

# Package ‘gauseR’

July 22, 2025

**Title** Lotka-Volterra Models for Gause's 'Struggle for Existence'

**Version** 1.3

**Description** A collection of tools and data for analyzing the Gause microcosm experiments, and for fitting Lotka-Volterra models to time series data. Includes methods for fitting single-species logistic growth, and multi-species interaction models, e.g. of competition, predator/prey relationships, or mutualism. See documentation for individual functions for examples. In general, see the `lv_optim()` function for examples of how to fit parameter values in multi-species systems. Note that the general methods applied here, as well as the form of the differential equations that we use, are described in detail in the Quantitative Ecology textbook by Lehman et al., available at <http://hdl.handle.net/11299/204551>, and in Lina K. Mühlbauer, Maximilienne Schulze, W. Stanley Harpole, and Adam T. Clark. 'gauseR': Simple methods for fitting Lotka-Volterra models describing Gause's 'Struggle for Existence' in the journal Ecology and Evolution.

**Imports** deSolve, stats, graphics

**Suggests** knitr, rmarkdown

**VignetteBuilder** knitr

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**Author** Adam Clark [aut, cre] (ORCID: <https://orcid.org/0000-0002-8843-3278>),  
Lina Mühlbauer [aut],  
Maximilienne Schulze [aut]

**Maintainer** Adam Clark <adam.tclark@gmail.com>

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gause_1931_AmN_f01	<i>Growth of population of the flour beetle Tribolium confusum in 16 and 64 grams of flour</i>
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Description

A dataset containing the abundance of Tribolium confusum, grown in monoculture with different quantities of food (flour). Gause’s goal was to determine the influence of ecological factors on population growth.

Usage

gause\_1931\_AmN\_f01

Format

A data frame with 18 rows and 6 variables:

- Paper

Paper from which data are drawn
- Figure

Figure number in paper
- Species

Name of Species: Tribolium confusum
- Time

Day of experiment
- Individuals

Number of Individuals
- Treatment

Treatments:16 and 64g flour per starting beetle pair

Source

Gause (1931) The influence of ecological factors on the size of population. The American Naturalist 65:696, 70-76

---

gause_1931_AmN_f02	<i>The influence of quantity of food on the asymptotic population of Tribolium confusum.</i>
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### Description

A dataset containing the population size of *Tribolium confusum* at the upper asymptote, as a characteristic for the population being in equilibrium, under different quantities of food (flour). Gause's goal was to determine the influence of ecological factors on population growth.

### Usage

gause\_1931\_AmN\_f02

### Format

A data frame with 4 rows and 5 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Tribolium confusum*

**Individuals** Number of Individuals at population equilibrium

**Treatment** Treatments: 16, 32, 64 and 128g flour per starting beetle pair

### Source

Gause (1931) The influence of ecological factors on the size of population. *The American Naturalist* 65:696, 70-76

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gause_1931_AmN_f03	<i>The influence of temperature on the asymptotic population of Moina macrocopa.</i>
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### Description

A dataset containing the population size of *Moina macrocopa* at the upper asymptote, as a characteristic for the population being in equilibrium, under different temperatures. Gause's goal was to determine the influence of ecological factors on population growth.

### Usage

gause\_1931\_AmN\_f03

**Format**

A data frame with 3 rows and 5 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Tribolium confusum*

**Individuals** Number of Individuals at population equilibrium

**Treatment** Treatments: 20, 25 and 35 degrees Celcius

**Source**

Gause (1931) The influence of ecological factors on the size of population. The American Naturalist 65:696, 70-76

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gause_1932_QR_t05	<i>The influence of temperature on the growth of the yeast Saccharomyces cerevisiae</i>
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**Description**

A dataset containing the abundance of *Saccharomyces cerevisiae*, grown in different temperatures (5.7 to 41 degrees C). The Volume is measured in "Amount of yeast", which refers to a standardized index, based on the alcohol production per Unit of Yeast.

**Usage**

gause\_1932\_QR\_t05

**Format**

A data frame with 102 rows and 7 variables:

**Paper** Paper from which data are drawn

**Table** Table number in paper

**Experiment** Number of series: 1, 2 or 3

**Species** Name of Species: *Saccharomyces cerevisiae*

**Time** Hour of experiment

**Volume** "Amount of Yeast" of Species

**Treatment** Treatments: Temperatures (5.7 to 41 degrees C)

**Source**

Gause (1932) Ecology of Populations. The Quarterly Review of Biology 7, vol. 1, pp. 27-46

---

gause\_1934\_book\_app\_t01

*Raw data on the abundances and volumes of Saccharomyces cerevisiae and Schizosaccharomyces kephir*

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## Description

A dataset containing the abundances (number of cells) and volumes of *Saccharomyces cerevisiae* and *Schizosaccharomyces kephir* grown in monoculture and in mixture. The data for two experiments with different time periods is reported.

## Usage

```
gause_1934_book_app_t01
```

## Format

A data frame with 60 rows and 10 variables:

**Paper** Paper from which data are drawn

**Table** Table number in paper

**Experiment** Number of experiment: 1 or 2

**Species** Name of Species: *Saccharomyces cerevisiae* and *Schizosaccharomyces kephir*

**Time** Day of experiment

**Volume\_Species** Volume of yeast species in the mixture, estimated from counted cells

**Squares** Number of Squares counted

**Individuals\_Square** Average Number of cells per Square

**Volume\_Total** Total volume of yeast

**Treatment** Treatments: Monoculture and Mixture

## Source

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

---

gause\_1934\_book\_app\_t02*Alcohol production of Saccharomyces cerevisiae and Schizosaccharomyces kephir*

---

**Description**

A dataset containing the alcohol production of *Saccharomyces cerevisiae* and *Schizosaccharomyces kephir* cultivated under anaerobic and aerobic conditions, in percent and per unit of yeast volume.

**Usage**

gause\_1934\_book\_app\_t02

**Format**

A data frame with 28 rows and 7 variables:

**Paper** Paper from which data are drawn

**Table** Table number in paper

**Species** Name of Species: *Saccharomyces cerevisiae*, *Schizosaccharomyces kephir*

**Time** Hour of experiment

**Alcohol** Alcohol production in percent

**Alcohol.Yeast\_Volume** Alcohol production per unit of yeast volume

**Treatment** Treatments: Anaerobic and Aerobic

**Source**

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

---

gause\_1934\_book\_app\_t03*Raw data of Paramecium caudatum and Paramecium aurelia grown in Monoculture and Mixture*

---

**Description**

A dataset containing the mean abundances of *Paramecium caudatum* and *Paramecium aurelia*, grown in mixture and monoculture. This dataset contains the mean abundances of three experiments. Note, that for day 20, single values are missing and only the mean is reported.

**Usage**

gause\_1934\_book\_app\_t03

**Format**

A data frame with 104 rows and 6 variables:

**Paper** Paper from which data are drawn

**Table** Table number in paper

**Species** Name of Species: Paramecium caudatum and Paramecium aurelia

**Time** Day of experiment

**Individuals** Number of Individuals

**Treatment** Treatments: Monoculture and Mixture

**Source**

Gause (1934) The Struggle for Existence. Dover Publications; Reprint edition.

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gause\_1934\_book\_app\_t04

*Raw data of Paramecium caudatum and Paramecium aurelia grown on different media*

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**Description**

A dataset containing the abundance of Paramecium caudatum and Paramecium aurelia, grown in monoculture and in mixture on buffered medium with high wild bacteria concentration ("one loop" medium) and low wild bacteria concentration ("half loop" medium). The number of individuals is reported for monoculture and the number of individuals of the species in the mixture.

**Usage**

gause\_1934\_book\_app\_t04

**Format**

A data frame with 68 rows and 7 variables:

**Paper** Paper from which data are drawn

**Table** Table number in paper

**Species** Name of Species: Paramecium caudatum and Paramecium aurelia

**Time** Day of experiment

**Individuals** Number of Individuals

**Individuals\_Mixture** Number of Individuals per Species in Mixture

**Treatment** Treatments: One Loop and Half Loop

**Source**

Gause (1934) The Struggle for Existence. Dover Publications; Reprint edition.

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gause\_1934\_book\_app\_t05*Raw data of Stylonychia pustulata in monoculture and mixture with  
and Paramecium aurelia and P. caudatum*

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**Description**

A dataset containing the abundances of Stylonychia pustulata grown in monoculture and mixture with P. aurelia and P. caudatum and the abundances of P. aurelia and P. caudatum in this mixtures on the medium of Osterhout. This dataset contains the raw data of three different experiments: Stylonychia pustulata grown in monoculture, in mixture with P.aurelia and in mixture wit P.caudatum. The abundances of three to five cultures per experiment and the calculated mean abundances of the experiments are reported. Note, that for day 20 - 25, single values are missing and only the mean is reported.

**Usage**

gause\_1934\_book\_app\_t05

**Format**

A data frame with 575 rows and 8 variables:

**Paper** Paper from which data are drawn

**Table** Table number in paper

**Time** Day of experiment

**Experiment** Number of experiment: 1,2 or 3

**Culture** Number of culture: 1,2,3,4,5 or Mean

**Species** Name of Species: Stylonychia pustulata, Paramecium caudatum and Paramecium aurelia

**Individuals** Number of Individuals

**Treatment** Treatments: Monoculture and Mixture P.aurelia and Mixture P.caudatum

**Source**

Gause (1934) The Struggle for Existence. Dover Publications; Reprint edition.

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gause_1934_book_f04	<i>Growth of Paramecium caudatum</i>
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**Description**

A dataset containing the growth in abundance of *Paramecium caudatum* over six days.

**Usage**

gause\_1934\_book\_f04

**Format**

A data frame with 8 rows and 5 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Paramecium caudatum*

**Time** Day of experiment

**Individuals** Number of Individuals

**Source**

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

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gause_1934_book_f09	<i>Growth of Saccharomyces cerevisiae</i>
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**Description**

A dataset containing the growth in volume of *Saccharomyces cerevisiae* under anaerobic conditions. The Volume is measured in "Amount of yeast", which refers to a standardized index, based on the alcohol production per Unit of Yeast.

**Usage**

gause\_1934\_book\_f09

**Format**

A data frame with 9 rows and 5 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Saccharomyces cerevisiae*

**Time** Hour of experiment

**Volume** "Amount of Yeast" of Species

**Source**

Gause (1934) The Struggle for Existence. Dover Publications; Reprint edition.

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gause_1934_book_f10	<i>Growth of Saccharomyces cerevisiae with medium change</i>
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**Description**

A dataset containing the abundance of *Saccharomyces cerevisiae* cultivated in monoculture with a medium change in different time periods under anaerobic conditions. The Number of Individuals is measured in Number of cells per 1/250 mm<sup>3</sup>.

**Usage**

gause\_1934\_book\_f10

**Format**

A data frame with 29 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Saccharomyces cerevisiae*

**Time** Hour of experiment

**Individuals** Number of cells per 1/250 mm<sup>3</sup>

**Treatment** Treatments: medium change every 3, 12, 24 hours and control

**Source**

Gause (1934) The Struggle for Existence. Dover Publications; Reprint edition.

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gause_1934_book_f11	<i>Gause Yeast Data</i>
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**Description**

A dataset containing yeast volume and alcohol concentration for two replicates of *S. cerevisiae* grown in monoculture.

**Usage**

gause\_1934\_book\_f11

**Format**

A data frame with 11 rows and 7 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Species name

**Time** Experiment time in hours

**Alcohol\_Percent** Alcohol concentration, in percent

**Yeast\_Volume** Yeast volume, listed in papers as 'amount'

**Treatment** Experiment replicate, under two 'somewhat different' growth medium concentrations

**Source**

Huffaker (1958) Experimental Studies on Predation: Dispersion Factors and Predator-Prey Oscillations. *Hilgardia* 27: 343-83.

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gause_1934_book_f12	<i>Growth of <i>Saccharomyces cerevisiae</i> with additional alcohol</i>
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**Description**

A dataset containing the growth in volume of *Saccharomyces cerevisiae* cultivated under anaerobic conditions with added alcohol. Gause measured the effect of alcohol on reaching a saturated population. The saturation is measured in percent of the saturated population grown without additional alcohol.

**Usage**

gause\_1934\_book\_f12

**Format**

A data frame with 6 rows and 5 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Saccharomyces cerevisiae*

**Alcohol** Additional alcohol in percent

**Population** Percentage of saturated population reached

**Source**

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

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gause_1934_book_f13	<i>Growth of Saccharomyces cerevisiae and Schizosaccharomyces kephir in mixed population</i>
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**Description**

A dataset containing the the growth in volume of *Saccharomyces cerevisiae* and *Schizosaccharomyces kephir* cultivated in the mixed population (two series of experiments) under anaerobic conditions. Gause also measured the volume of the mixed population. The Volume is measured in "Amount of yeast", which refers to a standardized index, based on the alcohol production per Unit of Yeast.

**Usage**

gause\_1934\_book\_f13

**Format**

A data frame with 47 rows and 5 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Saccharomyces cerevisiae*, *Schizosaccharomyces kephi* and Mixed Population

**Time** Hour of experiment

**Volume** "Amount of Yeast" of Species

**Source**

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

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gause_1934_book_f14	<i>Growth of Saccharomyces cerevisiae in mixed population</i>
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**Description**

A dataset containing the the growth in volume of *Saccharomyces cerevisiae* cultivated separately and in the mixed population (two series of experiments) with *Schizosaccharomyces kephir* under anaerobic conditions. The Volume is measured in "Amount of yeast", which refers to a standardized index, based on the alcohol production per Unit of Yeast.

**Usage**

gause\_1934\_book\_f14

**Format**

A data frame with 32 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Saccharomyces cerevisiae*

**Time** Hour of experiment

**Volume** "Amount of Yeast" of Species

**Treatment** Treatments: Monoculture and Mixture

**Source**

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

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gause\_1934\_book\_f15      *Growth of Schizosaccaromyces kephir in mixed population - anaerobic*

---

**Description**

A dataset containing the the growth in volume of *Schizosaccaromyces kephir* cultivated separately and in the mixed population (two series of experiments) with *Saccharomyces cerevisiae* under anaerobic conditions. The Volume is measured in "Amount of yeast", which refers to a standardized index, based on the alcohol production per Unit of Yeast.

**Usage**

gause\_1934\_book\_f15

**Format**

A data frame with 24 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Schizosaccaromyces kephir*

**Time** Hour of experiment

**Volume** "Amount of Yeast" of Species

**Treatment** Treatments: Monoculture and Mixture

**Source**

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

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gause_1934_book_f16	<i>Growth of Schizosaccaromyces kephir and Saccharomyces cerevisiae in mixed population -aerobic</i>
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**Description**

A dataset containing the the growth in volume of Schizosaccaromyces kephir cultivated separately and in the mixed population with Saccharomyces cerevisiae under aerobic conditions. The Volume is measured in "Amount of yeast", which refers to a standardized index, based on the alcohol production per Unit of Yeast.

**Usage**

gause\_1934\_book\_f16

**Format**

A data frame with 27 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: Schizosaccaromyces kephir, Saccharomyces cerevisiae and Total\_Yeast

**Time** Hour of experiment

**Volume** "Amount of Yeast" of Species

**Treatment** Treatments: Monoculture and Mixture

**Source**

Gause (1934) The Struggle for Existence. Dover Publications; Reprint edition.

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gause_1934_book_f18	<i>Growth of Paramecium caudatum and Stylonychia mytilis in Mixture</i>
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**Description**

A dataset containing the abundance of Paramecium caudatum and Stylonychia mytilis, grown in monoculture and in mixture on buffered medium without wild bacteria.

**Usage**

gause\_1934\_book\_f18

**Format**

A data frame with 28 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Paramecium caudatum* and *Stylonychia mytilis*

**Time** Day of experiment

**Individuals** Number of Individuals

**Treatment** Treatments: Monoculture and Mixture

**Source**

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

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gause_1934_book_f19	<i>Growth of Paramecium caudatum and Stylonychia mytilis in Mixture with Wild bacteria</i>
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**Description**

A dataset containing the abundance of *Paramecium caudatum* and *Stylonychia mytilis*, grown in monoculture and in mixture on buffered medium containing wild bacteria.

**Usage**

gause\_1934\_book\_f19

**Format**

A data frame with 17 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Paramecium caudatum* and *Stylonychia mytilis*

**Time** Day of experiment

**Individuals** Number of Individuals

**Treatment** Treatments: Monoculture and Mixture

**Source**

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

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gause_1934_book_f21	<i>Growth of Paramecium caudatum and Paramecium aurelia in Mono-culture</i>
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**Description**

A dataset containing the abundances and the volume of *Paramecium caudatum* and *Paramecium aurelia*, to determine the differences in reaching the saturating population regarding Volume and Number of individuals. "Volume" refers to a standardized index, meant to make the abundances of species comparable based on their relative sizes.

**Usage**

gause\_1934\_book\_f21

**Format**

A data frame with 87 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Paramecium caudatum* and *Paramecium aurelia*

**Time** Day of experiment

**Volume** "Volume" of Species

**Individuals** Number of Individuals

**Source**

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

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gause_1934_book_f22	<i>Paramecium competition experiment</i>
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**Description**

A dataset containing the abundances of two *Paramecium* species grown in monoculture and mixture. Note, is for the same experiment as gause\_1934\_science\_f02\_03, except that data were digitized separately, and therefore have small variations. These might be useful for estimating observation error in the data digitization process. "Volume" refers to a standardized index, meant to make the abundances of species comparable based on their relative sizes.

**Usage**

gause\_1934\_book\_f22

**Format**

A data frame with 72 rows and 4 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Day** Day of experiment

**Species1** Name of Species 1

**Volume\_Species1** Volume of *Paramecium caudatum*

**Species2** Name of Species 2

**Volume\_Species2** Volume of *Paramecium aurelia*

**Treatment** Treatments: Pa and Pc monocultures, or mixture

**Source**

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

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gause_1934_book_f23	<i>Growth of Paramecium caudatum and Paramecium aurelia with wild bacteria</i>
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**Description**

A dataset containing the volume of *Paramecium caudatum* and *Paramecium aurelia*, grown in monoculture on buffered medium with two different wild bacteria concentrations ("one" and "half loop"). "Volume" refers to a standardized index, meant to make the abundances of species comparable based on their relative sizes.

**Usage**

gause\_1934\_book\_f23

**Format**

A data frame with 61 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Paramecium caudatum* and *Paramecium aurelia*

**Time** Day of experiment

**Volume** "Volume" of Species

**Treatment** Treatments: One Loop and Half Loop

**Source**

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

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gause_1934_book_f24	<i>Growth of Paramecium caudatum and Paramecium aurelia in Mixture on Half Loop Medium</i>
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**Description**

A dataset containing the volume of *Paramecium caudatum* and *Paramecium aurelia*, grown in monoculture and in mixture on buffered medium with low wild bacteria concentration ("half loop" medium). "Volume" refers to a standardized index, meant to make the abundances of species comparable based on their relative sizes.

**Usage**

gause\_1934\_book\_f24

**Format**

A data frame with 56 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: *Paramecium caudatum* and *Paramecium aurelia*

**Time** Day of experiment

**Volume** "Volume" of Species

**Treatment** Treatments: Monoculture and Mixture

**Source**

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

---

gause_1934_book_f25	<i>Growth of Paramecium caudatum and Paramecium aurelia in Mixture on One Loop Medium</i>
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**Description**

A dataset containing the volume of *Paramecium caudatum* and *Paramecium aurelia*, grown in monoculture and in mixture on buffered medium with high wild bacteria concentration ("one loop" medium). "Volume" refers to a standardized index, meant to make the abundances of species comparable based on their relative sizes.

**Usage**

gause\_1934\_book\_f25

**Format**

A data frame with 57 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: Paramecium caudatum and Paramecium aurelia

**Time** Day of experiment

**Volume** "Volume" of Species

**Treatment** Treatments: Monoculture and Mixture

**Source**

Gause (1934) The Struggle for Existence. Dover Publications; Reprint edition.

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gause_1934_book_f26	<i>Growth of Stylorzychia pustulata in Monoculture and in Mixture</i>
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**Description**

A dataset containing the abundances of Stylorzychia pustulata cultivated separately, and in the mixed populations with Paramecium caudatum and Paramecium aurelia and the abundances of P. caudatum and P. aurelia grown in mixture with S. pustulata.

**Usage**

gause\_1934\_book\_f26

**Format**

A data frame with 104 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: Paramecium caudatum, Paramecium aurelia and Stylorzychia pustulata

**Time** Day of experiment

**Individuals** Number of Individuals

**Treatment** Treatments: Monoculture and Mixture(with Species)

**Source**

Gause (1934) The Struggle for Existence. Dover Publications; Reprint edition.

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gause_1934_book_f28	<i>Elementary interaction between Didinium nasutum and Paramecium caudatum</i>
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**Description**

A dataset containing the abundances of Paramecium caudatum and Didinium nasutum grown in mixture. Didinium was introduced at day two. "Individuals" refers to the number of individuals per 0.5 c.c..

**Usage**

gause\_1934\_book\_f28

**Format**

A data frame with 12 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: Paramecium caudatum and Didinium nasutum

**Time** Day of experiment

**Individuals** Number of Individuals

**Treatment** Treatments: Monoculture and Mixture

**Source**

Gause (1934) The Struggle for Existence. Dover Publications; Reprint edition.

---

gause_1934_book_f29	<i>Paramecium/Didinium predator-prey experiment</i>
---------------------	---

---

**Description**

A dataset containing the abundances of Paramecium caudatum and Didinium nasutum grown in mixture. Didinium was introduced at different days. "Volume" refers to a standardized index, meant to make the abundances of species comparable based on their relative sizes.

**Usage**

gause\_1934\_book\_f29

**Format**

A data frame with 62 rows and 7 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Name of Species: Didinium nasutum and Paramecium caudatum

**Time** Day of experiment

**Volume** Volume of Didinium

**Individuals** Number of Individuals

**Treatment** Treatments: D. nasutum introduced after 0, 24, 36 and 48 hrs

**Source**

Gause (1934) The Struggle for Existence. Dover Publications; Reprint edition.

---

gause_1934_book_f30	<i>The elementary interaction between Didinium nasutum and Paramecium caudatum</i>
---------------------	--

---

**Description**

A dataset containing the abundances of Didinium nasutum and Paramecium caudatum grown in mixture on the medium of Osterhout.

**Usage**

gause\_1934\_book\_f30

**Format**

A data frame with 16 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Time** Day of experiment

**Species** Name of Species: Didinium nasutum and Paramecium caudatum

**Individuals** Number of Individuals

**Treatment** Treatment: Osterhout medium

**Source**

Gause (1934) The Struggle for Existence. Dover Publications; Reprint edition.

---

gause_1934_book_f31	<i>The interaction between Didinium nasutum and Paramecium caudatum on oat medium</i>
---------------------	---

---

**Description**

A dataset containing the abundances of *Didinium nasutum* and *Paramecium caudatum* grown in mixture on oat medium with sediment.

**Usage**

gause\_1934\_book\_f31

**Format**

A data frame with 12 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Time** Day of experiment

**Species** Name of Species: *Didinium nasutum* and *Paramecium caudatum*

**Individuals** Number of Individuals

**Treatment** Treatment: Oat medium

**Source**

Gause (1934) *The Struggle for Existence*. Dover Publications; Reprint edition.

---

gause_1934_book_f32	<i>Didinium/Paramecium predator/prey experiment</i>
---------------------	---

---

**Description**

A dataset containing the abundances of *Paramecium caudatum* and *Didinium nasutum* grown in mixture. Note, is for the same experiment as gause\_1934\_science\_f01, except that data were digitized separately, and therefore have small variations. These might be useful for estimating observation error in the data digitization process.

**Usage**

gause\_1934\_book\_f32

**Format**

A data frame with 17 rows and 8 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Day** Day of experiment

**Prey** Name of Prey Species

**Individuals\_Prey** Number of Prey Individuals

**Predator** Name of Predator Species

**Individuals\_Predator** Number of Predator Individuals

**Immigration** Is immigration occurring in this time-step? (yes or no)

**Source**

Gause (1934) The Struggle for Existence. Dover Publications; Reprint edition.

---

gause\_1934\_book\_f39.1 *The interaction between Paramecium bursaria and Schizosaccharomyces pombe*

---

**Description**

A dataset containing the abundances of *Paramecium bursaria* and *Schizosaccharomyces pombe* grown in mixture.

**Usage**

```
gause_1934_book_f39.1
```

**Format**

A data frame with 36 rows and 5 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Time** Day of experiment

**Species** Name of Species: *Paramecium bursaria* and *Schizosaccharomyces pombe*

**Individuals** Number of Individuals

**Source**

Gause (1934) The Struggle for Existence. Dover Publications; Reprint edition.

---

gause\_1934\_science\_f01

*Didinium/Paramecium predator/prey experiment*


---

### Description

A dataset containing the abundances of *Paramecium caudatum* and *Didinium nasutum* grown in mixture. Note, is for the same experiment as gause\_1934\_book\_f32, except that data were digitized separately, and therefore have small variations. These might be useful for estimating observation error in the data digitization process.

### Usage

gause\_1934\_science\_f01

### Format

A data frame with 17 rows and 3 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Day** Day of experiment

**Prey** Name of Prey Species

**Individuals\_Prey** Number of Prey Individuals

**Predator** Name of Predator Species

**Individuals\_Predator** Number of Predator Individuals

**Immigration** Is immigration occurring in this time-step? (yes or no)

### Source

Gause (1934) Experimental Analysis of Vito Volterra's Mathematical Theory of the Struggle for Existence. Science 79:16-17.

---

gause\_1934\_science\_f02\_03

*Paramecium competition experiment*


---

### Description

A dataset containing the abundances of two *Paramecium* species grown in monoculture and mixture. Note, is for the same experiment as gause\_book\_1934\_f22, except that data were digitized separately, and therefore have small variations. These might be useful for estimating observation error in the data digitization process. "Volume" refers to a standardized index, meant to make the abundances of species comparable based on their relative sizes.

**Usage**

gause\_1934\_science\_f02\_03

**Format**

A data frame with 63 rows and 4 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Day** Day of experiment

**Species1** Name of Species 1

**Volume\_Species1** Volume of *Paramecium caudatum*

**Species2** Name of Species 2

**Volume\_Species2** Volume of *Paramecium aurelia*

**Treatment** Treatments: Pa and Pc monocultures, or mixture

**Source**

Gause (1934) Experimental Analysis of Vito Volterra's Mathematical Theory of the Struggle for Existence. *Science* 79:16-17.

---

gause_1936_AnE_f01	<i>Interaction between predators (Cheyletus eruditus) and prey (Aleuiroglyphus agilis) on millet, wheat flour and a mixture of these substances.</i>
--------------------	--

---

**Description**

A dataset containing the abundance of *Cheyletus eruditus* and *Aleuiroglyphus agilis*, as a predator-prey system under different food conditions for the prey (wheat and millet). Gause's goal was to determine the influence of ecological factors on predator-prey dynamics. The number of individuals is reported as Individuals per 0.2 g prey food.

**Usage**

gause\_1936\_AnE\_f01

**Format**

A data frame with 34 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Time** Day of experiment

**Species** Name of Species: *Cheyletus eruditus* and *Aleuiroglyphus agilis*

**Individuals** Number of Individuals per 0.2 g

**Treatment** Treatments: Wheat, Millet, Wheat+Millet

**Source**

Gause (1936) Further Studies of Interaction between Predators and Prey. Journal of Animal Ecology, vol. 5, pp. 1-18.

---

gause\_1936\_AnE\_f03.1    *Interaction between predators (Cheyletus eruditus) and prey (Aleuroglyphus agilis) with occasional immigration*

---

**Description**

A dataset containing the abundance of Cheyletus eruditus and Aleuiroglyphus agilis, as a predator-prey system with an occasional immigration of the prey on the 63rd day. The number of individuals is reported as Individuals per 0.2 g prey food. Wheat flour was used as food.

**Usage**

gause\_1936\_AnE\_f03.1

**Format**

A data frame with 22 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Time** Day of experiment

**Species** Name of Species: Cheyletus eruditus and Aleuiroglyphus agilis

**Individuals** Number of Individuals per 0.2 g

**Treatment** Treatments: Immigration or NA

**Source**

Gause (1936) Further Studies of Interaction between Predators and Prey. Journal of Animal Ecology, vol. 5, pp. 1-18.

---

gause\_1936\_AnE\_f03.3a *Interaction between predators (Cheyletus eruditus) and prey (Aleuroglyphus agilis) with artificial immigration*

---

### Description

A dataset containing the abundance of Cheyletus eruditus and Aleuiroglyphus agilis, as a predator-prey system with an artificial everyday immigration of predator and prey. The number of individuals is reported as Individuals per 0.2 g prey food. Wheat flour was used as food.

### Usage

gause\_1936\_AnE\_f03.3a

### Format

A data frame with 24 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Time** Day of experiment

**Species** Name of Species: Cheyletus eruditus and Aleuiroglyphus agilis

**Individuals** Number of Individuals per 0.2 g

**Treatment** Treatment: Immigration

### Source

Gause (1936) Further Studies of Interaction between Predators and Prey. Journal of Animal Ecology, vol. 5, pp. 1-18.

---

gause\_1936\_AnE\_f03.3b *Interaction between predators (Cheyletus eruditus) and prey (Aleuroglyphus agilis) with artificial immigration*

---

### Description

A dataset containing the abundance of Cheyletus eruditus and Aleuiroglyphus agilis, as a predator-prey system with an artificial immigration of predator and prey every 8th day. The number of individuals is reported as Individuals per 0.2 g prey food. Wheat flour was used as food.

### Usage

gause\_1936\_AnE\_f03.3b

**Format**

A data frame with 26 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Time** Day of experiment

**Species** Name of Species: *Cheyletus eruditus* and *Aleuiroglyphus agilis*

**Individuals** Number of Individuals per 0.2 g

**Treatment** Treatment: Immigration

**Source**

Gause (1936) Further Studies of Interaction between Predators and Prey. *Journal of Animal Ecology*, vol. 5, pp. 1-18.

---

gause_1936_AnE_t02	<i>Interaction between predators (<i>Cheyletus eruditus</i>) and prey (<i>Aleuiroglyphus agilis</i>)-Raw data</i>
--------------------	---

---

**Description**

A dataset containing the abundance of *Cheyletus eruditus* and *Aleuiroglyphus agilis*, as a predator-prey system on semoleta and wheat flour. A fraction at the beginning of each experiment shows the initial relation between predators and prey; e.g. 10/5 means 10 prey and 5 predators (reported in variable "Treatment"). Dataset includes age structured population abundances. The number of individuals is reported as Individuals per 0.2 g prey food. Wheat flour was used as food.

**Usage**

gause\_1936\_AnE\_t02

**Format**

A data frame with 191 rows and 12 variables:

**Paper** Paper from which data are drawn

**Table** Table number in paper

**Time** Day of experiment

**Species** Name of Species: *Cheyletus eruditus* and *Aleuiroglyphus agilis*

**Total\_Individuals** Number of all Individuals of Species per 0.2 g

**Female** Number of female individuals per 0.2 g

**Male** Number of male individuals per 0.2 g

**Imago** Number of adult Individuals per 0.2 g

**Hexapod** Number of hexapod larvae stage Individuals per 0.2 g

**Octapod** Number of octapod larvae stage Individuals per 0.2 g

**Initial\_Fraction** Initial Number of prey/predator

**Treatment** Treatments: Wheat and Semoleta

**Source**

Gause (1936) Further Studies of Interaction between Predators and Prey. Journal of Animal Ecology, vol. 5, pp. 1-18.

---

gause_1936_AnE_t03	<i>Interaction between predators (Paramecium bursaria) and prey (Saccharomyces exiguus)</i>
--------------------	---

---

**Description**

A dataset containing the abundance of Paramecium bursaria and Saccharomyces exiguus, as a predator-prey system. The primary difference among experimental replicates is the initial abundance of the two species. The number of individuals is reported as Individuals per 0.5 cm<sup>3</sup> for Paramecium, and as number of individuals per 0.1 cm<sup>3</sup> for Saccharomyces.

**Usage**

gause\_1936\_AnE\_t03

**Format**

A data frame with 266 rows and 6 variables:

**Paper** Paper from which data are drawn

**Table** Table number in paper

**Experiment** Experimental replicate number

**Time** Day of experiment

**Species** Name of Species: Cheyletus eruditus and Aleuiroglyphus agilis

**Individuals** Number of all Individuals of Species per 0.2 g

**Source**

Gause (1936) Further Studies of Interaction between Predators and Prey. Journal of Animal Ecology, vol. 5, pp. 1-18.

## Description

Automatically runs routine for finding starting values and optimal parameter values for a Lotka-Volterra interaction system. Using the default functions, species dynamics follow the form  $\text{dni}/\text{dt} = \text{ni} * (\text{ri} + \text{a}_{ii} * \text{ni} + \sum_j (\text{a}_{ij} * \text{nj}))$  where  $\text{ri}$  are the elements of vector  $\text{r}$ , and  $\text{a}_{ij}$  are the elements of matrix  $\text{A}$ .

## Usage

```
gause_wrapper(
  time,
  species,
  N_starting = NULL,
  r_starting = NULL,
  A_starting = NULL,
  doplot = TRUE,
  keeptimes = FALSE,
  parm_signs = NULL,
  doopt = TRUE,
  ...
)
```

## Arguments

time	Vector of time steps corresponding to observations in species data.frame.
species	A data.frame with one column per species to be fitted. Note - column names cannot include white spaces or non-standard special characters.
N_starting	Optional starting values for initial abundances.
r_starting	Optional starting values for species growth rates. If a value is set to zero, it #forces that parameter to zero in the fitting. Values of NA are ignored. Defaults to NULL (no starting values).
A_starting	Optional starting values for species interaction coefficients. If a value is set to zero, it #forces that parameter to zero in the fitting. Values of NA are ignored. Defaults to NULL (no starting values).
doplot	Logical. Should the resulting model be plotted? Defaults to TRUE.
keeptimes	Should predictions be given for the points in the "time" vector, or for a list of 100 evenly spaced time points? Defaults to FALSE.
parm_signs	Optional variable specifying signs for parameters. Defaults to NULL (automatically selected).
doopt	Should optimizer be used (if TRUE), or should the initial linearized estimates be applied (if FALSE)? Defaults to TRUE.
...	Optional additional arguments to be passed to ode and optim functions.

**Value**

A list with simulated time series (out), parameter estimates (parameter\_intervals), optimizer output (optout), and raw data used for fitting (rawdata).

**Examples**

```
#load competition data
data("gause_1934_science_f02_03")

#subset out data from species grown in mixture
mixturedat<-gause_1934_science_f02_03[gause_1934_science_f02_03$Treatment=="Mixture",]

#extract time and species data
time<-mixturedat$Day
species<-data.frame(mixturedat$Volume_Species1, mixturedat$Volume_Species2)
colnames(species)<-c("P-caudatum", "P-aurelia")

#run wrapper
gause_out<-gause_wrapper(time=time, species=species)
```

get\_lag

*Get timelag***Description**

Calculates time-lagged observations for variable x, separated by treatment.

**Usage**

```
get_lag(x, time, tau = 1, treatment = NULL, mindt = 0, maxdt = Inf)
```

**Arguments**

x	The time series from which time lagged observations are desired (e.g. population sizes)
time	The time steps corresponding to each observation
tau	Number of time steps to use between lagged components - defaults to 1
treatment	An optional vector of treatment conditions - time lags will only be computed separately within treatments - defaults to NULL (i.e. no treatments)
mindt	Minimum dt allowed between observations - defaults to 0
maxdt	Maximum dt allowed between observations - defaults to Inf

**Value**

Returns a data.frame with 7 columns: x (unlagged time series data); laggedx (lagged time series data); xmid (average of time series and lagged time series values); dt (time lag between x and laggedx); time (time for observation x); laggedtime (time for observation laggedx); treatment (treatment for observation)

**Examples**

```
data(gause_1934_science_f02_03)
lagged_data <- get_lag(x=gause_1934_science_f02_03$Volume_Species1,
  time = gause_1934_science_f02_03$Day,
  treatment = gause_1934_science_f02_03$Treatment)
```

get\_logistic

*Logistic Growth***Description**

Calculates logistic growth for population based on formula  $N_t = K * (N_0 * \exp(r * \text{time})) / (K + N_0 * (\exp(r * \text{time}) - 1))$

**Usage**

```
get_logistic(time, N0, r, K)
```

**Arguments**

time	The time steps corresponding to each observation
N0	Initial Population Size
r	Growth rate
K	Carying Capacity

**Value**

population size N for each time steps as a vector

**Examples**

```
# load Gause competition data
data(gause_1934_science_f02_03)
# extract monoculture data for P.c.
Pcmono<-gause_1934_science_f02_03[gause_1934_science_f02_03$Treatment=="Pc",]

# calculate lag and per-capita growth
lagged_data_Pc <- get_lag(x=Pcmono$Volume_Species1,
  time = Pcmono$Day)
Pcmono$dNNdt_Pc <- percap_growth(x=lagged_data_Pc$x, laggedx=lagged_data_Pc$laggedx,
  dt=lagged_data_Pc$dt)

# fit linear model to get dNNdt ~ r + s*N
mod_Pc<-lm(dNNdt_Pc~Volume_Species1, Pcmono)
rsn_pars<-coef(mod_Pc)

# transform into logistic growth parameters
logistic_pars<-c(r=unname(rsn_pars["(Intercept)"]),
```

```

K=unname(-rsn_pars["(Intercept)"]/rsn_pars["Volume_Species1"]))

#fit with nls, using linear model estimates as starting values for parameters
nls_mod<-nls(Volume_Species1~get_logistic(time = Day, N0, r, K),
            data=Pcmmono,
            start=c(N0=unname(Pcmmono$Volume_Species1[which.min(Pcmmono$Day)]),
                    r=unname(logistic_pars["r"]), K=unname(logistic_pars["K"])))
summary(nls_mod)

# plot results
plot(Volume_Species1~Day, Pcmmono, type="b", ylab="P. caudatum Volume")
timesq<-seq(0, 30, length=100)
Ntest<-get_logistic(time = timesq, N0=coef(nls_mod)["N0"], r=coef(nls_mod)["r"],
                    K=coef(nls_mod)["K"])

lines(timesq, Ntest, col="red")

```

huffaker\_1963

*Huffaker Mite Data*

## Description

A dataset containing the abundances mite species from some of the Huffaker experiments.

## Usage

```
huffaker_1963
```

## Format

A data frame with 168 rows and 6 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**Species** Species name

**Weeks** Experiment week

**Individuals** Number of individuals

**Treatment** 60 vs. 24-week experiments

## Source

Huffaker (1958) Experimental Studies on Predation: Dispersion Factors and Predator-Prey Oscillations. *Hilgardia* 27: 343-83.

---

lv_interaction	<i>Lotka-Volterra Interactions</i>
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---

**Description**

Calculates  $dn/dt$  for  $n$  species in a Lotka-Volterra system, following the form:  $dn_i/dt = n_i * (r_i + a_{ii} * n_i + \sum_j (a_{ij} * n_j))$ . Note that  $a_{ii}$  coefficients can be positive or negative, although positive coefficients risk having the system run to infinite population sizes, which will crash the function.

**Usage**

```
lv_interaction(time, n, parms)
```

**Arguments**

time	The time steps corresponding to each observation - exists to interface with ode function, but should be left blank.
n	A vector of species abundances
parms	A vector of parameters - the first $n$ elements should be the growth rates $r_1, r_2, \dots, r_n$ for all $n$ species. The remaining terms should be the elements of the interaction matrix $A$ , listed in the order $a_{11}, a_{12}, \dots, a_{1n}, a_{21}, a_{22}, \dots, a_{2n}, \dots, a_{n1}, a_{n2}, \dots, a_{nn}$ .

**Value**

vector of growth rates for each species

**Examples**

```
# load data from competition experiment
data(gause_1934_science_f02_03)

# subset data to include just mixtures
mixturedata<-gause_1934_science_f02_03[gause_1934_science_f02_03$Treatment=="Mixture",]

# get time-lagged observations for each species
Pc_lagged<-get_lag(x = mixturedata$Volume_Species1, time = mixturedata$Day)
Pa_lagged<-get_lag(x = mixturedata$Volume_Species2, time = mixturedata$Day)

# calculate per-capita growth rates
Pc_dNNdt<-percap_growth(x = Pc_lagged$x, laggedx = Pc_lagged$laggedx, dt = Pc_lagged$dt)
Pa_dNNdt<-percap_growth(x = Pa_lagged$x, laggedx = Pa_lagged$laggedx, dt = Pa_lagged$dt)

# fit linear models to dNNdt, based on average
# abundances between current and lagged time steps
Pc_mod_dat<-data.frame(Pc_dNNdt=Pc_dNNdt, Pc=Pc_lagged$laggedx, Pa=Pa_lagged$laggedx)
mod_comp_Pc<-lm(Pc_dNNdt~Pc+Pa, data=Pc_mod_dat)
```

```

Pa_mod_dat<-data.frame(Pa_dNNdt=Pa_dNNdt, Pa=Pa_lagged$laggedx, Pc=Pc_lagged$laggedx)
mod_comp_Pa<-lm(Pa_dNNdt~Pa+Pc, data=Pa_mod_dat)

# model summaries
summary(mod_comp_Pc)
summary(mod_comp_Pa)

# extract parameters
# note - linear regressions give us dynamics in the form:
# dni/nidt ~ (Intercept) + (n1_slope) * n1 + (n2_slope) n2
# and thus:
# dni/dt = n1*((Intercept) + (n1_slope) * n1 + (n2_slope) n2)

# growth rates
r1 <- unname(coef(mod_comp_Pc)["(Intercept)"])
r2 <- unname(coef(mod_comp_Pa)["(Intercept)"])

# self-limitation
a11 <- unname(coef(mod_comp_Pc)["Pc"])
a22 <- unname(coef(mod_comp_Pa)["Pa"])

# effect of Pa on Pc
a12 <- unname(coef(mod_comp_Pc)["Pa"])
# effect of Pc on Pa
a21 <- unname(coef(mod_comp_Pa)["Pc"])

# run ODE:
# make paramter vector:
parms <- c(r1, r2, a11, a12, a21, a22)
initialN <- c(1, 1)
out <- deSolve::ode(y=initialN, times=1:25, func=lv_interaction, parms=parms)
matplot(out[,1], out[, -1], type="l",
        xlab="time", ylab="N", col=c("black","red"), lty=c(1,3), lwd=2, ylim=c(0, 150))
legend("topleft", c("Pc", "Pa"), col=c(1,2), lwd=2, lty=c(1,3))

# now, plot in points from data
points(mixturedata$Day, mixturedata$Volume_Species1, col=1)
points(mixturedata$Day, mixturedata$Volume_Species2, col=2)

```

---

lv\_interaction\_log      *Lotka-Volterra Interactions in Log Space*

---

## Description

Calculates  $dn/dt$  for  $n$  species in a Lotka-Volterra system, in log space, following the form:  $d\log(n_i)/dt = (r_i + a_{ii} * n_i + \sum_j (a_{ij} * n_j))$  This form can be helpful for optimization routines where species abundances are close to zero.

## Usage

```
lv_interaction_log(time, n_log, parms)
```

**Arguments**

time	The time steps corresponding to each observation - exists to interface with ode function, but should be left blank.
n_log	A vector of species abundances, in log space
parms	A vector of parameters - the first n elements should be the growth rates r1, r2, ... rn for all n species. The remaining terms should be the elements of the interaction matrix A, listed in the order a11, a12, ... a1n, a21, a22, ... a2n, ... an1, an2, ... ann.

**Value**

vector of growth rates for each species in log space

---

lv_optim	<i>Optimizer for Lotka-Volterra Interactions</i>
----------	--

---

**Description**

Identifies optimal parameter values for a Lotka-Volterra interaction system.

**Usage**

```
lv_optim(
  pars,
  opt_data,
  parm_signs,
  standardize = TRUE,
  odefun = lv_interaction_log
)
```

**Arguments**

pars	A vector of parameter values in log space to be optimized. Must include a logged starting abundance for each species, followed by the logged absolute values of the growth rates, followed by the logged absolute value of the elements of the interaction matrix.
opt_data	Abundance data for optimization. Must include one column labeled 'time' with time steps, and a column for each species abundance.
parm_signs	A vector that provides the desired sign of each parameter (i.e. -1 or 1). If value is zero, then the term is held at zero (but should be left out of the pars vector).
standardize	A logical, defaulting to TRUE - should error be calculated based on standardized values of outputs? Allows for more equal weighting of observed variabls.
odefun	The function to use to simulate the ODE - defaults to lv_interaction_log

**Value**

squared error between model fits for given parameter values, and observations

**Examples**

```
# load data from competition experiment
data(gause_1934_book_f32)

# keep all data - no separate treatments exist for this experiment
predatorpreydata<-gause_1934_book_f32

# get time-lagged observations for each species
prey_lagged<-get_lag(x = predatorpreydata$Individuals_Prey, time = predatorpreydata$Day)
predator_lagged<-get_lag(x = predatorpreydata$Individuals_Predator, time = predatorpreydata$Day)

# calculate per-capita growth rates
prey_dNNdt<-percap_growth(x = prey_lagged$x, laggedx = prey_lagged$laggedx, dt = prey_lagged$dt)
predator_dNNdt<-percap_growth(x = predator_lagged$x,
  laggedx = predator_lagged$laggedx, dt = predator_lagged$dt)

# fit linear models to dNNdt, based on average
# abundances between current and lagged time steps
prey_mod_dat<-data.frame(prey_dNNdt=prey_dNNdt, prey=prey_lagged$laggedx,
  predator=predator_lagged$laggedx)
mod_prey<-lm(prey_dNNdt~prey+predator, data=prey_mod_dat)

predator_mod_dat<-data.frame(predator_dNNdt=predator_dNNdt,
  predator=predator_lagged$laggedx, prey=prey_lagged$laggedx)
mod_predator<-lm(predator_dNNdt~predator+prey, data=predator_mod_dat)

# model summaries
summary(mod_prey)
summary(mod_predator)

# extract parameters
# growth rates
r1 <- unname(coef(mod_prey)["(Intercept)"])
r2 <- unname(coef(mod_predator)["(Intercept)"])

# self-limitation
a11 <- unname(coef(mod_prey)["prey"])
a22 <- unname(coef(mod_predator)["predator"])

# effect of Pa on Pc
a12 <- unname(coef(mod_prey)["predator"])
# effect of Pc on Pa
a21 <- unname(coef(mod_predator)["prey"])

# run ODE:
# make parameter vector:
parms <- c(r1, r2, a11, a12, a21, a22)
initialN <- c(4, 0.1)
```

```

out <- deSolve::ode(y=initialN, times=seq(1, 17, length=100), func=lv_interaction, parms=parms)
matplot(out[,1], out[,-1], type="l",
        xlab="time", ylab="N", col=c("black","red"), lty=c(1,3), lwd=2, ylim=c(0, 60))
legend("topright", c("Pc", "Dn"), col=c(1,2), lwd=2, lty=c(1,3))

# now, plot in points from data
points(predatorpreydata$Day, predatorpreydata$Individuals_Predator , col=2)
points(predatorpreydata$Day, predatorpreydata$Individuals_Prey, col=1)

# uh-oh - This is a bad fit. This suggests that our linear model
# approximation isn't very good. Instead, we should try optimizing
# directly using the ode solver

# Re-run using an optimizer
# Data for the optimizer:
# Must have a column with time steps labeled 'time', and
# columns for each species in the community.
opt_data<-data.frame(time=predatorpreydata$Day, Prey=predatorpreydata$Individuals_Prey,
                    Predator=predatorpreydata$Individuals_Predator)

# Save the signs of the parameters -
# optimizer works in log space, so these
# must be specified separately
parm_signs<-sign(parms)

# parameter vector for optimizer -
# must be a vector with, first, the
# starting abundances in log space,
# and second, the parameter values,
# again in log space
pars<-c(log(initialN), log(abs(parms)))

# run optimizer
optout<-optim(par = pars, fn = lv_optim, hessian = TRUE,
             opt_data=opt_data, parm_signs=parm_signs)

# extract parameter vector:
parms <- exp(optout$par[-c(1:2)])*parm_signs
initialN <- exp(optout$par[1:2])

out <- deSolve::ode(y=initialN, times=seq(1, 17, length=100), func=lv_interaction, parms=parms)
matplot(out[,1], out[,-1], type="l",
        xlab="time", ylab="N", col=c("black","red"), lty=c(1,3), lwd=2, ylim=c(0, 60))
legend("topright", c("Pc", "Dn"), col=c(1,2), lwd=2, lty=c(1,3))

# now, plot in points from data
points(predatorpreydata$Day, predatorpreydata$Individuals_Predator , col=2)
points(predatorpreydata$Day, predatorpreydata$Individuals_Prey, col=1)

# get rough estimate of confidence intervals
fisher_info<-solve(-optout$hessian)
optout$par_sd<-sqrt(abs(diag(fisher_info)))

```

```

parm_signs_sp<-c(rep(1, ncol(opt_data)-1), parm_signs)
parameter_intervals<-data.frame(lower_sd=exp(optout$par-optout$par_sd)*parm_signs_sp,
                                mu=exp(optout$par)*parm_signs_sp,
                                upper_sd=exp(optout$par+optout$par_sd)*parm_signs_sp)

rownames(parameter_intervals)<-c("prey", "predator", "r1", "r2", "a11", "a12", "a21", "a22")
parameter_intervals

```

---

mclaren\_1994\_f03

*Wolf, Moose, and Fir dynamics from Isle Royale*


---

### Description

A dataset containing the abundances of wolves, moose, and fir trees from the Isle Royale study of McLaren et al.

### Usage

```
mclaren_1994_f03
```

### Format

A data frame with 140 rows and 7 variables:

**Paper** Paper from which data are drawn

**Figure** Figure number in paper

**year** Year of measurements

**Species** Species name

**width** Width of tree rings

**individuals** Number of wolf or moose individuals

**AET.mm.** AET water availability index

### Source

McLaren & Peterson (1994) Wolves, Moose, and Tree Rings on Isle Royale. *Science* 266:1555-1558.

---

ode_prediction	<i>Optimizer extension</i>
----------------	----------------------------

---

## Description

Takes in parameter values in the form returned by the `gause_wrapper` function, and calculates expected abundances for all  $n$  species, returned as a single vector. This function is potentially useful in combination with other optimizer software, e.g. as might be used for hypothesis testing.

## Usage

```
ode_prediction(pars_full, time, N)
```

## Arguments

<code>pars_full</code>	Initial Population Size
<code>time</code>	A vector of times. Must be repeated once per species.
<code>N</code>	Number of species. Can be either a number, or a vector the same length as <code>time</code> .

## Value

a stacked vector with predicted abundances for all species

## Examples

```
#load competition data
data("gause_1934_science_f02_03")

#subset out data from species grown in mixture
mixturedata<-gause_1934_science_f02_03[gause_1934_science_f02_03$Treatment=="Mixture",]

#extract time and species data
time<-mixturedata$Day
species<-data.frame(mixturedata$Volume_Species1, mixturedata$Volume_Species2)
colnames(species)<-c("P_caudatum", "P_aurelia")

#run wrapper
gause_out<-gause_wrapper(time=time, species=species)

# number of species
N<-ncol(gause_out$rawdata)-1
# parameters
pars_full<-c(gause_out$parameter_intervals$mu)
# data.frame for optimization
fittigdata<-data.frame(y=unlist(gause_out$rawdata[,-1]),
                      time=gause_out$rawdata$time,
                      N=N)
```

```

yest<-ode_prediction(pars_full, time=fittigdata$time, N=fittigdata$N)
plot(fittigdata$y, yest, xlab="observation", ylab="prediction")
abline(a=0, b=1, lty=2)

#example of how to apply function, using nls()
mod<-nls(y~ode_prediction(pars_full, time, N),
        start = list(pars_full=pars_full),
        data=fittigdata)
summary(mod)

```

---

percap_growth	<i>Per-capita growth rate</i>
---------------	-------------------------------

---

### Description

Calculates per-capita growth rate, using log ratios following the formula  $dN/Ndt = \log(N(t)/N_0)/dt$ .

### Usage

```
percap_growth(x, laggedx, dt)
```

### Arguments

x	Abundance
laggedx	Lagged abundance
dt	Time lag between observations

### Value

Per-capita growth rate

### Examples

```

data(gause_1934_science_f02_03)
lagged_data <- get_lag(x=gause_1934_science_f02_03$Volume_Species1,
                      time = gause_1934_science_f02_03$Day,
                      treatment = gause_1934_science_f02_03$Treatment)
dNNdt <- percap_growth(x=lagged_data$x, laggedx=lagged_data$laggedx,
                      dt=lagged_data$dt)

```

---

test\_goodness\_of\_fit    *Test goodness of fit*


---

### Description

Tests goodness of fit for predictions vs. observations. This statistic can be thought of in the same way as a classic "R2", except that it measures scatter around the 1-1 line, rather than around a fitted regression line of observed vs. predicted values. Value close to 1 indicate a that predictions match observations closely. Values at or below zero indicate that predictions do not match observations any better than the grand mean taken across all observations.

### Usage

```
test_goodness_of_fit(observed, predicted, bycolumn = FALSE, droptimecol = TRUE)
```

### Arguments

observed	A vector or matrix of observed values.
predicted	A vector or matrix of predicted values.
bycolumn	If TRUE, then separate values are calculated for each column in observed and predicted.
droptimecol	If TRUE, will automatically remove the column labeled "time" in the predicted variable. This is useful for dealing with the default output of the <code>gause_wrapper</code> function. Defaults to FALSE.

### Examples

```
#load competition data
data("gause_1934_science_f02_03")

#subset out data from species grown in mixture
mixturedat<-gause_1934_science_f02_03[gause_1934_science_f02_03$Treatment=="Mixture",]

#extract time and species data
time<-mixturedat$Day
species<-data.frame(mixturedat$Volume_Species1, mixturedat$Volume_Species2)
colnames(species)<-c("P_caudatum", "P_aurelia")

#run wrapper
#note - keeptimes=TRUE is needed, so that predicted time steps match
#observed time steps
gause_out<-gause_wrapper(time=time, species=species, keeptimes = TRUE)

#calculate goodness of fit
test_goodness_of_fit(observed=species, predicted=gause_out)

# > 0.9 for both time series - these are good fits!
```

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