Population dynamics – a source of diversity

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Models with continuous time
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Leonhard Euler: *Introductio in analysin infinitorum* (1748)

Geometric growth of population

- The increase of population is necessarily limited by the means of subsistence,
- population does invariably increase when the means of subsistence increase,
- the superior power of population is repressed, and the actual population kept equal to the means of subsistence, by misery and vice.
Pierre-François Verhulst: *Recherches mathématiques sur la loie d’accroissement de la population* (1845)

Self-limited (logistic) growth of population
Alfred J. Lotka: *Analytical note on certain rhythmic relations in organic systems* (1920)
A bit of history

Alfred J. Lotka: *Analytical note on certain rhythmic relations in organic systems* (1920)

Vito Volterra: *Variazioni e fluttuazioni del numero d'individui in specie animali conviventi.* (1926)
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Alfred J. Lotka: *Elements of physical biology* (1925)

Vito Volterra: *Leçons sur la théorie mathématique de la lutte pur la vie* (1931)
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Vito Volterra: *Leçons sur la théorie mathématique de la lutte pur la vie* (1931)
Georgij F. Gause: *The Struggle for existence* (1934)
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Vito Volterra: *Leçons sur la théorie mathématique de la lutte pur la vie* (1931)
Georgij F. Gause: *The Struggle for existence* (1934)
Andrej N. Kolmogorov: *Sula teoria di Volterra della lota per l’esistenza* (1936)
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Charles S. Elton: *Animal ecology* (1927)

food chain, ecological niche, pyramid of numbers
Charles S. Elton: *Animal ecology* (1927)
density (in)dependent growth
Charles S. Elton: *Animal ecology* (1927)

Charles S. Elton: *Animal ecology* (1927)


Ernest T. Seton: *The arctic prairies* (1912)
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Charles S. Elton: *Animal ecology* (1927)


Crawford S. Holling: *The functional response of predator to prey density and its role in mimicry and population regulation* (1965)
Patrick H. Leslie: *On the use of matrices in certain population mathematics* (1945)

structured population
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John G. Skellam: *Random Dispersal in Theoretical Populations* (1951)

dispersal of population in space, random walk, biological invasion
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General theory of population dynamics

Principles of population

1st principle

2nd principle

“Fundamental equations”

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General theory of population dynamics
Principles of population

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Principles of population

1st principle

2nd principle

“Fundamental equations”

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Principles of population

1. A size of population sustains in the exponential increase or decrease until environmental conditions cause a change of the status.
1. A size of population sustains in the exponential increase or decrease until environmental conditions cause a change of the status.

2. The relative change of a population size equals to the impact of environmental conditions.
1\textsuperscript{st} principle

A size of population sustains in the exponential increase or decrease until environmental conditions cause a change of the status.

\[ x(t) = x_0q^t \]
1st principle

A size of population sustains in the exponential increase or decrease until environmental conditions cause a change of the status.

\[ x(t) = x_0 q^t \]

\[ x(t + 1) = x_0 q^{t+1}. \]
A size of population sustains in the exponential increase or decrease until environmental conditions cause a change of the status.

\[ x(t) = x_0 q^t \]

\[ x(t + 1) = qx(t) \]
1st principle

A size of population sustains in the exponential increase or decrease until environmental conditions cause a change of the status.

\[ x(t) = x_0 q^t \]

\[ x(t + 1) = q x(t), \quad \frac{x(t + 1) - x(t)}{x(t)} = q - 1 \]
1st principle

A size of population sustains in the exponential increase or decrease until environmental conditions cause a change of the status.

\[ x(t) = x_0 q^t \]

\[ x(t + 1) = qx(t), \quad \frac{x(t + 1) - x(t)}{x(t)} = q - 1 \]

\[ x'(t) = x_0 q^t \ln q, \]
1\textsuperscript{st} principle

A size of population sustains in the exponential increase or decrease until environmental conditions cause a change of the status.

\[ x(t) = x_0 q^t \]

\[ x(t + 1) = qx(t), \quad \frac{x(t + 1) - x(t)}{x(t)} = q - 1 \]

\[ x'(t) = (\ln q)x(t), \]
A size of population sustains in the exponential increase or decrease until environmental conditions cause a change of the status.

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\[ x(t + 1) = qx(t), \quad \frac{x(t + 1) - x(t)}{x(t)} = q - 1 \]

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\[ x(t + 1) = qx(t), \quad \frac{x(t + 1) - x(t)}{x(t)} = q - 1 \]

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A size of population sustains in the exponential increase or decrease until environmental conditions cause a change of the status.

$$x(t) = x_0 q^t$$

$$x(t + 1) = qx(t), \quad \frac{x(t + 1) - x(t)}{x(t)} = r$$

$$x'(t) = (\ln q)x(t), \quad \frac{x'(t)}{x(t)} = r$$
2\textsuperscript{nd} principle

The relative change of a population size equals to the impact of environmental conditions.
The relative change of a population size equals to the impact of environmental conditions.

\[ \frac{x'(t)}{x(t)} = r \]
The relative change of a population size equals to the impact of environmental conditions.

\[
\frac{d x_i(t)}{x_i(t)} = q_i(x_1(t), x_2(t), \ldots, x_n(t)), \quad i = 1, 2, \ldots, n
\]
2nd principle

The relative change of a population size equals to the impact of environmental conditions.

\[
\frac{x_i'(t)}{x_i(t)} = \varrho_i(x_1(t), x_2(t), \ldots, x_n(t)), \quad i = 1, 2, \ldots, n
\]

\[
\frac{x(t+1) - x(t)}{x(t)} = r
\]
2nd principle

The relative change of a population size equals to the impact of environmental conditions.

\[
\frac{x_i'(t)}{x_i(t)} = q_i(x_1(t), x_2(t), \ldots, x_n(t)), \quad i = 1, 2, \ldots, n
\]

\[
\frac{x_i(t + 1) - x_i(t)}{x_i(t)} = q_i(x_1(t), x_2(t), \ldots, x_n(t)), \quad i = 1, 2, \ldots, n
\]
The relative change of a population size equals to the impact of environmental conditions.

\[ \frac{x'_i(t)}{x_i(t)} = \varphi_i(x_1(t), x_2(t), \ldots, x_n(t)), \quad i = 1, 2, \ldots, n \]

\[ \frac{x_i(t + 1) - x_i(t)}{x_i(t)} = \varphi_i(x_1(t), x_2(t), \ldots, x_n(t)), \quad i = 1, 2, \ldots, n \]

\[ x(t + 1) = qx(t) \]
2nd principle

The relative change of a population size equals to the impact of environmental conditions.

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\frac{x_i'(t)}{x_i(t)} = \varphi_i(x_1(t), x_2(t), \ldots, x_n(t)), \quad i = 1, 2, \ldots, n
\]

\[
\frac{x_i(t + 1) - x_i(t)}{x_i(t)} = \varphi_i(x_1(t), x_2(t), \ldots, x_n(t)), \quad i = 1, 2, \ldots, n
\]

\[x(t + 1) = e^r x(t)\]
The relative change of a population size equals to the impact of environmental conditions.

\[
\frac{x'_i(t)}{x_i(t)} = \phi_i(x_1(t), x_2(t), \ldots, x_n(t)), \quad i = 1, 2, \ldots, n
\]

\[
\frac{x_i(t+1) - x_i(t)}{x_i(t)} = \phi_i(x_1(t), x_2(t), \ldots, x_n(t)), \quad i = 1, 2, \ldots, n
\]

\[
x_i(t+1) = e^{\phi_i(x_1(t), x_2(t), \ldots, x_n(t))} x(t), \quad i = 1, 2, \ldots, n
\]
“Fundamental equations”

Populations with overlapping generations

\[ x'_i = x_i \varrho_i(x_1, x_2, \ldots, x_n), \quad i = 1, 2, \ldots, n \]

Populations with non-overlapping generations

\[ x_i(t + 1) = e^{\varrho_i(x_1(t), x_2(t), \ldots, x_n(t))} x_i(t), \quad i = 1, 2, \ldots, n \]
“Fundamental equations”

Populations with overlapping generations

\[ x'_i = x_i \rho_i(x_1, x_2, \ldots, x_n), \quad i = 1, 2, \ldots, n \]

Populations with non-overlapping generations

\[ x_i(t + 1) = e^{\rho_i(x_1(t), x_2(t), \ldots, x_n(t))} x_i(t), \quad i = 1, 2, \ldots, n \]

\[ \rho_i \] linear functions – Lotka-Volterra systems
\[ \rho_i \] general functions – Kolmogorov systems
"Fundamental equations"

Populations with overlapping generations

\[ x'_i = x_i \left( r_i - f_i(x_1, x_2, \ldots, x_n) \right), \quad i = 1, 2, \ldots, n \]

Populations with non-overlapping generations

\[ x_i(t + 1) = e^{r_i - f_i(x_1(t), x_2(t), \ldots, x_n(t))} x_i(t), \quad i = 1, 2, \ldots, n \]

- \( f_i \) linear functions – Lotka-Volterra systems
- \( f_i \) general functions – Kolmogorov systems

\[ f(0, 0, \ldots, 0) = 0 \]
“Fundamental equations”

Populations with overlapping generations

\[ x'_i = x_i \left( r_i - f_i(x_1, x_2, \ldots, x_n) \right), \quad i = 1, 2, \ldots, n \]

Populations with non-overlapping generations

\[ x_i(t + 1) = e^{r_i - f_i(x_1(t), x_2(t), \ldots, x_n(t))} x_i(t), \quad i = 1, 2, \ldots, n \]

Lotka-Volterra systems

\[ f_i(x_1, x_2, \ldots, x_n) = \sum_{j=1}^{n} a_{ij}x_j = Ax \]
“Fundamental equations”

Populations with overlapping generations

\[ x'_i = x_i (r_i - f_i(x_1, x_2, \ldots, x_n)), \quad i = 1, 2, \ldots, n \]

Populations with non-overlapping generations

\[ x_i(t + 1) = e^{r_i - f_i(x_1(t), x_2(t), \ldots, x_n(t))} x_i(t), \quad i = 1, 2, \ldots, n \]

Lotka-Volterra systems

\[ f_i(x_1, x_2, \ldots, x_n) = \sum_{j=1}^{n} a_{ij} x_j = A \mathbf{x} \]

\[ A = (a_{ij}) \ - \ community \ matrix \]
Models with discrete time

- One population
- Two populations – Lotka-Volterra system

Models with continuous time

Introduction

General theory of population dynamics
One population

\[ x(t + 1) = e^{rt} x(t), \quad x(0) = x_0 \quad \Rightarrow \quad x(t) = x_0 e^{rt} \]
One population

\[ x(t + 1) = e^r x(t), \quad x(0) = x_0 \quad \Rightarrow \quad x(t) = x_0 e^{rt} \]

\[ x(t + 1) = e^{p(x(t))} x(t), \quad x(0) = x_0 \]

\( p \) decreasing – intra-specific competition
\( p \) increasing – Allee effect
One population

\[ x(t + 1) = e^{rt}x(t), \quad x(0) = x_0 \quad \Rightarrow \quad x(t) = x_0 e^{rt} \]

\[ x(t + 1) = e^{p(x(t))}x(t), \quad x(0) = x_0 \]

\( p \) decreasing – intra-specific competition

\( p \) increasing – Allee effect

\[ p(x) = r \left(1 - \frac{x}{K}\right) \quad \text{– logistic equation} \]

\[ x > K \quad \Rightarrow \quad e^{p(x)} > 1, \quad x < K \quad \Rightarrow \quad e^{p(x)} < 1 \]

\( K \) – carrying capacity
One population

\[ x(t + 1) = e^{rx(t)}, \quad x(0) = x_0 \quad \Rightarrow \quad x(t) = x_0 e^{rt} \]

\[ x(t + 1) = e^{p(x(t))} x(t), \quad x(0) = x_0 \]

\( p \) decreasing – intra-specific competition

\( p \) increasing – Allee effect

\[ p(x) = r \left( 1 - \frac{x}{K} \right) \] – logistic equation

\[ x > K \Rightarrow e^{p(x)} > 1, \quad x < K \Rightarrow e^{p(x)} < 1 \]

\( K \) – carrying capacity

\[ e^{p(x)} = \frac{q}{(1 + (q - 1)x/K)^b} \] – basic equation
Two populations – Lotka-Volterra system

\[
\begin{align*}
x(t + 1) &= x(t)e^{r_1 - a_{11}x(t) - a_{12}y(t)} \\
y(t + 1) &= y(t)e^{r_2 - a_{21}x(t) - a_{22}y(t)}
\end{align*}
\]
Two populations – Lotka-Volterra system

\[
\begin{align*}
    x(t + 1) &= x(t) e^{r_1 - a_{11} x(t) - a_{12} y(t)} \\
    y(t + 1) &= y(t) e^{r_2 - a_{21} x(t) - a_{22} y(t)}
\end{align*}
\]

- \( a_{ii} > 0 \) – intra-specific competition
- \( a_{ii} < 0 \) – Allee effect
- \( a_{ij} > 0 \) – inter-specific competition
- \( a_{ij} < 0 \) – mutualism
- \( a_{ij} a_{ji} < 0 \) – predation
Models with continuous time

Models with continuous time

One population
Two populations – Lotka-Volterra system
Gause-type predator-prey system
One population

\[ x' = rx, \quad x(0) = x_0 \quad \Rightarrow \quad x(t) = x_0 e^{rt} \]
One population

$x' = rx, \ x(0) = x_0 \Rightarrow x(t) = x_0 e^{rt}$

$x' = xp(x), \ x(0) = x_0$

$p$ decreasing – intra-specific competition
$p$ increasing – Allee effect
One population

\[ x' = rx, \quad x(0) = x_0 \quad \Rightarrow x(t) = x_0 e^{rt} \]

\[ x' = xp(x), \quad x(0) = x_0 \]

- \( p \) decreasing – intra-specific competition
- \( p \) increasing – Allee effect

\[ p(x) = r \left( 1 - \frac{x}{K} \right) \] – logistic equation
One population

$x' = rx, \ x(0) = x_0 \ \Rightarrow \ x(t) = x_0e^{rt}$

$x' = xp(x), \ x(0) = x_0$

$p$ decreasing – intra-specific competition
$p$ increasing – Allee effect

$p(x) = r \left(1 - \frac{x}{K}\right)$ – logistic equation

$p(x) = rx^{a-1} \left(1 - \left(\frac{x}{K}\right)^b\right)$ – generalized logistic equation
Two populations – Lotka-Volterra system

\[ x' = x(r_1 - a_{11}x - a_{12}y) \]
\[ y' = y(r_2 - a_{21}x - a_{22}y) \]
Two populations – Lotka-Volterra system

\[ x' = x(r_1 - a_{11}x - a_{12}y) \]
\[ y' = y(r_2 - a_{21}x - a_{22}y) \]

- \( a_{ii} > 0 \) – intra-specific competition
- \( a_{ii} < 0 \) – Allee effect
- \( a_{ij} > 0 \) – inter-specific competition
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Gause-type predator-prey system
Gause-type predator-prey system

\[
x' = xp(x), \\
y' = -dy
\]

- \(x\) – size of prey population
- \(y\) – size of predator population
- \(p(x)\) – prey growth rate
- \(d\) – predator death rate
Gause-type predator-prey system

\[ x' = xp(x) - S\varphi(x)y, \]
\[ y' = -dy \]

- \( x \) – size of prey population
- \( y \) – size of predator population
- \( p(x) \) – prey growth rate
- \( d \) – predator death rate
- \( \varphi(x) \) – trophic function; increasing, \( \varphi(0) = 0, \lim_{x \to \infty} \varphi(x) = 1 \)
- \( S \) – predator level of satiety

**Holling I**
\[
\varphi(x) = \begin{cases} 
0 & \text{if } x < a \\
1 & \text{if } x \geq 2a
\end{cases}
\]

**Holling II**
\[
\varphi(x) = \frac{x}{b} \quad \text{for } 0 \leq x \leq b
\]

**Holling III**
\[
\varphi(x) = \frac{x}{b + 2a} \quad \text{for } 0 \leq x \leq b + 2a
\]
Gause-type predator-prey system

\[
\begin{align*}
  x' &= xp(x) - S\varphi(x)y, \\
  y' &= -dy + \kappa S\varphi(x)y \\
\end{align*}
\]

- $x$ – size of prey population
- $y$ – size of predator population
- $p(x)$ – prey growth rate
- $d$ – predator death rate
- $\varphi(x)$ – trophic function; increasing, $\varphi(0) = 0$, $\lim_{x \to \infty} \varphi(x) = 1$
- $S$ – predator level of satiety
- $\kappa$ – efficiency of conversion: prey into predator growth rate
Gause-type predator-prey system

\[ \begin{align*}
x' &= x \left( p(x) - \frac{S \varphi(x)}{x} y \right), \\
y' &= y \left( -d + \kappa S \varphi(x) \right)
\end{align*} \]
Gause-type predator-prey system

\[ x' = x \left( p(x) - S \frac{\varphi(x)}{x} y \right), \]
\[ y' = y \left( -d + \kappa S \varphi(x) \right) \]

\[ \varphi(x) = \begin{cases} 
\frac{x}{2a}, & x < 2a \\
1, & x \geq 2a 
\end{cases} \]
Gause-type predator-prey system

\[
x' = x \left( p(x) - S \frac{\varphi(x)}{x} y \right),
\]
\[
y' = y \left( -d + \kappa S \varphi(x) \right)
\]

\[
\varphi(x) = \begin{cases} 
\frac{x}{2a}, & x < 2a \\
1, & x \geq 2a 
\end{cases}
\]

\[
\varphi(x) = \frac{x^k}{x^k + a^k}
\]

\[
\varphi(x) = 1 - 2^{-\left(\frac{x}{a}\right)^k}
\]
Gause-type predator-prey system

\[
x' = x \left( p(x) - S \frac{\varphi(x)}{x} y \right),
\]
\[
y' = y \left( -d + \kappa S \varphi(x) \right)
\]

\[
\varphi(x) = \begin{cases} 
  x/(2a), & x < 2a \\
  1, & x \geq 2a 
\end{cases} \quad \text{– Holling I}
\]

\[
\varphi(x) = \frac{x^k}{x^k + a^k} \quad \text{– Michaelis-Menten}
\]

\[
\varphi(x) = 1 - 2^{-(x/a)^k} \quad \text{– Ivlev}
\]

\(a\) – level of “half saturation”