

# Package ‘cyr’

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**Type** Package

**Title** A Toolbox for Modelling Species Coexistence in R

**Version** 0.1

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**Description** Recent developments in modern coexistence theory has advanced our understanding on how species are able to persist and co-occur with other species at varying abundances. However, applying this mathematical framework to empirical data is still challenging, precluding a larger adoption of the theoretical tools developed by empiricists. This package provides a complete toolbox for modelling competitive effects between species, calculate fitness and niche differences, and calculate coexistence regions. The functions are flexible and can include covariates and different fitting algorithms can be used.

**License** MIT + file LICENCE

**Depends** R (>= 3.5)

**Imports** stats, nlme

**RoxygenNote** 6.1.1

**Suggests** ggplot2, tidy, dplyr, magrittr, knitr, stringr, rmarkdown, testthat (>= 0.8.0), hydroPSO, GenSA, DEoptimR, nloptr

**VignetteBuilder** knitr

**NeedsCompilation** no

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abundance	<i>Abundance measurements</i>
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## Description

A dataset containing abundances for each plant species, where each species was sampled at its developmental peak.

## Usage

```
data(abundance)
```

## Format

A data frame with 5832 rows and 7 variables

**Details**

- year: year
- month: month of sampling
- day: day of sampling
- plot: plot
- subplot: subplot code
- species: plant species
- individuals: number of individuals

**Note**

For details, see Lanuza et al. 2018 Ecology Letters.

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AvgFitnessRatio	<i>Average fitness differences between a pair of species</i>
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**Description**

Calculates the product of (1) the demographic ratio, and (2) the competitive response ratio between two species according to their vital rates and competition coefficients. First species in the parameters is numerator (j in eq. 4 of Godoy et al. 2014). If germ.rate and survival.rate are provided, it calculates the ratio according to eq. 4 of Godoy et al. (2014), for annual plants. Otherwise, if only lambda is provided, it returns the general version of the demographic ratio, where nu = lambda

**Usage**

```
AvgFitnessRatio(lambda, germ.rate = NULL, survival.rate = NULL,
  pair.matrix)
```

**Arguments**

lambda	vector of length 2, per capita fecundity of the species in the absence of competition
germ.rate	optional vector of length 2, germination rate of the two species
survival.rate	optional vector of length 2, annual survival of ungerminated seed in the soil
pair.matrix	2x2 matrix, competition coefficients between the two species and intraspecific terms

**Value**

list with three numeric values, giving 1) the demographic ratio, 2) the competitive response ratio, and 3) the average fitness ratio between the two species

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competition	<i>Competition measurements</i>
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**Description**

A dataset containing fitness and neighbours for each plant individual

**Usage**

```
data(competition)
```

**Format**

A data frame with 42948 rows and 11 variables

**Details**

- year: year
- month: month
- day: day
- plot: plot
- subplot: subplot code
- focal: focal plant species identity
- individual\_ID: unique identifier for each individual focal plant
- fruit: total fruits produced by the focal individual
- seed: total seeds produced by the focal individual
- competitor: competitor identity
- number: number of competitors

**Note**

For details, see Lanuza et al. 2018 Ecology Letters.

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cxr	<i>cxr</i>
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**Description**

Tools and functions for evaluating multi-species coexistence.

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cxr_er_bootstrap	<i>standard error estimates for effect and response parameters</i>
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## Description

Computes bootstrap standard errors for a given effect/response function

## Usage

```
cxr_er_bootstrap(effect.response.model, optim.method, sp.data, init.par,
  lower.bounds, upper.bounds, covariates, optimize.lambda, lambda.vector,
  nsamples)
```

## Arguments

effect.response.model	effect/response function
optim.method	optimization method to use. One of the following: "optim_NM","optim_L-BFGS-B","nloptr_CRS2_LM", "nloptr_ISRES","nloptr_DIRECT_L_RAND","GenSA","hydroPSO","D"
sp.data	dataframe with all the necessary information in long format. It should have the following columns: - site: character ID - focal: character ID of the focal species. Any number of focal species is allowed, but the number of focal species must match the number of initial parameters (one lambda, e, and r per species). - fitness: numeric, a fitness metric - competitor: character, ID of a competitor for that observation. The set of competitors must be, for now, the same as the set of focal species. - number: number of neighbouring/competitor individuals from the associated species. Observations without competitors of a given species must be explicit, i.e. setting number to zero.
init.par	1d vector of initial parameters
lower.bounds	1d vector of lower bounds
upper.bounds	1d vector of upper bounds
covariates	dataframe/matrix with observations in rows and covariates in columns. Each cell is the value of a covariate from an observation.
optimize.lambda	boolean, whether to optimize the values of lambda or not.
lambda.vector	in case lambda is not to be optimized, fixed values for it.
nsamples	how many bootstrap samples to compute.

## Value

1d vector, the standard error of each parameter in init.par

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cxr_init_params	<i>Join parameters in a 1d vector</i>
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### Description

Generate a 1d vector from a series of parameters in a certain order. It also returns the same vector for lower and upper bounds. This function is intended to work with parameters for a single species (i.e. a single lambda value, etc). Note that lambda.cov and alpha.cov must be consistent with num.covariates.

### Usage

```
cxr_init_params(init.lambda = NULL, init.sigma = 0,
  init.alpha = NULL, init.lambda.cov = NULL, init.alpha.cov = NULL,
  lower.lambda = 1, upper.lambda = 1e+05, lower.sigma = 1e-05,
  upper.sigma = 1e+05, lower.alpha = 1e-05, upper.alpha = 1e+05,
  lower.lambda.cov = 1e-05, upper.lambda.cov = 1e+05,
  lower.alpha.cov = 1e-05, upper.alpha.cov = 1e+05, num.competitors,
  num.covariates)
```

### Arguments

init.lambda	numeric, lambda
init.sigma	numeric, sigma
init.alpha	1d vector, interaction coefficients over the species
init.lambda.cov	1d vector, initial values for lambda.cov
init.alpha.cov	1d vector, initial values for alpha.cov
lower.lambda	lower bound for lambda
upper.lambda	upper bound for lambda
lower.sigma	lower bound for sigma
upper.sigma	upper bound for sigma
lower.alpha	lower bound for alpha
upper.alpha	upper bound for alpha
lower.lambda.cov	lower bound for lambda.cov
upper.lambda.cov	upper bound for lambda.cov
lower.alpha.cov	lower bound for alpha.cov
upper.alpha.cov	upper bound for alpha.cov
num.competitors	number of competitors
num.covariates	number of covariates

**Value**

list with three 1d vectors, ready for passing to the optim methods, consistent with the functions model\_BH1-5

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cxr\_pm\_bootstrap

*Standard error estimates for model parameters*


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**Description**

Computes bootstrap standard errors for a given population dynamics model.

**Usage**

```
cxr_pm_bootstrap(fitness.model, optim.method, param.list, fixed.terms,
  log.fitness, init.par, lower.bounds, upper.bounds, focal.comp.matrix,
  focal.covariates, nsamples)
```

**Arguments**

fitness.model    function returning a single value to minimize, given a set of parameters and a fitness metric

optim.method    optimization method to use. One of the following: "optim\_NM", "optim\_L-BFGS-B", "nloptr\_CRS2\_LM", "nloptr\_ISRES", "nloptr\_DIRECT\_L\_RAND", "GenSA", "hydroPSO", "D"

param.list       string vector giving the parameters that are to be optimized for the fitness model.

fixed.terms      string vector giving the parameters that are NOT optimized for the fitness model.

log.fitness       1d vector, log of the fitness metric for every observation

init.par           1d vector of initial parameters

lower.bounds      1d vector of lower bounds

upper.bounds      1d vector of upper bounds

focal.comp.matrix       matrix with observations in rows and neighbours in columns. Each cell is the number of neighbours of a given species in a given observation.

focal.covariates       optional matrix with observations in rows and covariates in columns. Each cell is the value of a covariate in a given observation.

nsamples           how many bootstrap samples to compute.

**Value**

1d vector, the standard error of each parameter in init.par

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cxr_retrieve_params	<i>Retrieve parameters from the vector returned by the optimization procedures</i>
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### Description

Retrieve parameters from the vector returned by the optimization procedures

### Usage

```
cxr_retrieve_params(optim.params, param.list, alpha.length,
  alpha.cov.length, num.competitors, num.covariates)
```

### Arguments

optim.params	1d vector, the result of an optimization method
param.list	character vector, which parameters are present. Possible elements are "lambda", "lambda.cov", "alpha", "alpha.cov".
alpha.length	if alpha is to be retrieved, its length
alpha.cov.length	if alpha.cov is to be retrieved, its length
num.competitors	how many competitor species
num.covariates	how many covariates

### Value

list with elements "lambda", "alpha", "lambda.cov", "alpha.cov", "sigma". If one of these elements is not present, returns NULL.

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er_optim	<i>Estimate competition effects and responses for a set of species</i>
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### Description

This function is similar in spirit to pm\_optim, in that it optimizes a set of parameters via maximum likelihood. See vignette 'Obtain competitive responses and effects' for an example of its use.



**Usage**

```
er_optim(lambda.vector, e.vector, r.vector, lambda.cov = NULL,
  e.cov = NULL, r.cov = NULL, sigma, lower.lambda = 0,
  upper.lambda = 1000, lower.e, upper.e, lower.r, upper.r,
  lower.lambda.cov = NULL, upper.lambda.cov = NULL,
  lower.e.cov = NULL, upper.e.cov = NULL, lower.r.cov = NULL,
  upper.r.cov = NULL, lower.sigma, upper.sigma, effect.response.model,
  optim.method, sp.data, covariates = NULL, optimize.lambda = FALSE,
  generate.errors = FALSE, bootstrap.samples = 0)
```

**Arguments**

lambda.vector	1d vector of lambda estimates/initial values (depending on whether lambda values are optimized or not)
e.vector	1d vector of competitive effect initial values
r.vector	1d vector of competitive response initial values
lambda.cov	numeric matrix of num.sp x num.covariates, effect of every covariate on species' lambda. Discarded if covariates are not passed.
e.cov	numeric matrix of num.sp x num.covariates, effect of every covariate on species' competitive effect. Discarded if covariates are not passed.
r.cov	numeric matrix of num.sp x num.covariates, effect of every covariate on species' competitive response. Discarded if covariates are not passed.
sigma	initial value for variation estimate.
lower.lambda	lower bound for lambda, in case it is optimized. Either length 1 or same length as lambda.vector
upper.lambda	upper bound for lambda, in case it is optimized. Either length 1 or same length as lambda.vector
lower.e	lower bound for competitive effects. Either length 1 or same length as e.vector
upper.e	upper bound for competitive effects. Either length 1 or same length as e.vector
lower.r	lower bound for competitive responses. Either length 1 or same length as r.vector
upper.r	upper bound for competitive responses. Either length 1 or same length as r.vector
lower.lambda.cov	lower bound for covariate effects on lambda. Either length 1 or same length as lambda.cov. Discarded if covariates are not passed.
upper.lambda.cov	upper bound for covariate effects on lambda. Either length 1 or same length as lambda.cov. Discarded if covariates are not passed.
lower.e.cov	lower bound for covariate effects on e. Either length 1 or same length as e.cov. Discarded if covariates are not passed.
upper.e.cov	upper bound for covariate effects on e. Either length 1 or same length as e.cov. Discarded if covariates are not passed.
lower.r.cov	lower bound for covariate effects on r. Either length 1 or same length as r.cov. Discarded if covariates are not passed.

<code>upper.r.cov</code>	upper bound for covariate effects on r. Either length 1 or same length as <code>r.cov</code> . Discarded if covariates are not passed.
<code>lower.sigma</code>	lower bound for sigma. Length 1.
<code>upper.sigma</code>	upper bound for sigma. Length 1.
<code>effect.response.model</code>	function returning a value to optimize over, e.g. maximum likelihood
<code>optim.method</code>	optimization method to use. One of the following: "optim_NM", "optim_L-BFGS-B", "nloptr_CRS2_LM", "nloptr_ISRES", "nloptr_DIRECT_L_RAND", "GenSA", "hydroPSO", "D"
<code>sp.data</code>	dataframe with all the necessary information in long format. It should have the following columns: - site: character ID - focal: character ID of the focal species. Any number of focal species is allowed, but the number of focal species must match the number of initial parameters (one lambda, e, and r per species). - fitness: numeric, a fitness metric - competitor: character, ID of a competitor for that observation. The set of competitors must be, for now, the same as the set of focal species. - number: number of neighbouring/competitor individuals from the associated species. Observations without competitors of a given species must be explicit, i.e. setting number to zero.
<code>covariates</code>	optional matrix/dataframe with as many rows as the <code>sp.data</code> dataframe, and covariates in columns.
<code>optimize.lambda</code>	boolean, whether we want to optimize lambda values or not.
<code>generate.errors</code>	boolean, whether to compute bootstrap errors for the fitted parameters. Note that, depending on the data and optimization method, this may be computationally expensive.
<code>bootstrap.samples</code>	how many bootstrap samples to compute.

## Value

list with estimated species values for e, r, lambda (optional), and if covariates are given, the effects of covariates on lambda, r, and e.

---

GenerateTestData	<i>Generate simulated competition data</i>
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---

## Description

Generate simulated competition data

## Usage

```
GenerateTestData(focal.sp = 1, num.sp = 2, num.cov = 2,
  num.obs = 10, fitness.model = 1, focal.lambda, alpha,
  alpha.cov = NULL, lambda.cov = NULL)
```

**Arguments**

focal.sp	number of focal species
num.sp	total number of species, including focal ones
num.cov	number of covariates
num.obs	number of observations/sites
fitness.model	scalar representing the model to generate data from, from BH1 to BH5 in increasing levels of complexity.
focal.lambda	1d vector with lambdas of the focal sp
alpha	interaction matrix, num.sp x num.sp
alpha.cov	list of dimension num.cov. Each component of the list is a matrix of different dimensions depending on fitness.model. If fitness.model is 4, each component should be a single value, giving the effect of each covariate over every interaction; if fitness.model is 5, each component should be a matrix num.sp x num.sp, giving the effect of the covariate in question over each element of the interaction matrix.
lambda.cov	matrix of num.sp x num.cov giving the effect of each covariate over the fecundity (lambda) of each species

**Value**

dataset with a fitness metric calculated for each focal species and observation, according to the fitness model selected

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model_abundBH1	<i>Project abundance of individuals according to the Beverton-Holt fist model</i>
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**Description**

Project abundance of individuals according to the Beverton-Holt fist model

**Usage**

```
model_abundBH1(sp.par, init.abund, cov.values, alpha.matrix,
               lambda.cov.matrix, alpha.cov.matrix, return.seeds = TRUE)
```

**Arguments**

sp.par	dataframe with species in rows, and the following columns: lambda: fecundity term germ.rate: seed germination rate survival.rate: annual survival of ungerminated seed
init.abund	number of individuals at time t
cov.values	Not used in BH_abundances_1
alpha.matrix	Not used in BH_1

lambda.cov.matrix	Not used in BH_abundances_1
alpha.cov.matrix	Not used in BH_abundances_1
return.seeds	boolean flag, whether the prediction should return number of seeds (i.e. $N_{i,t+1}$ , eq. 1 of Lanuza et al. 2018), or number of adult individuals, (i.e. $N_{i,t+1} * g$ )

**Value**

1d vector with number of individuals of each species at time t+1

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model_abundBH2	<i>Project abundance of individuals according to the Beverton-Holt second model</i>
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**Description**

Project abundance of individuals according to the Beverton-Holt second model

**Usage**

```
model_abundBH2(sp.par, init.abund, cov.values, alpha.matrix,
               lambda.cov.matrix, alpha.cov.matrix, return.seeds = TRUE)
```

**Arguments**

sp.par	dataframe with species in rows, and the following columns: lambda: fecundity term germ.rate: seed germination rate survival.rate: annual survival of ungerminated seed
init.abund	number of individuals at time t
cov.values	Not used in model_abundBH2
alpha.matrix	competition value, same for all interactions
lambda.cov.matrix	Not used in model_abundBH2
alpha.cov.matrix	Not used in model_abundBH2
return.seeds	boolean flag, whether the prediction should return number of seeds (i.e. $N_{i,t+1}$ , eq. 1 of Lanuza et al. 2018), or number of adult individuals, (i.e. $N_{i,t+1} * g$ )

**Value**

1d vector with number of individuals of each species at time t+1

---

model_abundBH3	<i>Project abundance of individuals according to the Beverton-Holt third model</i>
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---

**Description**

Project abundance of individuals according to the Beverton-Holt third model

**Usage**

```
model_abundBH3(sp.par, init.abund, cov.values, alpha.matrix,
               lambda.cov.matrix, alpha.cov.matrix, return.seeds = TRUE)
```

**Arguments**

sp.par	dataframe with species in rows, and the following columns: lambda: fecundity term germ.rate: seed germination rate survival.rate: annual survival of ungerminated seed
init.abund	number of individuals at time t
cov.values	Not used in model_abundBH3
alpha.matrix	competition matrix
lambda.cov.matrix	Not used in model_abundBH3
alpha.cov.matrix	Not used in model_abundBH3
return.seeds	boolean flag, whether the prediction should return number of seeds (i.e. $N_{i,t+1}$ , eq. 1 of Lanuza et al. 2018), or number of adult individuals, (i.e. $N_{i,t+1} * g$ )

**Value**

1d vector with number of individuals of each species at time t+1

---

model_abundBH4	<i>Project abundance of individuals according to the Beverton-Holt fourth model</i>
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---

**Description**

Project abundance of individuals according to the Beverton-Holt fourth model

**Usage**

```
model_abundBH4(sp.par, init.abund, cov.values, alpha.matrix,
               lambda.cov.matrix, alpha.cov.matrix, return.seeds = TRUE)
```

**Arguments**

sp.par	dataframe with species in rows, and the following columns: lambda: fecundity term germ.rate: seed germination rate survival.rate: annual survival of ungerminated seed
init.abund	number of individuals at time t
cov.values	1d vector with values of each covariate
alpha.matrix	competition matrix
lambda.cov.matrix	matrix of num.sp x num.cov giving the effect of each covariate over the fecundity (lambda) of each species
alpha.cov.matrix	list of dimension number of covariates. Each component of the list is a single value, giving the effect of the covariate in question over the interaction matrix.
return.seeds	boolean flag, whether the prediction should return number of seeds (i.e. $N_{i,t+1}$ , eq. 1 of Lanuza et al. 2018), or number of adult individuals, (i.e. $N_{i,t+1} * g$ )

**Value**

1d vector with number of individuals of each species at time t+1

---

model_abundBH5	<i>Project abundance of individuals according to the Beverton-Holt fifth model</i>
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**Description**

Project abundance of individuals according to the Beverton-Holt fifth model

**Usage**

```
model_abundBH5(sp.par, init.abund, cov.values, alpha.matrix,
               lambda.cov.matrix, alpha.cov.matrix, return.seeds = TRUE)
```

**Arguments**

sp.par	dataframe with species in rows, and the following columns: lambda: fecundity term germ.rate: seed germination rate survival.rate: annual survival of ungerminated seed
init.abund	number of individuals at time t
cov.values	1d vector with values of each covariate
alpha.matrix	competition matrix
lambda.cov.matrix	matrix of num.sp x num.cov giving the effect of each covariate over the fecundity (lambda) of each species

<code>alpha.cov.matrix</code>	list of dimension number of covariates. Each component of the list is a matrix of <code>num.sp</code> x <code>num.sp</code> , giving the effect of the covariate in question over the interaction matrix.
<code>return.seeds</code>	boolean flag, whether the prediction should return number of seeds (i.e. $N_{i,t+1}$ , eq. 1 of Lanuza et al. 2018), or number of adult individuals, (i.e. $N_{i,t+1} * g$ )

**Value**

1d vector with number of individuals of each species at time t+1

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<code>model_BH1</code>	<i>Title Beverton-Holt fecundity, first model</i>
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**Description**

These functions return the negative log-likelihood of the data given the model and parameters. `model_BH1` is  $F_i = \lambda_i$

**Usage**

```
model_BH1(par, param.list = NULL, log.fitness,
  focal.comp.matrix = NULL, num.covariates = NULL,
  num.competitors = NULL, focal.covariates = NULL,
  fixed.terms = NULL)
```

**Arguments**

<code>par</code>	vector containing lambda of focal sp and sigma value
<code>param.list</code>	not used in <code>model_BH1</code>
<code>log.fitness</code>	log of fitness value
<code>focal.comp.matrix</code>	not used in <code>model_BH1</code>
<code>num.covariates</code>	not used in <code>model_BH1</code>
<code>num.competitors</code>	not used in <code>model_BH1</code>
<code>focal.covariates</code>	not used in <code>model_BH1</code>
<code>fixed.terms</code>	not used in <code>model_BH1</code>

**Value**

log-likelihood value

model\_BH2

*Title Beverton-Holt fecundity, second model***Description**

These functions return the negative log-likelihood of the data given the model and parameters.

model\_BH2 is  $F_i = \frac{\lambda_i}{1+\alpha \sum_j N_j}$

**Usage**

```
model_BH2(par, param.list = c("lambda", "alpha"), log.fitness,
  focal.comp.matrix, num.covariates = NULL, num.competitors = NULL,
  focal.covariates = NULL, fixed.terms = NULL)
```

**Arguments**

par	vector of variable length, with the following order: first, lambda of focal sp; second alpha, single interaction coefficient; last, sigma value. If any element is not to be optimized, it must not be present in this vector, but rather in the "fixed.terms" list
param.list	string listing parameters to optimize. Possible elements are lambda, lambda.cov, alpha, alpha.cov.
log.fitness	log of fitness value
focal.comp.matrix	dataframe with as many rows as observations, and one column for each competitor sp. Values of the dataframe are number of competitors of each sp per observation.
num.covariates	not used in model_BH2
num.competitors	not used in model_BH2
focal.covariates	not used in model_BH2.
fixed.terms	list with elements lambda, lambda.cov, alpha, alpha.cov. It contains parameters not to be optimized. Each element of the list must be of its appropriate length. Note that adding an element in "param.list" will force the function to look for it in par, and will not consider it here. In this model, lambda.cov and alpha.cov are not considered.

**Value**

log-likelihood value



model\_BH3

*Title Beverton-Holt fecundity, third model***Description**

These functions return the negative log-likelihood of the data given the model and parameters.

model\_BH3 is  $F_i = \frac{\lambda_i}{1 + \sum_j \alpha_{ij} N_j}$

**Usage**

```
model_BH3(par, param.list = c("lambda", "alpha"), log.fitness,
  focal.comp.matrix, num.covariates = NULL, num.competitors = NULL,
  focal.covariates = NULL, fixed.terms = NULL)
```

**Arguments**

par	vector of variable length, with the following order: first, lambda of focal sp; second alpha, interaction coefficients with every species; last, sigma value. If any element is not to be optimized, it must not be present in this vector, but rather in the fixed.terms list
param.list	string listing parameters to optimize. Possible elements are lambda, lambda.cov, alpha, alpha.cov.
log.fitness	log of fitness value
focal.comp.matrix	dataframe with as many rows as observations, and one column for each competitor sp. Values of the dataframe are number of competitors of each sp per observation.
num.covariates	not used in model_BH3
num.competitors	number of competitor species
focal.covariates	not used in model_BH3.
fixed.terms	list with elements lambda, lambda.cov, alpha, alpha.cov. It contains parameters not to be optimized. Each element of the list must be of its appropriate length. Note that adding an element in "param.list" will force the function to look for it in par, and will not consider it here. In this model, lambda.cov and alpha.cov are not considered.

**Value**

log-likelihood value

model\_BH4

*Title Beverton-Holt fecundity, fourth model***Description**

These functions return the negative log-likelihood of the data given the model and parameters.

$$\text{model\_BH4 is } F_i = \frac{\lambda_i + \sum_k b_k \Theta_{i,k}}{1 + \sum_j (\alpha_{ij} + \sum_k b_k \phi_k) N_j}$$

**Usage**

```
model_BH4(par, param.list, log.fitness, focal.comp.matrix, num.covariates,
          num.competitors, focal.covariates, fixed.terms)
```

**Arguments**

par	vector of variable length, with the following order: first, lambda of focal sp; second lambda.cov, effects of every covariate on lambda; third alpha, interaction coefficients with every species; fourth alpha.cov, effects of every covariate on alpha values (single effect for each covariate); last, sigma value. If any element is not to be optimized, it must not be present in this vector, but rather in the fixed.terms list
param.list	string listing parameters to optimize. Possible elements are lambda, lambda.cov, alpha, alpha.cov.
log.fitness	log of fitness value
focal.comp.matrix	dataframe with as many rows as observations, and one column for each competitor sp. Values of the dataframe are number of competitors of each sp per observation.
num.covariates	number of covariates
num.competitors	number of competitor species
focal.covariates	dataframe/matrix with as many rows as observations, and one column for each covariate. Values of the dataframe are covariate values for every observation.
fixed.terms	list with elements lambda, lambda.cov, alpha, alpha.cov. It contains parameters not to be optimized. Each element of the list must be of its appropriate length. Note that adding an element in "param.list" will force the function to look for it in par, and will not consider it here. In this model, lambda.cov and alpha.cov are not considered.

**Value**

log-likelihood value

model\_BH5

*Title Beverton-Holt fecundity, fifth model***Description**

These functions return the negative log-likelihood of the data given the model and parameters.

$$\text{model\_BH5 is } F_i = \frac{\lambda_i + \sum_k b_k \Theta_{i,k}}{1 + \sum_j (\alpha_{ij} + \sum_k b_k \phi_{i,j,k}) N_j}$$

**Usage**

```
model_BH5(par, param.list, log.fitness, focal.comp.matrix, num.covariates,
          num.competitors, focal.covariates, fixed.terms)
```

**Arguments**

par	vector of variable length, with the following order: first, lambda of focal sp; second lambda.cov, effects of every covariate on lambda; third alpha, interaction coefficients with every species; fourth alpha.cov, effects of every covariate on alpha values (varying effect of every covariate over every interaction coefficient); last, sigma value. If any element is not to be optimized, it must not be present in this vector, but rather in the fixed.terms list
param.list	string listing parameters to optimize. Possible elements are lambda, lambda.cov, alpha, alpha.cov.
log.fitness	log of fitness value
focal.comp.matrix	dataframe with as many rows as observations, and one column for each competitor sp. Values of the dataframe are number of competitors of each sp per observation.
num.covariates	number of covariates
num.competitors	number of competitor species
focal.covariates	dataframe with as many rows as observations, and one column for each covariate. Values of the dataframe are covariate values for every observation.
fixed.terms	list with elements lambda, lambda.cov, alpha, alpha.cov. It contains parameters not to be optimized. Each element of the list must be of its appropriate length. Note that adding an element in "param.list" will force the function to look for it in par, and will not consider it here. In this model, lambda.cov and alpha.cov are not considered.

**Value**

log-likelihood value

---

model\_ER

*Estimation of competitive effects and responses*


---

### Description

Calculates the log-likelihood of a Beverton-Holt model parameterized with given values with respect to a fitness metric. The function for calculating fecundity given effect and response values is taken from Godoy et al. (2014). Note that, as e and r are not pair-specific, all species parameters are fit in the same function. In this version, lambda values are fixed.

### Usage

```
model_ER(init.par, lambda, target_all, density_all, log.fitness,
         covariates = NULL)
```

### Arguments

init.par	1d vector of initial parameters: r values, e values, and single sigma term. If covariates are given, this vector must include also lambda.cov, response.cov, and effect.cov terms, after the e values and before the sigma term.
lambda	1d vector of lambda values
target_all	matrix giving which species is calculated with which values. See er_optim
density_all	matrix giving the densities of each species at each observation. See er_optim
log.fitness	log of the fitness metric
covariates	if present, it is a dataframe/matrix with as many rows as observations, and one column for each covariate. Values are covariate values for every observation.

### Value

single numeric value giving the sum of negative log-likelihoods

---

model\_ER\_lambda

*Estimation of competitive effects and responses*


---

### Description

Calculates the log-likelihood of a Beverton-Holt model parameterized with given values with respect to a fitness metric. The function for calculating fecundity given effect and response values is taken from Godoy et al. (2014). Note that, as e is not pair-specific, all species parameters are fit in the same function. In this version, lambda values are also fit.

### Usage

```
model_ER_lambda(init.par, target_all, density_all, log.fitness,
                covariates = NULL)
```

**Arguments**

<code>init.par</code>	1d vector of initial parameters: lambda values, r values, e values, and single sigma term. If covariates are given, this vector must include also lambda.cov, response.cov, and effect.cov terms, after the e values and before the sigma term.
<code>target_all</code>	matrix giving which species is calculated with which values. See <code>er_optim</code>
<code>density_all</code>	matrix giving the densities of each species at each observation. See <code>er_optim</code>
<code>log.fitness</code>	log of the fitness metric
<code>covariates</code>	if present, it is a dataframe/matrix with as many rows as observations, and one column for each covariate. Values are covariate values for every observation.

**Value**

single numeric value giving the sum of negative log-likelihoods

---

NicheOverlap	<i>Niche overlap between two species</i>
--------------	--

---

**Description**

quoting Godoy et al. (2014): reflects the average degree to which species limit individuals of their own species relative to competitors. Low niche overlap causes species to have greater per capita growth rates when rare than when common. If species limit individuals of their own species and their competitors equally, then niche overlap is 1, and coexistence is not possible unless species are otherwise identical. At the other extreme, if species have no interspecific effects, then niche overlap is 0.

**Usage**

```
NicheOverlap(pair.matrix)
```

**Arguments**

<code>pair.matrix</code>	2x2 matrix with competition coefficients between the two species, and intraspecific terms
--------------------------	---

**Value**

niche overlap value, in the range 0-1.

---

param_estimates	<i>Population model parameters</i>
-----------------	------------------------------------

---

## Description

A dataset containing estimated parameters for the competition dataset. The dataset is generated by code similar to that of the vignette `Multi-species parameter optimization`. It is structured as a nested list with three levels, of the form: `param_estimates[[species]][[fecundity model]][[optimization method]]`. In the provided dataset, we include models 1 to 5, estimated with optimization method "optim\_L-BFGS-B". For each combination of species, model, and method, all model parameters are given. If a parameter is not estimated (e.g. upper/lower errors), the value stored is NA.

## Usage

```
data(param_estimates)
```

## Format

A nested list with three levels

## Details

- `lambda`: per germinant fecundity
- `lambda.lower.error`:
- `lambda.upper.error`:
- `sigma`:
- `alpha`: effect of every competitor species on the focal species
- `alpha.lower.error`:
- `alpha.upper.error`:
- `lambda.cov`: effect of every covariate on `lambda`
- `lambda.cov.lower.error`:
- `lambda.cov.upper.error`:
- `alpha.cov`: effect of every covariate on `alpha`
- `alpha.cov.lower.error`:
- `alpha.cov.upper.error`:
- `log.likelihood`: log-likelihood of the fitted parameters and model

## Note

For details, see vignette `Multi-species parameter optimization`

pm\_optim

*General optimization for population models***Description**

Wrapper for optimization procedures. It accepts a population dynamics model, defined as a function, and a series of parameters. It returns the optimal value for the parameters given a fitness metric and an optimization method. Optionally, bootstrap confidence intervals can also be computed.

**Usage**

```
pm_optim(fitness.model, optim.method, param.list, log.fitness,
  init.lambda = NULL, lower.lambda = 1, upper.lambda = 1e+05,
  init.sigma = NULL, lower.sigma = 1e-10, upper.sigma = 1e+05,
  init.alpha = 1e-04, lower.alpha = 0, upper.alpha = 1e+05,
  init.lambda.cov = 0.001, lower.lambda.cov = 1e-04,
  upper.lambda.cov = 1e+05, init.alpha.cov = 0.001,
  lower.alpha.cov = 1e-04, upper.alpha.cov = 1e+05, focal.comp.matrix,
  focal.covariates = NULL, generate.errors = FALSE,
  bootstrap.samples = 0, verbose = FALSE)
```

**Arguments**

fitness.model	function giving the population dynamics model. Any functional form is allowed, but the model must be constrained to free parameters lambda (fecundity of each sp in absence of competition), alpha (interaction coefficients), lambda.cov (effect of covariates on lambda), alpha.cov (effect of covariates on alpha)
optim.method	optimization method to use. One of the following: "optim_NM", "optim_L-BFGS-B", "nloptr_CRS2_LM", "nloptr_ISRES", "nloptr_DIRECT_L_RAND", "GenSA", "hydroPSO", "D"
param.list	string vector giving the parameters that are to be optimized for the fitness model (to choose among "lambda", "alpha", "lambda.cov", and "alpha.cov").
log.fitness	1d vector, log of the fitness metric for every observation
init.lambda	1d vector, initial value of lambda
lower.lambda	lower bound for lambda
upper.lambda	upper bound for lambda
init.sigma	initial value for sigma (standard deviation)
lower.sigma	lower bound for sigma
upper.sigma	upper bound for sigma
init.alpha	initial value for the alpha vector/matrix
lower.alpha	lower bound for alpha
upper.alpha	upper bound for alpha
init.lambda.cov	initial value for the lambda.cov matrix. Discarded if no covariates are given.

`lower.lambda.cov`  
                     lower bound for lambda.cov  
`upper.lambda.cov`  
                     upper bound for lambda.cov  
`init.alpha.cov` initial value for the alpha.cov matrix. Discarded if no covariates are given.  
`lower.alpha.cov`  
                     lower bound for alpha.cov  
`upper.alpha.cov`  
                     upper bound for alpha.cov  
`focal.comp.matrix`  
                     matrix with observations in rows and neighbours in columns. Each cell is the  
                             number of neighbours of a given species in a given observation.  
`focal.covariates`  
                     optional matrix with observations in rows and covariates in columns. Each cell  
                             is the value of a covariate in a given observation.  
`generate.errors`  
                     boolean, whether to compute bootstrap errors for the fitted parameters. Note  
                             that, depending on the data, model, and optimization method, this may be com-  
                             putationally expensive.  
`bootstrap.samples`  
                     how many bootstrap samples to compute.  
`verbose`            work in progress

### Value

list with the fitted parameters, and the loglikelihood of the fit. If a parameter is taken as a constant, the list will return the original value given.

---

pollinators	<i>Pollinators measurments</i>
-------------	--------------------------------

---

### Description

A dataset containing the overall pollinator visitation over the season for each plant species.

### Usage

```
data(pollinators)
```

### Format

A data frame with x rows and 9 variables



**Details**

- plot: plot number
- subplot: subplot code
- plant\_species: plant species
- year: year of measurement
- bees: total bee visits recieved
- flies: total flies visits recieved
- beetles: total beetles visits recieved
- butterflies: total butterflies visits recieved
- other: total other visits recieved

**Note**

For details, see Lanuza et al. 2018 Ecology Letters.

---

PredictAbundances

*Project abundances according to specified models and parameters*


---

**Description**

Project abundances according to specified models and parameters

**Usage**

```
PredictAbundances(par, timesteps, abundance.model, return.seeds = TRUE)
```

**Arguments**

- |                 |  |
|-----------------|--|
| par             | <p>list with the following components:</p> <ul style="list-style-type: none"> <li>• dataframe sp.par, with the parameters to be passed to the predictive model</li> <li>• dataframe initial.values, with fields "site","species","abundance"</li> <li>• covariates, either 0 if there are no covariates, or a dataframe with fields "site","timestep","covariate","value"</li> <li>• list other.par, other parameters to abundance model, such as alpha.matrix, lambda.cov.matrix, alpha.cov.matrix.</li> </ul> <p>Note that the fields "species", "site", and "covariate" should be unique identifiers, character or numeric.</p> |
| timesteps       | number of timesteps to project   |
| abundance.model | a function that accepts parameters from sp.par, a set of initial abundances, and optionally other parameters. The function returns the projected abundances at t+1   |
| return.seeds    | boolean flag, whether the prediction should return number of seeds (i.e. $N_{i,t+1}$ , eq. 1 of Lanuza et al. 2018), or number of adult individuals, (i.e. $N_{i,t+1} * g$ )   |

**Value**

dataframe with fields "timestep", "site", "sp", "abundance", giving the expected abundance for each species, timestep, and site.

---

salinity	<i>Salinity measurements</i>
----------	------------------------------

---

**Description**

A dataset containing the integrated salinity over the season for each plant species.

**Usage**

```
data(salinity)
```

**Format**

A data frame with 324 rows and 5 variables

**Details**

- plot: plot number
- subplot: subplot code
- year: year of measurement
- precip: anual precipitation
- sum\_salinity: summatory of the salinity values integrated through the species lifespan.

**Note**

For details, see Lanuza et al. 2018 Ecology Letters.

---

SpeciesFitness	<i>Fitness of a species</i>
----------------	-----------------------------

---

**Description**

Calculates the fitness of a species following eq. S2 of Godoy et al. (2014). If germ.rate and survival.rate are provided, it calculates nu according to eq. 4 of Godoy et al. (2014), for annual plants. Otherwise, if only lambda is provided, nu = lambda

**Usage**

```
SpeciesFitness(lambda, germ.rate = NULL, survival.rate = NULL,
  competitive.response)
```

**Arguments**

- lambda            per capita fecundity of the species in the absence of competition
- germ.rate        optional, germination rate of the species
- survival.rate    optional, annual survival of ungerminated seed in the soil
- competitive.response        parameter reflecting the species' sensitivity to competition

**Value**

single numeric value, species fitness

---

species_rates	<i>Species germination and survival rates</i>
---------------	---

---

**Description**

A dataset containing germination and survival rates for each plant species. It also includes a column with the scientific names, and their associated codes.

**Usage**

```
data(species_rates)
```

**Format**

A data frame with 20 rows and 4 variables

**Details**

- species: binomial name
- code: four-letter code used in other datasets
- germination: germination rate
- seed.survival: annual survival of ungerminated seed in the soil

**Note**

For details, see Lanuza et al. 2018 Ecology Letters.

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