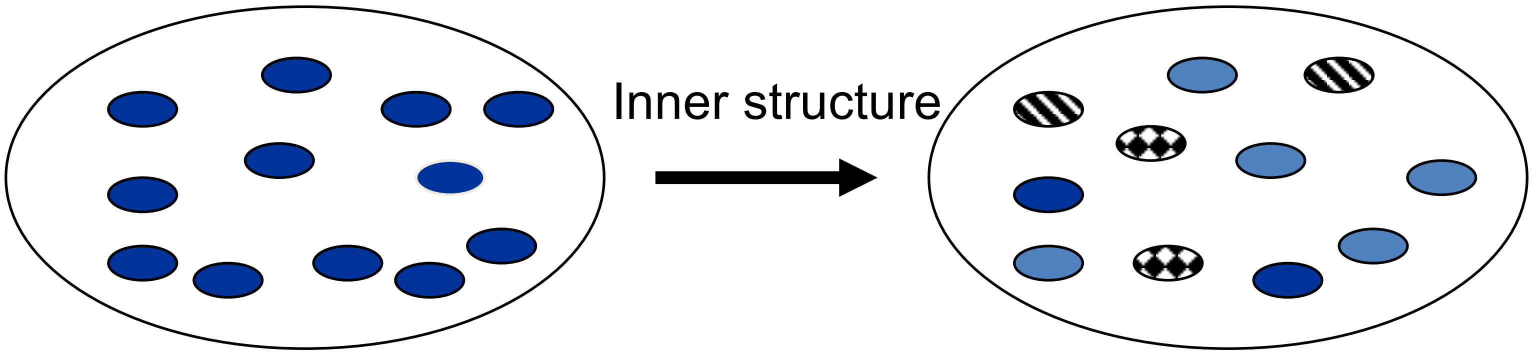
Biological meaning of population matrix model

Section 1　Age structure

Count No. of individuals simply.



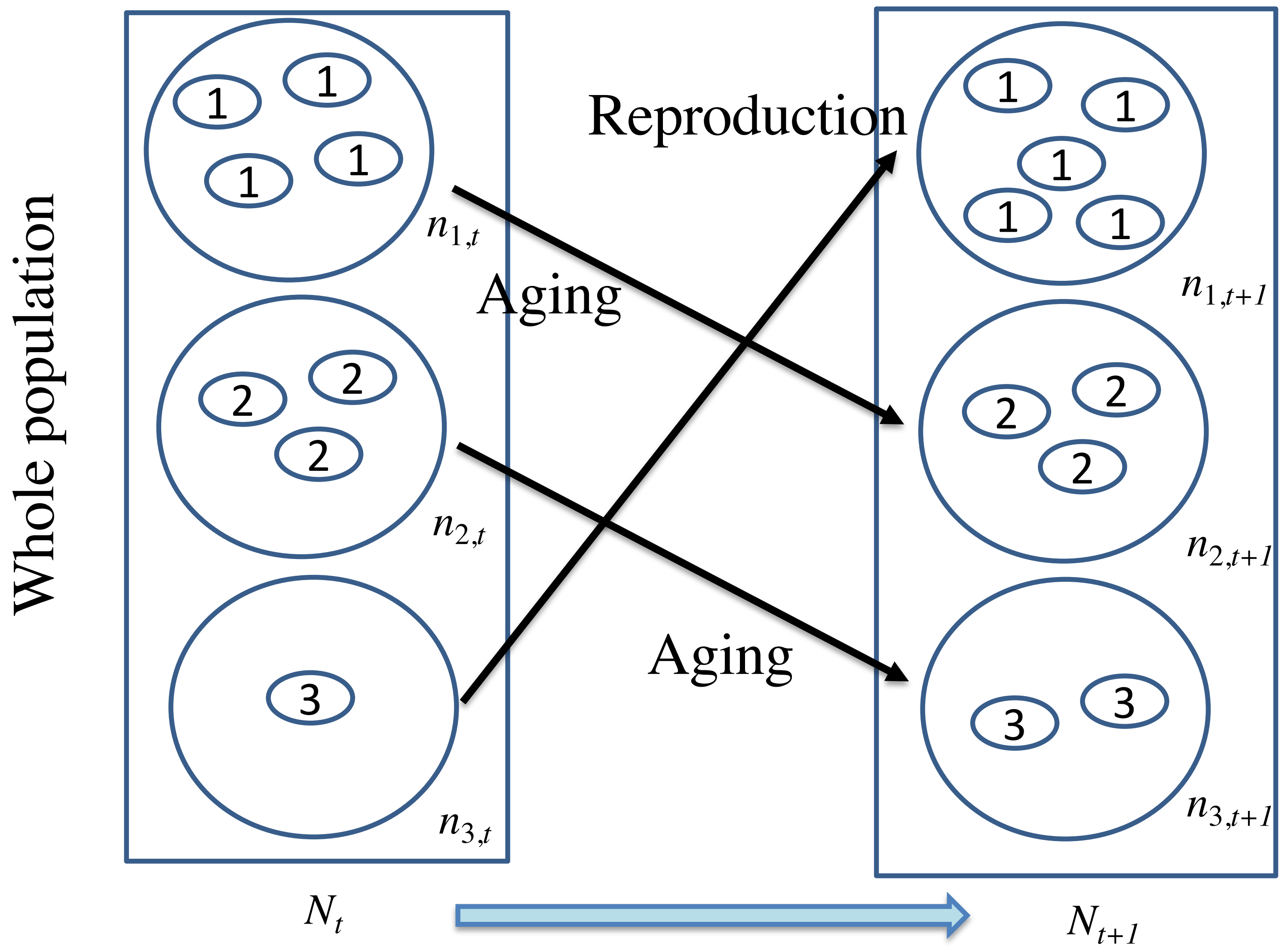
Age structure

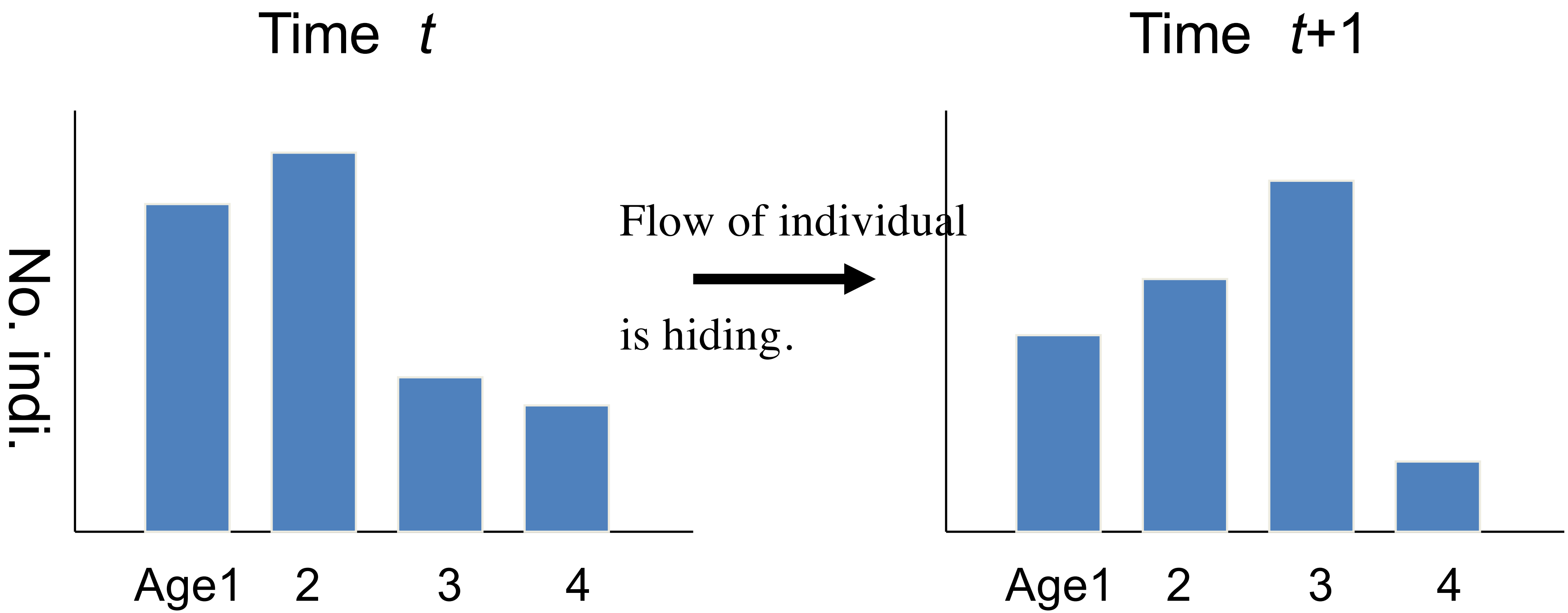


No inner structure
（Homogeneity among individuals）

Inner structure
- Genetic structure
- Age structure
- Size structure

Inner structure (Age)

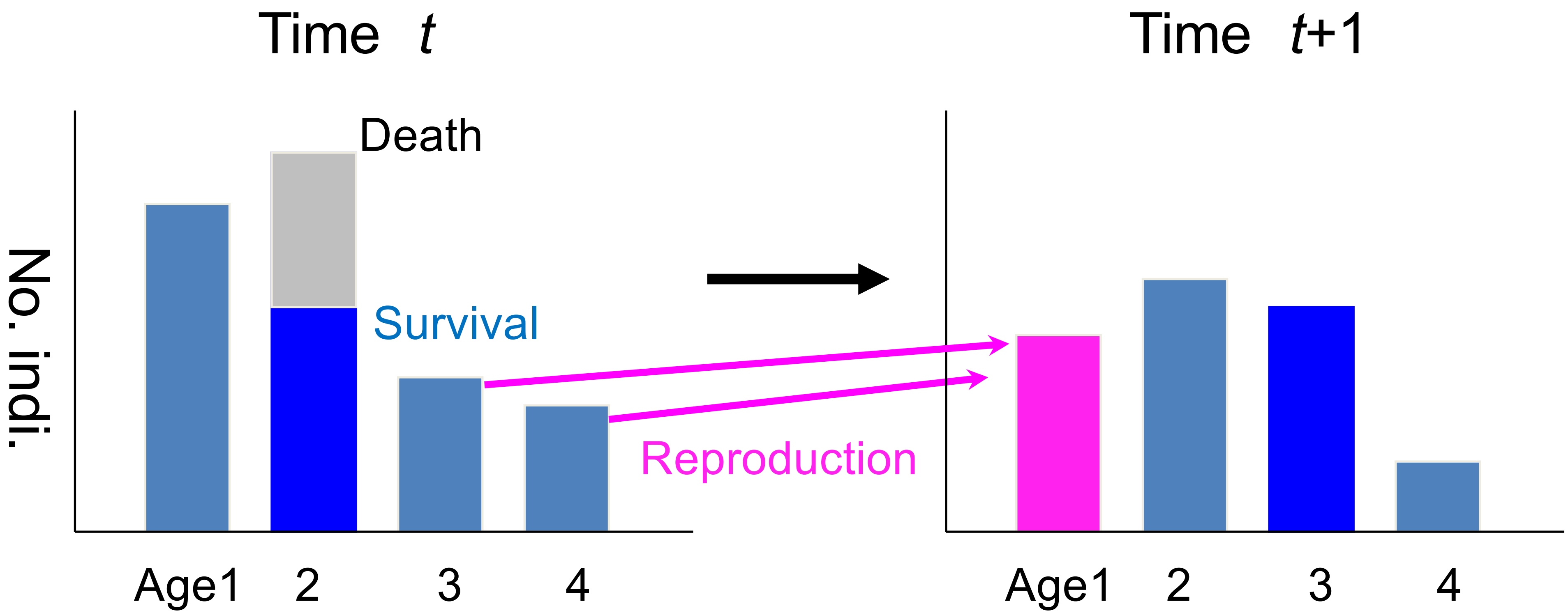




Time t
Time t+1
No. indi.
Flow of individual
is hiding.
Age1 2 3 4
Age1 2 3 4

The dynamics of a population with age structure

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

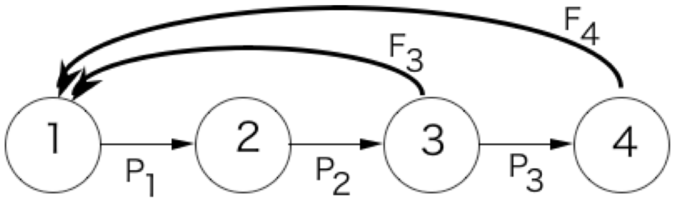


Mortality, survival, fecundity leads to the description of all the processes.

Matrix A is a summarized table of those parameters.

Age-structured model
by Lewis (1942), Leslie (1945)

∗ Flow chart



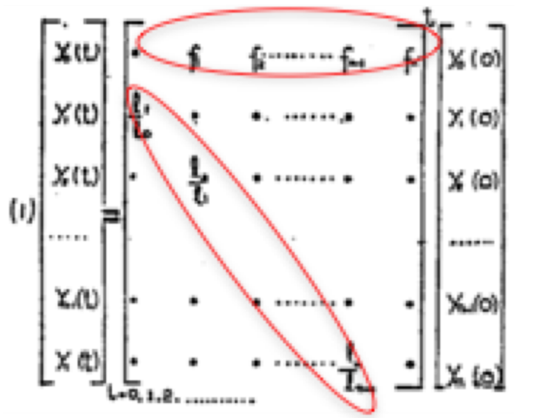
P_i: Survival at age *i*
(you can get them from life table)
F_i:Fecundity at age *i*

Parameters attached with arrows from state *j* to state *i* are assigned in (*i*, *j*) element of matrix.

$$
\begin{array}{cc}
 & \text{This year} \\
\text{Succeeding year} & \begin{matrix} 0 & 0 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{matrix}
\end{array}
$$

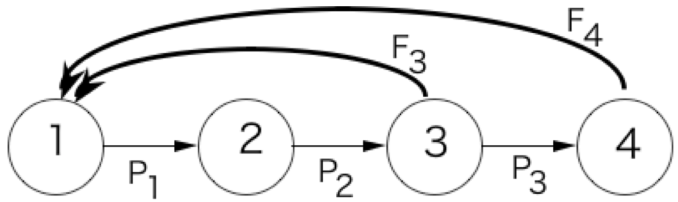
Matrix A
(Leslie matrix)

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



From Bernardelli (1941)

Biological meaning



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

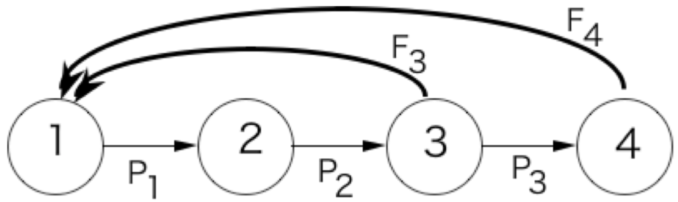
$$\begin{pmatrix} \#\text{of stage 1} \\ \#\text{of stage 2} \\ \#\text{of stage 3} \\ \#\text{of stage 4} \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & 0 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{pmatrix} \begin{pmatrix} \#\text{of stage 1} \\ \#\text{of stage 2} \\ \#\text{of stage 3} \\ \#\text{of stage 4} \end{pmatrix}_t$$

$$= \begin{pmatrix} \#\text{of stage } 3 \times F_3 + \#\text{of stage } 4 \times F_4 \\ \#\text{of stage } 1 \times P_1 \\ \#\text{of stage } 2 \times P_2 \\ \#\text{of stage } 3 \times P_3 \end{pmatrix}_t$$

Blue : Ageing
Red : reproduction

Forecasting the population vector at the next time step

Age-structured model
by Lewis (1942), Leslie (1945)



$$\mathbf{A} = \begin{pmatrix} 0 & 0 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{pmatrix}$$

Eigenvalue equation

$$\det(\lambda \mathbf{E} - \mathbf{A}) = 0 \Rightarrow 1 = \sum_{i=1}^{4} F_i l_i \lambda^{-i}$$

Same as Euler-Lotka equation

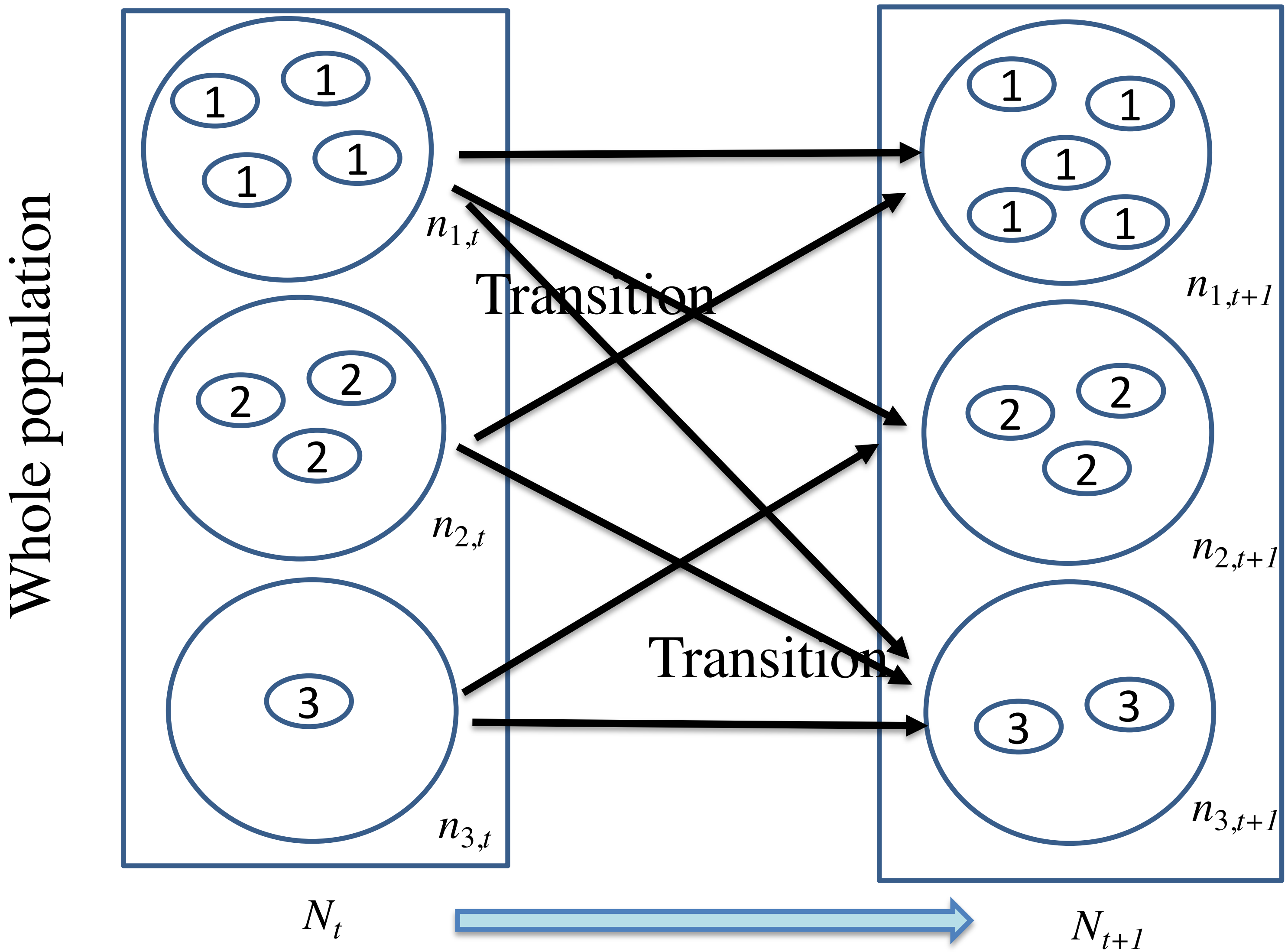
Nishimura Part

$$l_i = P_1 P_2 \cdots P_{i-1}$$

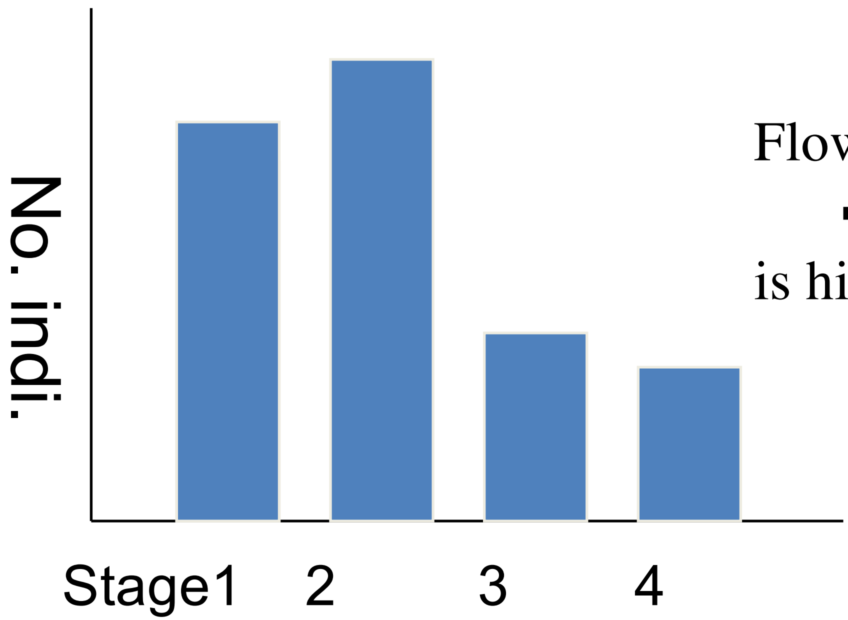
The eigenvalues is a multi-variable function of P_i and F_i .

Section 2 Stage structure

Inner structure (Stage)



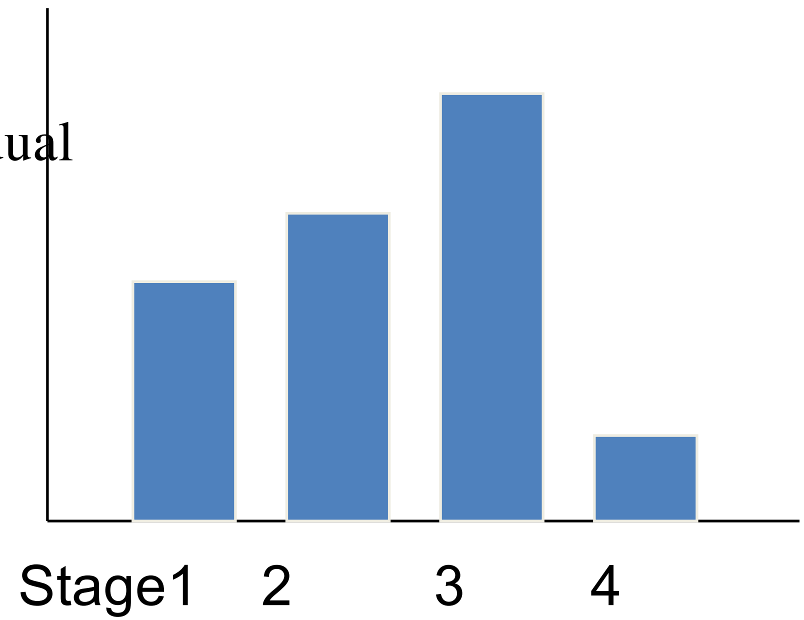
Time t



Flow of individual

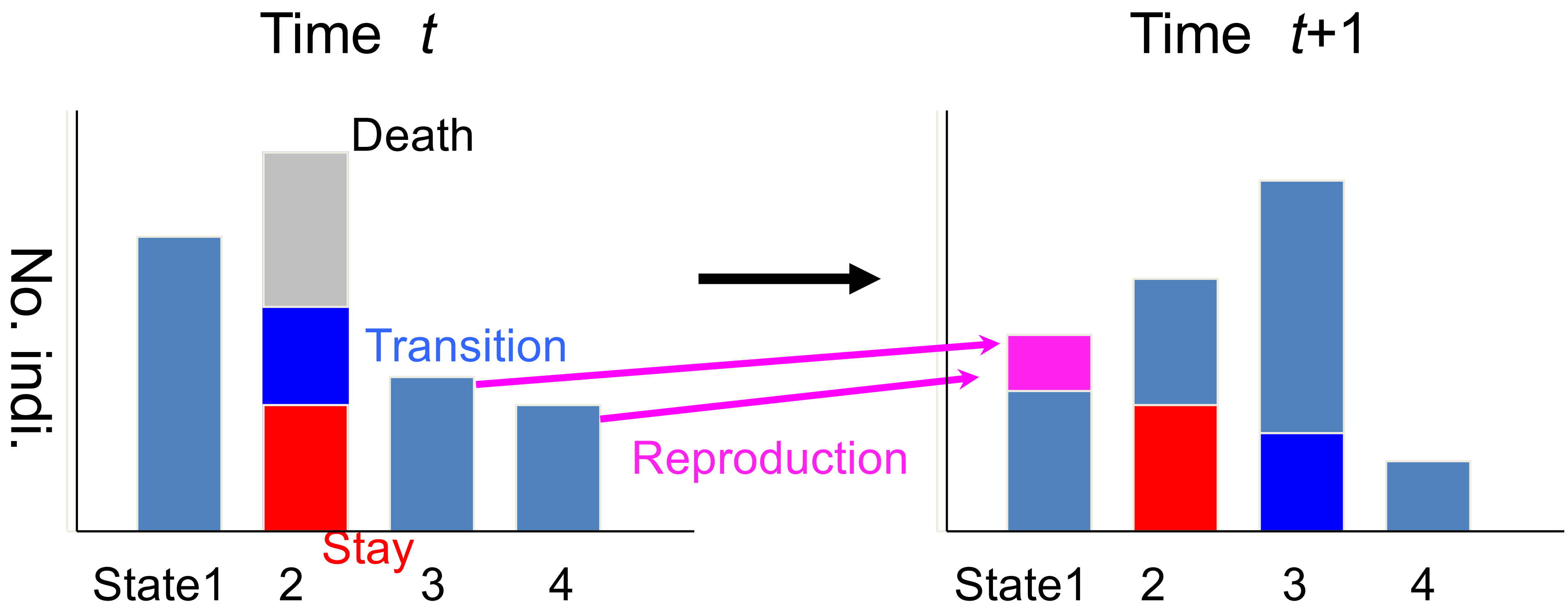
is hiding.

Time t+1



Linear model describing the dynamics with multiple states

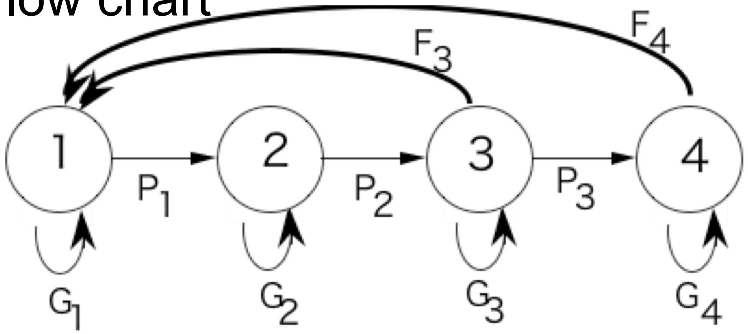
$$\vec{x}_{t+1} = A\vec{x}_t$$



Mortality, transition, stay, fecundity leads to the description of all the processes.
Matrix A is a summarized table of those parameters.

Multiple-state model
(size- or stage-structured model)
by Lefkovitch (1965)

* Flow chart



P_i: transition probability at stage i
F_i: fecundity at stage i
G_i: staying probability at stage i

$P_i + G_i$:survival at stage i

* Matrix (called as Lefkovitch matrix)

This year

Succeeding year

$$\begin{matrix} G_1 & 0 & F_3 & F_4 \\ P_1 & G_2 & 0 & 0 \\ 0 & P_2 & G_3 & 0 \\ 0 & 0 & P_3 & G_4 \end{matrix}$$

All the elements could be positive.

Difference?

$$\begin{matrix} 0 & 0 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{matrix}$$

Age-structured

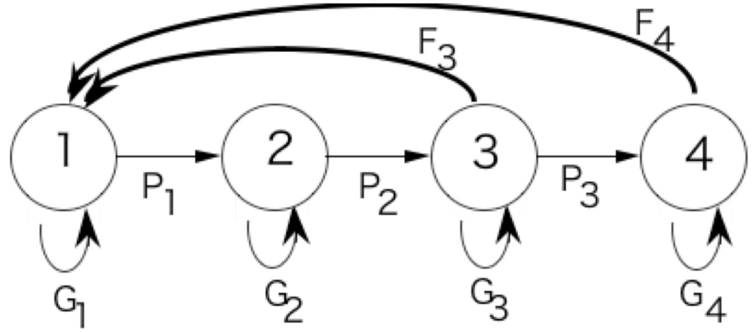
They are different, and "Age" is a special case of "Stage".

$$\underset{\text{Stage-structured}}{\begin{pmatrix} g_1 & * & b_3 & b_4 \\ s_1 & g_2 & * & * \\ * & s_2 & g_3 & * \\ * & * & s_3 & g_4 \end{pmatrix}} \xleftarrow{\text{General-ization}} \underset{\text{Age-structured}}{\begin{pmatrix} 0 & 0 & b_3 & b_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{pmatrix}}$$

Merit in stage-structured model

1) Too difficult to know the ages of individuals (fish, trees, herbs)
2) Survival and fecundity depend on size (or stage) rather than age.
3) "Stage" is an abstract concept. Applied more widely.

Stage



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

$$\begin{pmatrix} \#\text{of stage 1} \\ \#\text{of stage 2} \\ \#\text{of stage 3} \\ \#\text{of stage 4} \end{pmatrix}_{t+1} = \begin{pmatrix} G_1 & 0 & F_3 & F_4 \\ P_1 & G_2 & 0 & 0 \\ 0 & P_2 & G_3 & 0 \\ 0 & 0 & P_3 & G_4 \end{pmatrix} \begin{pmatrix} \#\text{of stage 1} \\ \#\text{of stage 2} \\ \#\text{of stage 3} \\ \#\text{of stage 4} \end{pmatrix}_t$$

$$= \begin{pmatrix} \#\text{of stage } 1 \times G_1 + \#\text{of stage } 3 \times F_3 + \#\text{of stage } 4 \times F_4 \\ \#\text{of stage } 1 \times P_1 + \#\text{of stage } 2 \times G_2 \\ \#\text{of stage } 2 \times P_2 + \#\text{of stage } 3 \times G_3 \\ \#\text{of stage } 3 \times P_3 + \#\text{of stage } 4 \times G_4 \end{pmatrix}_t$$

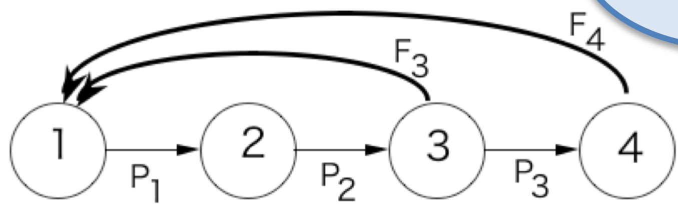
Forecasting the population vector at the next time step

Black : stay
Blue : transition
Red : reproduction

Age

Again

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



$$\begin{pmatrix} \#\text{of stage 1} \\ \#\text{of stage 2} \\ \#\text{of stage 3} \\ \#\text{of stage 4} \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & 0 & F_3 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & 0 \end{pmatrix} \begin{pmatrix} \#\text{of stage 1} \\ \#\text{of stage 2} \\ \#\text{of stage 3} \\ \#\text{of stage 4} \end{pmatrix}_t$$

$$= \begin{pmatrix} \#\text{of stage } 3 \times F_3 + \#\text{of stage } 4 \times F_4 \\ \#\text{of stage } 1 \times P_1 \\ \#\text{of stage } 2 \times P_2 \\ \#\text{of stage } 3 \times P_3 \end{pmatrix}_t$$

Blue : Ageing

Red : reproduction

Forecasting the population vector at the next time step

◆Survival and fecundity

- Survival at a state (Calculated by the row-sum of transition prob.)

- Fecundity ：Number of offspring per individual

$$
\begin{pmatrix} G_1 & 0 & F_3 & F_4 \\ P_1 & G_2 & 0 & 0 \\ 0 & P_2 & G_3 & 0 \\ 0 & 0 & P_3 & G_4 \end{pmatrix} = \begin{pmatrix} G_1 & 0 & 0 & 0 \\ P_1 & G_2 & 0 & 0 \\ 0 & P_2 & G_3 & 0 \\ 0 & 0 & P_3 & G_4 \end{pmatrix} + \begin{pmatrix} 0 & 0 & F_3 & F_4 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}
$$

Population Matrix A	Transition matrix T	Reproduction matrix F

Divided into two qualitatively different matrices.

Do it yourself !

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

$$\begin{pmatrix} \#\text{of stage 1} \\ \#\text{of stage 2} \\ \#\text{of stage 3} \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & 0 & 5 \\ 0.5 & 0.2 & 0 \\ 0 & 0.7 & 0.2 \end{pmatrix} \begin{pmatrix} 1 \\ 0.1 \\ 0.1 \end{pmatrix}_t$$

$$= \begin{pmatrix} 1\times 0 + 0.1\times 0 + {\color{red}0.1\times 5} \\ {\color{blue}1\times 0.5} + 0.1\times 0.2 \\ {\color{blue}0.1\times 0.7} + 0.1\times 0.2 \end{pmatrix} = \begin{pmatrix} 0.5 \\ 0.52 \\ 0.09 \end{pmatrix}$$

Not only the number of individuals at each stage,
But also the total number (population size)

Black : stay
Blue : transition
Red : reproduction

Chapter 4

Solving population matrix model

Theorem on non-negative matrix

$$\mathbf{A} = \{a_{ij}\} \qquad a_{ij} \geq 0 \text{ for all } i, j$$

<u>Peron-Frobenius theorem</u>

In irreducible non-negative matrix,

(1) it has simple root of positive and real eigenvalue. ～～> not always one

(2) Denoting the maximum eigenvalue among positive ones as λ_1(dominant eigenvalue), then the right eigenvector corresponding to λ_1 is a positive vector.

(3) The absolute value of other eigenvalues is equal to or less than λ_1

EX.

				Positive, real		
λ	$1+i$	$1-i$	-2	1	2	3 ← λ_1 Dominant
Absolute value	$\sqrt{2}$	$\sqrt{2}$	2	1	2	3
Eigenvector (**u**)	·	·	· ·	$\begin{pmatrix}+\\-\\+\end{pmatrix}$	$\begin{pmatrix}+\\-\\-\end{pmatrix}$	$\begin{pmatrix}+\\+\\+\end{pmatrix}$ ← positive vector

Cf. Gantmacher (1959) Applications of the theory of matrices.Chap. 3

(3) The absolute value of other eigenvalues is equal to or less than λ_1

Solution: $$\vec{x}_t = \sum_{i=1}^{n} c_i(\lambda_i)^t \vec{\mathbf{u}}_i = c_1(\lambda_1)^t \vec{\mathbf{u}}_1 + \sum_{i=2}^{n} c_i(\lambda_i)^t \vec{\mathbf{u}}_i$$

If the absolute value of other eigenvalues is less than λ_1 ⇒ the behavior of $\mathbf{x}(t)$ is dominated by $c_1(\lambda_1)^t \vec{\mathbf{u}}_1$ Dominant

$\lambda_1 > 1$	--->	increase exponentially
$\lambda_1 < 1$	--->	decrease exponentially

EX.

$$\mathbf{A} = \begin{pmatrix} 2 & 4 \\ 5 & 3 \end{pmatrix}$$

$$\lambda = 7, -2$$

$$\vec{\mathbf{u}} = \begin{pmatrix} 4\alpha \\ 5\alpha \end{pmatrix}, \begin{pmatrix} \beta \\ -\beta \end{pmatrix}$$

$$\vec{x}_t = \sum_{i=1}^{2} c_i(\lambda_i)^t \vec{u}_i = c_1(\lambda_1)^t \vec{u}_1 + c_2(\lambda_2)^t \vec{u}_2$$

$$= c_1 7^t \begin{pmatrix} 4 \\ 5 \end{pmatrix} + c_2(-2)^t \begin{pmatrix} 1 \\ -1 \end{pmatrix}$$

$$\approx c_1 7^t \begin{pmatrix} 4 \\ 5 \end{pmatrix}$$

Let's examine Peron-Frobenius theorem!!

Again

Obtain the eigenvalues (λ) and the corresponding right eigenvectors (u) of the following matrices.

(a) $\begin{pmatrix} 2 & 4 \\ 5 & 3 \end{pmatrix}$ (b) $\begin{pmatrix} 0.7 & 1.2 \\ 0.1 & 0.6 \end{pmatrix}$ (c) $\begin{pmatrix} 1 & -2 \\ 4 & -5 \end{pmatrix}$ (d) $\begin{pmatrix} 1 & 1 & 0 \\ 1 & 4 & 3 \\ 0 & 3 & 1 \end{pmatrix}$

Village example

Answer

(a) $\lambda = 7, -2$

$$\vec{\mathbf{u}} = \begin{pmatrix} 4\alpha \\ 5\alpha \end{pmatrix}, \begin{pmatrix} \beta \\ -\beta \end{pmatrix}$$

(b) $\lambda = 1,\ 0.3$

$$\vec{\mathbf{u}} = \begin{pmatrix} 0.97\alpha \\ 0.24\alpha \end{pmatrix}, \begin{pmatrix} 0.95\beta \\ -0.32\beta \end{pmatrix}$$

(c) $\lambda = -1, -3$

$$\vec{\mathbf{u}} = \begin{pmatrix} \alpha \\ \alpha \end{pmatrix}, \begin{pmatrix} \beta \\ 2\beta \end{pmatrix}$$

(d) $\lambda = 6,\ 1,\ -1$

$$\vec{\mathbf{u}} = \begin{pmatrix} \alpha \\ 5\alpha \\ 3\alpha \end{pmatrix}, \begin{pmatrix} -3\beta \\ 0 \\ \beta \end{pmatrix}, \begin{pmatrix} \gamma \\ -2\gamma \\ 3\gamma \end{pmatrix}$$

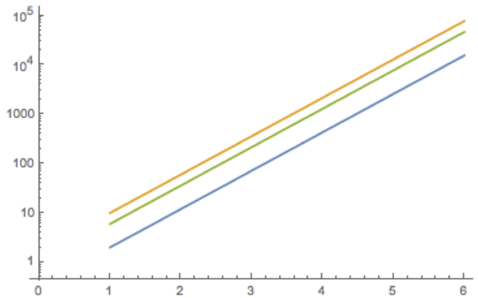
The eigenvalues with maximum absolute value are real and positive in (a), (b), (d) . The corresponding eigenvectors are positive vectors.

Let's make figures to show the dynamics of 4th example in the previous slide.

$$\vec{x}_{t+1} = \mathbf{A}\vec{x}_t \qquad \mathbf{A} = \begin{pmatrix} 1 & 1 & 0 \\ 1 & 4 & 3 \\ 0 & 3 & 1 \end{pmatrix}$$

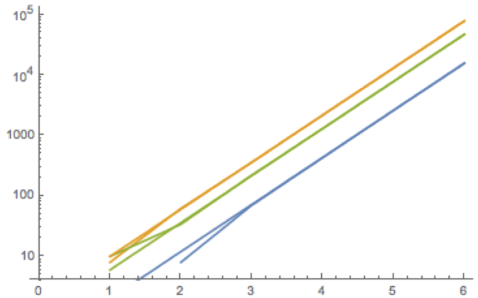
```
In[113]:= zuxt = xt /. {g1 -> 2, g2 → 0, g3 → 0};                    (* If we neglect 2nd and 3rd terms.....

          fig4 = ListLogPlot[{Flatten[zuxt[[1]]], Flatten[zuxt[[2]]], Flatten[zuxt[[3]]]}, Joined → True]
```

Out[113]=




```
In[114]:= Show[fig2, fig4]                    (*        Let's compare these two        *)
```

Out[114]=



(1) λ_1 times at every timestep

$$\begin{pmatrix} x_{1,t} \\ x_{2,t} \\ x_{3,t} \end{pmatrix} \approx c_1 \ (\lambda_1)^t \begin{pmatrix} u_{11} \\ u_{12} \\ u_{13} \end{pmatrix}$$

$$x_{i,t+1} \approx c_1 \ (\lambda_1)^{t+1} u_{1i}$$

$$x_{i,t} \approx c_1 \ (\lambda_1)^t u_{1i}$$

for all i

$$\frac{x_{i,t+1}}{x_{i,t}} \approx \frac{c_1 \ (\lambda_1)^{t+1} u_{1i}}{c_1 \ (\lambda_1)^t u_{1i}} = \lambda_1$$

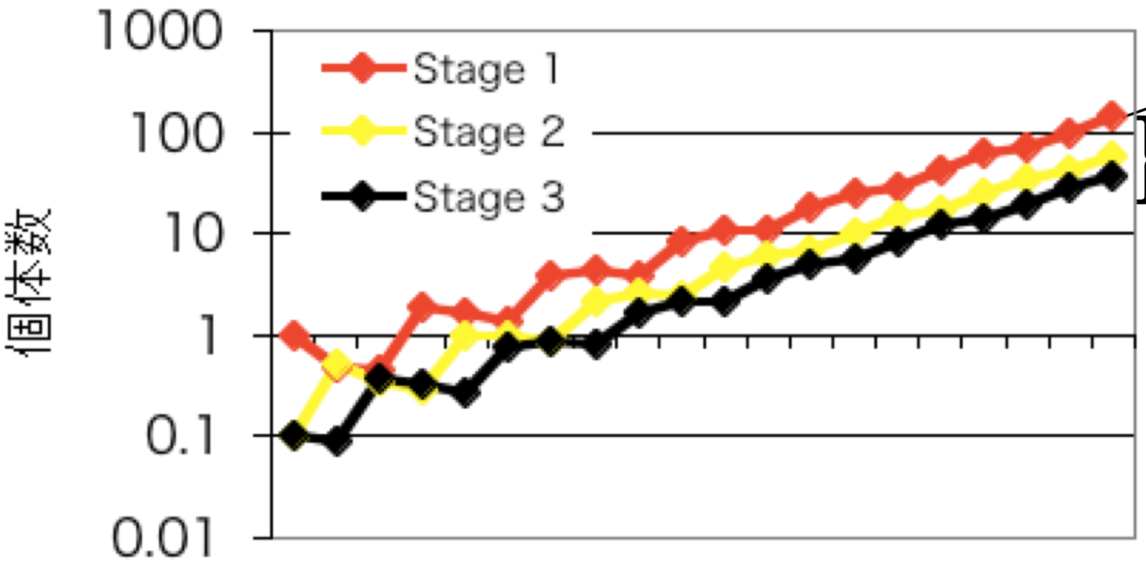
Dominant eigenvalue
means
“Population growth rate”.

(2) $\vec{x}_t$ is proportional to **u**$_1$

$$x_{1,t} : x_{2,t} : x_{3,t} = c_1 \ (\lambda_1)^t u_{11} : c_1 \ (\lambda_1)^t u_{12} : c_1 \ (\lambda_1)^t u_{13} = u_{11} : u_{12} : u_{13}$$

The right eigenvector means “Stable stage distribution”
if the element–sum is equal to 1.

Dynamics of No. of individuals



Year

Slope
(logarithm of increase rate)
logarithm of dominant eigenvalue

% Ratio of each stage
(stable stage distribution)
right eigenvector

Linear curve in semi-logarithmic ordinate means "Exponential increase".

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

$$A = \begin{pmatrix} 0 & 0 & 5 \\ 0.5 & 0.2 & 0 \\ 0 & 0.7 & 0.2 \end{pmatrix}$$

When t is large, the behavior of a solution is approximately the same as the dominant term $c_1(\lambda_1)^t \vec{\mathbf{u}}_1$

$\lambda_1 > 1$ ---> exponential increase

$\lambda_1 < 1$ ---> exponential decrease

Matrix model is like Malthus model (time-discrete and state-discrete.

! The dominant eigenvalue and the eigenvector dominate the system !

Mathematica Program

```
mat = {{0, 0, 5}, {0.5, 0.2, 0}, {0, 0.7, 0.2}}; MatrixForm[mat]
```

$$\begin{pmatrix} 0 & 0 & 5 \\ 0.5 & 0.2 & 0 \\ 0 & 0.7 & 0.2 \end{pmatrix}$$

Initial value $\vec{x}_0 = \begin{pmatrix} 1 \\ 0.1 \\ 0.1 \end{pmatrix} = \sum_{i=1}^{n} c_i \vec{\mathbf{u}}_i$

(* Eigenvalues and vectors *)

```
Eigensystem[mat]
{{1.34196, -0.470978 + 1.04031 i, -0.470978 - 1.04031 i},
 {{0.889551, 0.389485, 0.238748},
  {0.907107 + 0. i, -0.198586 - 0.307895 i, -0.0854455 + 0.188734 i},
  {0.907107 + 0. i, -0.198586 + 0.307895 i, -0.0854455 - 0.188734 i}}}
```

(* Stable stage distribution *)

```
{0.8895508471088555`, 0.3894852807368841`, 0.2387477884656794`} /
 Total[{0.8895508471088555`, 0.3894852807368841`, 0.2387477884656794`}]
{0.586085, 0.256614, 0.1573}
```

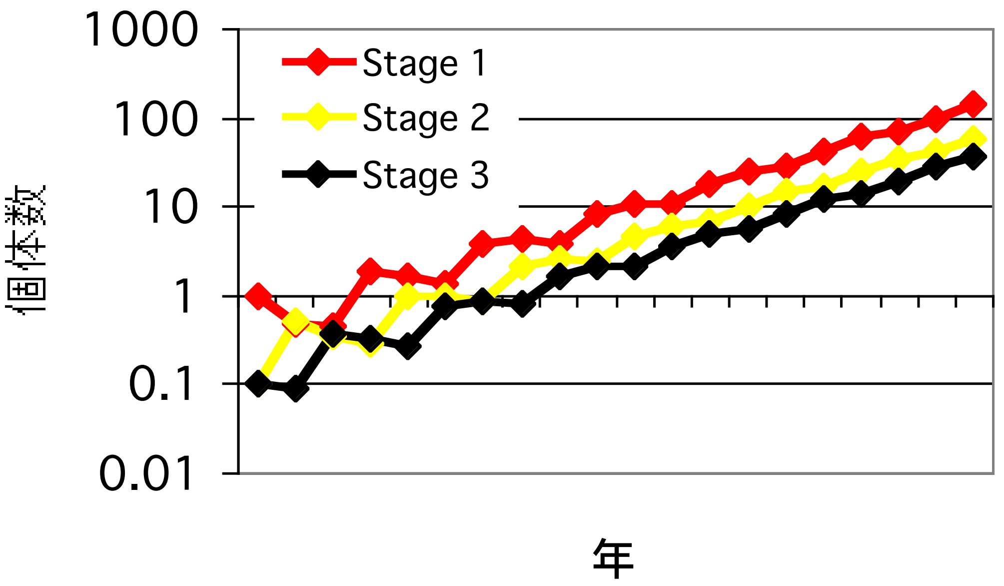
Normalized vector (element-sum equals one)

(* Obtain the coeffi. c1 from initial value *)

```
olve[{1, 0.1, 0.1} ==
  c1 {0.5860853034144075`, 0.2566144472550746 5`, 0.1573002493305178 4`} +
   c2 {0.9071066901394358` + 0.` i, -0.1985860083296788 2` - 0.3078951461899872` i,
     -0.0854455451853625 1` + 0.1887344371347877 7` i} +
   c3 {0.9071066901394358` + 0.` i, -0.1985860083296788 2` + 0.3078951461899872` i,
     -0.0854455451853625 1` - 0.1887344371347877 7` i}, {c1, c2, c3}]
{{c1 → 0.868956 + 0. i, c2 → 0.270485 - 0.0252643 i, c3 → 0.270485 + 0.0252643 i}}
```

Again

Dynamics of No. of individuals



Slope = log(1.34196)

logarithm of dominant eigenvalue

Proportional to right eigenvector

$$\vec{u} = \begin{pmatrix} 0.586085 \\ 0.256614 \\ 0.1573 \end{pmatrix}$$

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

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 5 \\ 0.5 & 0.2 & 0 \\ 0 & 0.7 & 0.2 \end{pmatrix}$$

Right eigenvector

Dominant eigenvalue

When t is large, the behavior of a solution is approximately the same as the dominant term

$$0.868956\,(1.34196)^t \begin{pmatrix} 0.586085 \\ 0.256614 \\ 0.1573 \end{pmatrix}$$

(1) Increases by 1.34196 times very timestep

(2) $\vec{x}_t$ at each timestep is proportional to $\vec{u}$

Summary

＊Transition prob.: P_i *(growing)* , G_i (staying)

＊The sum of *i*-th row elements equals survival prob. at *i*-th stage.

＊If individuals grow faster, then P_i increase (transition prob. to next stage)

＊Dominant eigenvalue（λ_1）: population growth rate（fitness per year）

＊Normalized right eigenvector (i. e. the sum of elements =1; **u**=(u_1, u_2, …,))
: Proportion of numbers at each stage (stable stage distribution）.

＊ Population growth rate (PGR) and stable stage distribution are two basic population metrics.