# Package: cxr (via r-universe)

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Type Package

Title A Toolbox for Modelling Species Coexistence in R

Version 1.1.1

Description Recent developments in modern coexistence theory have 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 interaction effects between species, and calculate fitness and niche differences. The functions are flexible, may accept covariates, and different fitting algorithms can be used. A full description of the underlying methods is available in García-Callejas, D., Godoy, O., and Bartomeus, I. (2020) <doi:10.1111/2041-210X.13443>. Furthermore, the package provides a series of functions to calculate dynamics for stage-structured populations across sites.

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URL https://github.com/RadicalCommEcol/cxr

BugReports https://github.com/RadicalCommEcol/cxr/issues

**Depends** R (>= 3.5)

**Imports** Matrix, mytnorm, optimx, stats

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# **Description**

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

- plot: one of 9 plots of the study area
- subplot: one of 36 1x1 m subplots of each plot
- species: plant species
- individuals: number of individuals observed

# Usage

```
data(abundance)
```

### **Format**

A data frame with 5184 rows and 4 variables

### Note

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

### **Description**

The function projects a number of steps of a time-discrete model, with model parameters taken from a 'cxr\_pm\_multifit' object or as function arguments.

# Usage

```
abundance_projection(
  cxr_fit = NULL,
 model_family = NULL,
  alpha_form = NULL,
  lambda_cov_form = NULL,
  alpha_cov_form = NULL,
  lambda = NULL,
  alpha_matrix = NULL,
  lambda_cov = NULL,
  alpha_cov = NULL,
  covariates = NULL,
  timesteps = 2,
  initial_abundances = 0
)
```

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# Arguments

cxr\_fit object of type 'cxr\_pm\_multifit'. If this is not specified, all parameters below

are needed.

model\_family acronym for model family. Included by default in 'cxr' are 'BH' (Beverton-

Holt), 'RK' (Ricker), 'LW' (Law-Watkinson), 'LV' (Lotka-Volterra).

alpha\_form character, either "none", "global", or "pairwise".

lambda\_cov\_form

character, either "none" or "global".

alpha\_cov\_form character, either "none", "global", or "pairwise".

lambda named vector with lambda values for all taxa to be projected.

alpha\_matrix square matrix with taxa names in rows and columns.

lambda\_cov optional named matrix with covariates in columns and taxa in rows, representing

the effect of each covariate on the lambda parameter of each taxa.

alpha\_cov optional list. Each element of the named list represents the effects of a covariate

over alpha values. Thus, each list element contains a square matrix of the same dimensions as 'alpha\_matrix', as returned from the function 'cxr\_pm\_fit'. Note that for alpha\_cov\_form = "global", all columns in this matrix are the same, as

there is a single value per species.

covariates matrix or dataframe with covariates in columns and timesteps in rows.

timesteps number of timesteps to project.

initial\_abundances

named vector of initial abundances for all taxa.

#### Value

named matrix with projected abundance values for each taxa at each timestep.

avg\_fitness\_diff
Average fitness differences

#### Description

computes the average fitness differences among two or more species according to the formulation of the MCT (Chesson 2012, Godoy and Levine 2014), and according to the structural approach (Saavedra et al. 2017). For the MCT version, the average fitness ratio is decomposed in a 'demographic ratio' and a 'competitive response ratio', the product of which is the average fitness ratio (Godoy and Levine 2014). This formulation is only valid for competitive interaction coefficients (i.e. positive alpha values in the interaction matrix). The structural analog can be computed for any interaction matrix, on the other hand. Note that the 'demographic ratio' is model-specific (Hart et al. 2018).

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# Usage

```
avg_fitness_diff(
  cxr_multifit = NULL,
  cxr_sp1 = NULL,
  cxr_sp2 = NULL,
  pair_lambdas = NULL,
  pair_matrix = NULL,
  model_family = NULL
)
```

#### **Arguments**

```
cxr_multifit cxr_pm_multifit object, with parameters for a series of species.

cxr_sp1 cxr_pm_fit object giving the parameters from the first species.

cxr_sp2 cxr_pm_fit object giving the parameters from the second species.

pair_lambdas numeric vector of length 2 giving lambda values for the two species.

2x2 matrix with intra and interspecific interaction coefficients between the two species.

model_family model family for which to calculate fitness differences.
```

### **Details**

This function, as in niche\_overlap and competitive\_ability, accepts three different parameterizations:

- A cxr\_pm\_multifit object, from which average fitness differences will be computed across all species pairs.
- two cxr\_pm\_fit objects, one for each species.
- explicit lambda and alpha values, as well as the model family from which these parameters were obtained.

If using the third parameterization, the function will try to find a model-specific function for obtaining the demographic ratio, by looking at the 'model\_family' parameter. If this specific function is not found, it will resort to the standard Lotka-Volterra formulation (lambda in the numerator term). Overall, we strongly suggest that you use the standard formulation ONLY if you are completely confident that your custom model is consistent with it. Otherwise, you should include your own formulation of the demographic ratio (see vignette 4).

# Value

data frame with variable number of rows, and columns specifying the different components of the MCT average fitness ratio, as well as its structural analog. The average fitness ratio informs quantitatively about the better competitor. If the ratio is < 1, sp2 is the better competitor; if = 1, both species are equivalent competitors, if > 1, sp1 is the better competitor.

### **Examples**

```
{\tt BH\_er\_lambdacov\_global\_effectcov\_global\_responsecov\_global}
```

Effect response Beverton-Holt model with covariate effects on lambda, effect, and response

# Description

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.

#### Usage

```
BH_er_lambdacov_global_effectcov_global_responsecov_global(
  par,
  fitness,
  target,
  density,
  covariates,
  fixed_parameters
)
```

#### **Arguments**

par 1d vector with initial parameters in the order: lambda,lambda\_cov,effect,effect\_cov,response,response\_co

fitness 1d vector with fitness observations

target matrix with species in rows, observations in columns. Value is 1 if a species is

focal for a given observation, 0 otherwise.

density matrix with species in rows, observations in columns. Value is density of each

sp as neighbour for each observation.

covariates numeric dataframe or matrix with observations in rows and covariates in columns.

Each cell is the value of a covariate in a given observation

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "lambda\_cov", "effect", "eff "response", "response\_cov".

### Value

log-likelihood value

```
BH_er_lambdacov_none_effectcov_none_responsecov_none

*Effect response model without covariate effects*
```

# **Description**

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.

# Usage

```
BH_er_lambdacov_none_effectcov_none_responsecov_none(
  par,
  fitness,
  target,
  density,
  covariates,
  fixed_parameters
)
```

# **Arguments**

par 1d vector with initial parameters in the order: lambda,effect,response,sigma.

fitness 1d vector with fitness observations.

target matrix with species in rows, observations in columns. Value is 1 if a species is

focal for a given observation, 0 otherwise.

density matrix with species in rows, observations in columns. Value is density of each

sp as neighbour for each observation.

covariates included for compatibility, not used in this model.

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "effect", "response".

#### Value

log-likelihood value

```
BH_pm_alpha_global_lambdacov_none_alphacov_none

Beverton-Holt model with a global alpha and no covariate effects
```

# Description

Beverton-Holt model with a global alpha and no covariate effects

### Usage

```
BH_pm_alpha_global_lambdacov_none_alphacov_none(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

# **Arguments**

# Value

log-likelihood value

```
BH_pm_alpha_none_lambdacov_none_alphacov_none

Beverton-Holt model with no alphas and no covariate effects
```

# **Description**

Beverton-Holt model with no alphas and no covariate effects

### Usage

```
BH_pm_alpha_none_lambdacov_none_alphacov_none(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

### Arguments

#### Value

log-likelihood value

```
BH_pm_alpha_pairwise_lambdacov_global_alphacov_global

Beverton-Holt model with pairwise alphas and global covariate effects
on lambda and alpha
```

# **Description**

Beverton-Holt model with pairwise alphas and global covariate effects on lambda and alpha

# Usage

```
BH_pm_alpha_pairwise_lambdacov_global_alphacov_global(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

# **Arguments**

par 1d vector of initial parameters: lambda, lambda\_cov, alpha, alpha\_cov, and

sigma

fitness 1d vector of fitness observations, in log scale

neigh\_intra\_matrix

optional matrix of one column, number of intraspecific neighbours for each ob-

servation

neigh\_inter\_matrix

matrix of arbitrary columns, number of interspecific neighbours for each obser-

vation

covariates optional matrix with observations in rows and covariates in columns. Each cell

is the value of a covariate in a given observation

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "alpha\_intra", "alpha\_inter"

#### Value

log-likelihood value

```
BH_pm_alpha_pairwise_lambdacov_global_alphacov_pairwise
```

Beverton-Holt model with pairwise alphas, covariate effects on lambda, and pairwise covariate effects on alpha

# Description

Beverton-Holt model with pairwise alphas, covariate effects on lambda, and pairwise covariate effects on alpha

### Usage

```
BH_pm_alpha_pairwise_lambdacov_global_alphacov_pairwise(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

# Arguments

par 1d vector of initial parameters: lambda, lambda\_cov, alpha, alpha\_cov, and

sigma

fitness 1d vector of fitness observations, in log scale

```
neigh_intra_matrix
```

optional matrix of one column, number of intraspecific neighbours for each ob-

servation

neigh\_inter\_matrix

matrix of arbitrary columns, number of interspecific neighbours for each obser-

vation

covariates

optional matrix with observations in rows and covariates in columns. Each cell

is the value of a covariate in a given observation

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "alpha\_intra", "alpha\_inter"

#### Value

log-likelihood value

```
BH_pm_alpha_pairwise_lambdacov_none_alphacov_none
```

Beverton-Holt model with pairwise alphas and no covariate effects

# Description

Beverton-Holt model with pairwise alphas and no covariate effects

# Usage

```
BH_pm_alpha_pairwise_lambdacov_none_alphacov_none(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

#### Arguments

par 1d vector of initial parameters: 'lambda', 'alpha\_intra' (optional), 'alpha\_inter',

and 'sigma'

fitness 1d vector of fitness observations, in log scale

neigh\_intra\_matrix

optional matrix of one column, number of intraspecific neighbours for each ob-

servation

neigh\_inter\_matrix

matrix of arbitrary columns, number of interspecific neighbours for each obser-

vation

covariates included for compatibility, not used in this model

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "alpha\_intra", "alpha\_inter"

# Value

log-likelihood value

```
BH_project_alpha_global_lambdacov_none_alphacov_none

Beverton-Holt model for projecting abundances, with a global alpha

and no covariate effects
```

# Description

Beverton-Holt model for projecting abundances, with a global alpha and no covariate effects

# Usage

```
BH_project_alpha_global_lambdacov_none_alphacov_none(
    lambda,
    alpha_intra,
    alpha_inter,
    lambda_cov,
    alpha_cov,
    abundance,
    covariates
)
```

# Arguments

lambda	numeric lambda value.
alpha_intra	included for compatibility, not used in this model.
alpha_inter	single numeric value.
lambda_cov	included for compatibility, not used in this model.
alpha_cov	included for compatibility, not used in this model.
abundance	named numeric vector of abundances in the previous timestep.
covariates	included for compatibility, not used in this model.

# Value

numeric abundance projected one timestep

```
BH_project_alpha_none_lambdacov_none_alphacov_none

Beverton-Holt model for projecting abundances, with no alpha and no covariate effects
```

# **Description**

Beverton-Holt model for projecting abundances, with no alpha and no covariate effects

### Usage

```
BH_project_alpha_none_lambdacov_none_alphacov_none(
    lambda,
    alpha_intra,
    alpha_inter,
    lambda_cov,
    alpha_cov,
    abundance,
    covariates
)
```

# **Arguments**

```
lambda numeric lambda value.

alpha_intra included for compatibility, not used in this model.

alpha_inter included for compatibility, not used in this model.

lambda_cov included for compatibility, not used in this model.

alpha_cov included for compatibility, not used in this model.

abundance named numeric vector of abundances in the previous timestep.

covariates included for compatibility, not used in this model.
```

### Value

numeric abundance projected one timestep

```
BH_project_alpha_pairwise_lambdacov_global_alphacov_global

Beverton-Holt model for projecting abundances, with specific alpha

values and global covariate effects on alpha and lambda
```

### **Description**

Beverton-Holt model for projecting abundances, with specific alpha values and global covariate effects on alpha and lambda

# Usage

```
BH_project_alpha_pairwise_lambdacov_global_alphacov_global(
    lambda,
    alpha_intra,
    alpha_inter,
    lambda_cov,
    alpha_cov,
    abundance,
    covariates
)
```

# **Arguments**

```
lambda numeric lambda value.

alpha_intra single numeric value.

alpha_inter numeric vector with interspecific alpha values.

lambda_cov numeric vector with effects of covariates over lambda.

alpha_cov named list of numeric values with effects of each covariate over alpha.

abundance named numeric vector of abundances in the previous timestep.

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

#### Value

numeric abundance projected one timestep

```
BH_project_alpha_pairwise_lambdacov_global_alphacov_pairwise

Beverton-Holt model for projecting abundances, with specific alpha

values and global covariate effects on alpha and lambda
```

# **Description**

Beverton-Holt model for projecting abundances, with specific alpha values and global covariate effects on alpha and lambda

# Usage

```
BH_project_alpha_pairwise_lambdacov_global_alphacov_pairwise(
  lambda,
  alpha_intra,
  alpha_inter,
  lambda_cov,
  alpha_cov,
  abundance,
  covariates
)
```

# **Arguments**

lambda named numeric lambda value. alpha\_intra single numeric value. alpha\_inter numeric vector with interspecific alpha values. lambda\_cov numeric vector with effects of covariates over lambda. alpha\_cov named list of named numeric vectors with effects of each covariate over alpha values. abundance named numeric vector of abundances in the previous timestep. covariates matrix with observations in rows and covariates in named columns. Each cell is the value of a covariate in a given observation.

### Value

numeric abundance projected one timestep

```
BH_project_alpha_pairwise_lambdacov_none_alphacov_none

Beverton-Holt model for projecting abundances, with specific alpha

values and no covariate effects
```

# **Description**

Beverton-Holt model for projecting abundances, with specific alpha values and no covariate effects

# Usage

```
BH_project_alpha_pairwise_lambdacov_none_alphacov_none(
    lambda,
    alpha_intra,
    alpha_inter,
    lambda_cov,
    alpha_cov,
    abundance,
    covariates
)
```

#### **Arguments**

lambda	numeric lambda value.
alpha_intra	included for compatibility, not used in this model.
alpha_inter	single numeric value.
lambda_cov	included for compatibility, not used in this model.
alpha_cov	included for compatibility, not used in this model.
abundance	named numeric vector of abundances in the previous timestep.
covariates	included for compatibility, not used in this model.

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# Value

numeric abundance projected one timestep

param
•

# Description

Builds a nested list for the parameters of a given metapopulation

# Usage

```
build_param(sp, sites, rates, env, num.params = NULL)
```

# Arguments

sp	character vector with species names
sites	character vector with site names
rates	character vector, vital rate names
env	boolean, whether environment is accounted for
num.params	optional, integer giving the number of parameters to account for. If not specified, it will include environment interactions with all species densities. E.g. if 3 sp and env = TRUE, there will be 7 params (intercept + 6 betas)

# Value

nested list of the form 'list[[sp]][[site]]'. Each of these elements is a NA matrix with vital rates in rows and expected parameters in columns.

# **Examples**

```
sp <- c("s1","s2","s3")
sites <- c("sa","sb")
rates <- c("Sj","Sn","Sr","Rn","Rr","D","0")
env <- TRUE
param <- build_param(sp = sp,sites = sites,rates = rates,env = env)</pre>
```

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calculate\_densities

Obtain species densities from transition matrices

### **Description**

Using the vec-permutation approach as defined in: Hunter and Caswell 2005, doi:10.1016/j.ecolmodel.2005.05.002, Ozgul et al. 2009, doi: 10.1086/597225 In particular, it uses the arrangement by patches, and calculates first demography, then dispersal (Table 1 of Hunter and Caswell 2005).

#### Usage

```
calculate_densities(focal.sp, vpm, current.densities)
```

### **Arguments**

focal.sp integer, focal species

vpm data structure holding all vector-permutation matrices; see 'vec\_permutation\_matrices'.

If not in an appropriate format, it is likely to fail without warning.

current.densities

list of length sp, each element is a matrix sites\*stages. If not in that format, it is

likely to fail without warning.

#### Value

matrix of sites x stages, each element is the density of a given life stage (juvenile, non-reproductive adult, reproductive adult) at a given site.

competitive\_ability

Competitive ability among pairs of species

# Description

Computes the competitive ability among two species, as defined by Hart et al. (2018). This metric, as others in MCT, is model-specific; the formulation for a series of Lotka-Volterra-like models is given in table A1 of Hart et al. (2018). We include in cxr by default the formulation for Beverton-Holt, Ricker, Law-Watkinson, and Lotka-Volterra families.

# Usage

```
competitive_ability(
  cxr_multifit = NULL,
  cxr_sp1 = NULL,
  cxr_sp2 = NULL,
  lambda = NULL,
  pair_matrix = NULL,
  model_family = NULL
)
```

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# Arguments

cxr_multifit	cxr_pm_multifit object, with parameters for a series of species.
cxr_sp1	cxr_pm_fit object giving the parameters from the first species.
cxr_sp2	cxr_pm_fit object giving the parameters from the second species.
lambda	numeric lambda value of the focal species.
pair_matrix	2x2 matrix with intra and interspecific interaction coefficients between the focal and competitor species.
model_family	model family for which to calculate competitive ability.

### **Details**

The function, as in avg\_fitness\_diff and niche\_overlap, accepts three different parameterizations:

- A cxr\_pm\_multifit object, from which competitive ability of a focal species relative to a given competitor will be computed across all species pairs.
- two cxr\_pm\_fit objects, one for a focal species and one for a competitor.
- explicit lambda and alpha values, as well as the model family from which these parameters were obtained.

If the third parameterization is used, the function will try to find a model-specific function for obtaining the competitive ability, by looking at the 'model\_family' parameter. If this specific function is not found, it will resort to the standard Lotka-Volterra formulation (lambda - 1 in the numerator term, Hart et al. 2018). Overall, we strongly suggest that you use the standard formulation ONLY if you are completely confident that the model from which you obtained your parameters is consistent with it. Otherwise, you should include your own formulation of competitive ability (see vignette 4).

### Value

data frame with variable number of rows and three columns, specifying taxa identity and the competitive ability of focal species (sp1) relative to the competitor (sp2).

### **Examples**

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cxr\_er\_bootstrap

standard error estimates for effect and response parameters

# Description

Computes bootstrap standard errors for a given effect/response function. This function is provided for completeness, but error calculation is integrated in the function cxr\_er\_fit.

# Usage

```
cxr_er_bootstrap(
  fitness_model,
  optimization_method,
  data,
  covariates,
  init_par,
  lower_bounds,
  upper_bounds,
  fixed_parameters,
  bootstrap_samples
)
```

### **Arguments**

fitness\_model effect/response function, see cxr\_er\_fit
optimization\_method

numerical optimization method.

data

either a list of dataframes or a single dataframe. if 'data' is a list, each element is a dataframe with the following columns:

- fitness: fitness metric for each observation
- neighbours: named columns giving the number of neighbours of each column the names of the list elements are taken to be the names of the focal species.

If 'data' is a dataframe, it also needs a 'focal' column. Regardless of the data structure, all focal species need to have the same number of observations (i.e. same number of rows), and the set of neighbour species needs to be the same as the set of focal species, so that the neighbours columns correspond to the names of the list elements or, if 'data' is a dataframe, to the values of the 'focal' column. Future versions will relax this requirement.

covariates

a data structure equivalent to 'data', in which each column are the values of a covariate.

init\_par initial values for parameters

lower\_bounds o

optional list with single values for "lambda", "effect", "response", and optionally "lambda\_cov", "effect\_cov", "response\_cov".

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```
upper_bounds optional list with single values for "lambda", "effect", "response", and optionally "lambda_cov", "effect_cov", "response_cov".

fixed_parameters
    list with values for fixed parameters, or NULL.

bootstrap_samples
    number of bootstrap samples for error calculation. Defaults to 0, i.e. no error is calculated.
```

#### Value

1d vector, the standard error of each parameter in init\_par

cxr\_er\_fit

General optimization for effect-response models

# Description

Estimates parameters of user-specified models of competitive effects and responses. NOTE: including covariates on competitive effects is still under development, in this version it is suggested not to use that feature.

# Usage

```
cxr_er_fit(
  data,
  model_family = c("BH"),
  covariates = NULL,
 optimization_method = c("Nelder-Mead", "BFGS", "CG", "ucminf", "L-BFGS-B", "nlm",
  "nlminb", "Rcgmin", "Rvmmin", "spg", "bobyqa", "nmkb", "hjkb", "nloptr_CRS2_LM",
    "nloptr_ISRES", "nloptr_DIRECT_L_RAND", "DEoptimR", "GenSA"),
  lambda_cov_form = c("none", "global"),
  effect_cov_form = c("none", "global"),
  response_cov_form = c("none", "global"),
 initial_values = list(lambda = 1, effect = 1, response = 1, lambda_cov = 0, effect_cov
    = 0, response_cov = 0),
  lower_bounds = NULL,
  upper_bounds = NULL,
  fixed_terms = NULL,
  bootstrap_samples = 0
)
```

# Arguments

data

either a list of dataframes or a single dataframe. if 'data' is a list, each element is a dataframe with the following columns:

• fitness: fitness metric for each observation

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> • neighbours: named columns giving the number of neighbours of each column the names of the list elements are taken to be the names of the focal species.

If 'data' is a dataframe, it also needs a 'focal' column. Regardless of the data structure, all focal species need to have the same number of observations (i.e. same number of rows), and the set of neighbour species needs to be the same as the set of focal species, so that the neighbours columns correspond to the names of the list elements or, if 'data' is a dataframe, to the values of the 'focal' column. Future versions will relax this requirement.

model\_family

family of model to use. Available families are BH (Beverton-Holt), LV (Lotka-Volterra), RK (Ricker), and LW (Law-Watkinson). Users may also define their own families and models (see vignette 4).

covariates

a data structure equivalent to 'data', in which each column are the values of a covariate.

optimization\_method

numerical optimization method.

lambda\_cov\_form

form of the covariate effects on lambda. Either "none" (no covariate effects) or "global" (one estimate per covariate).

effect\_cov\_form

form of the covariate effects on competitive effects. Either "none" (no covariate effects) or "global" (one estimate per covariate)

response\_cov\_form

form of the covariate effects on competitive responses. Either "none" (no covariate effects) or "global" (one estimate per covariate)

initial\_values list with components "lambda", "effect", "response", and optionally "lambda\_cov", "effect\_cov", "response\_cov", specifying the initial values for numerical optimization. Single values are allowed.

lower\_bounds

optional list with single values for "lambda", "effect", "response", and optionally "lambda\_cov", "effect\_cov", "response\_cov".

upper\_bounds

optional list with single values for "lambda", "effect", "response", and optionally "lambda\_cov", "effect\_cov", "response\_cov".

fixed\_terms

optional list specifying which model parameters are fixed.

bootstrap\_samples

number of bootstrap samples for error calculation. Defaults to 0, i.e. no error is calculated.

# Value

an object of class 'cxr\_er\_fit' which is a list with the following components:

• model\_name: string with the name of the fitness model

· model: model function

• data: data supplied

· taxa: names of the taxa fitted

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- · covariates: covariate data supplied
- · optimization\_method: optimization method used
- initial\_values: list with initial values
- fixed\_terms: list with fixed terms
- lambda: fitted values for lambdas, or NULL if fixed
- effect: fitted values for competitive effects, or NULL if fixed
- response: fitted values for competitive responses, or NULL if fixed
- lambda\_cov: fitted values for effect of covariates on lambdas, or NULL if fixed
- effect\_cov: fitted values for effect of covariates on competitive effects, or NULL if fixed
- · response\_cov: fitted values for effect of covariates on competitive responses, or NULL if fixed
- lambda\_standard\_error: standard errors for lambdas, if calculated
- effect\_standard\_error: standard errors for competitive effects, if calculated
- response\_standard\_error: standard errors for competitive responses, if calculated
- lambda\_cov\_standard\_error: standard errors for effect of covariates on lambdas, if calculated
- effect\_cov\_standard\_error: standard errors for effect of covariates on competitive effects, if calculated
- response\_cov\_standard\_error: standard errors for effect of covariates on competitive responses, if calculated
- log\_likelihood: log-likelihood of the fits

# **Examples**

```
# fit three species at once
data("neigh_list")
# these species all have >250 observations
example_sp <- c("BEMA","LEMA","HOMA")</pre>
sp.pos <- which(names(neigh_list) %in% example_sp)</pre>
data <- neigh_list[sp.pos]</pre>
n.obs <- 250
# keep only fitness and neighbours columns
for(i in 1:length(data)){
 data[[i]] <- data[[i]][1:n.obs,c(2,sp.pos+2)]#2:length(data[[i]])]</pre>
# covariates: salinity
data("salinity_list")
salinity <- salinity_list[example_sp]</pre>
# keep only salinity column
for(i in 1:length(salinity)){
  salinity[[i]] <- salinity[[i]][1:n.obs,2:length(salinity[[i]])]</pre>
initial_values = list(lambda = 1,
                      effect = 1,
                      response = 1
                      # lambda_cov = 0,
```

cxr\_generate\_test\_data

```
# effect_cov = 0,
                     # response_cov = 0
lower_bounds = list(lambda = 0,
                   effect = 0,
                   response = 0
                   # lambda_cov = 0,
                   # effect_cov = 0,
                   # response_cov = 0
)
upper_bounds = list(lambda = 100,
                    effect = 10,
                    response = 10
                   # lambda_cov = 0,
                   # effect_cov = 0,
                   # response_cov = 0
)
er_3sp <- cxr_er_fit(data = data,
                     model_family = "BH",
                     # fit without covariates,
                     # as it may be very computationally expensive
                     # covariates = salinity,
                     optimization_method = "bobyqa",
                     lambda_cov_form = "none",
                     effect_cov_form = "none",
                     response_cov_form = "none",
                     initial_values = initial_values,
                     lower_bounds = lower_bounds,
                     upper_bounds = upper_bounds,
                     # syntaxis for fixed values
                     # fixed_terms = list("response"),
                     bootstrap_samples = 3)
# brief summary
summary(er_3sp)
```

cxr\_generate\_test\_data

Generate simulated interaction data

# Description

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Model fitness responses to neighbours and covariates using a Beverton-Holt functional form. This function is fairly restricted and under development, but can be used to generate simple test data to run the main functions of cxr.

# Usage

```
cxr_generate_test_data(
```

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```
focal_sp = 1,
  neigh_sp = 1,
  covariates = 0.
  observations = 10,
  alpha_form = c("pairwise", "none", "global"),
  lambda_cov_form = c("none", "global"),
  alpha_cov_form = c("none", "global", "pairwise"),
  focal_lambda = NULL,
 min lambda = 0.
 max_lambda = 10,
 alpha = NULL,
 min_alpha = 0,
 max_alpha = 1,
  alpha_cov = NULL,
 min_alpha_cov = -1,
 max_alpha_cov = 1,
  lambda_cov = NULL,
 min_lambda_cov = -1,
 max_lambda_cov = 1,
 min_cov = 0,
 max\_cov = 1
)
```

number of focal species, defaults to 1.

#### **Arguments**

focal\_sp

number of neighbour species, defaults to 1. neigh\_sp number of covariates, defaults to 0. covariates observations number of observations, defaults to 10. alpha\_form what form does the alpha parameter take? one of "none" (no alpha in the model), "global" (a single alpha for all pairwise interactions), or "pairwise" (one alpha value for every interaction). lambda\_cov\_form form of the covariate effects on lambda. Either "none" (no covariate effects) or "global" (one estimate per covariate). alpha\_cov\_form form of the covariate effects on alpha. One of "none" (no covariate effects), "global" (one estimate per covariate on every alpha), or "pairwise" (one estimate per covariate and pairwise alpha). focal\_lambda optional 1d vector with lambdas of the focal sp. min\_lambda if no focal\_lambda is provided, lambdas are taken from a uniform distribution with min lambda and max lambda as minimum and maximum values. if no focal\_lambda is provided, lambdas are taken from a uniform distribution max\_lambda with min lambda and max lambda as minimum and maximum values. alpha optional interaction matrix, neigh\_sp x neigh\_sp min\_alpha if no focal alpha is provided, alphas are taken from a uniform distribution with min\_alpha and max\_alpha as minimum and maximum values.

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max_alpha	if no focal_alpha is provided, alphas are taken from a uniform distribution with min_alpha and max_alpha as minimum and maximum values.
alpha_cov	Under development
min_alpha_cov	if no focal_alpha_cov is provided, alpha_covs are taken from a uniform distribution with min_alpha_cov and max_alpha_cov as minimum and maximum values.
max_alpha_cov	if no focal_alpha_cov is provided, alpha_covs are taken from a uniform distribution with min_alpha and max_alpha as minimum and maximum values.
lambda_cov	optional matrix of neigh_sp x covariates giving the effect of each covariate over the fecundity (lambda) of each species.
min_lambda_cov	if no focal_lambda_cov is provided, lambda_covs are taken from a uniform distribution with min_lambda_cov and max_lambda_cov as minimum and maximum values.
max_lambda_cov	if no focal_lambda_cov is provided, lambda_covs are taken from a uniform distribution with min_lambda and max_lambda as minimum and maximum values.
min_cov	minimum value for covariates
max_cov	maximum value for covariates

### Value

list with two components: 'observations' is a list with as many components as focal species. Each component of 'observations' is a dataframe with stochastic number of neighbours and associated fitness. The second component, 'covariates', is again a list with one component per focal species. Each component of 'covariates' is a dataframe with the values of each covariate for each associated observation.

# **Examples**

cxr\_pm\_bootstrap

Standard error estimates for model parameters

# **Description**

Computes bootstrap standard errors for a given population dynamics model. This function is provided for completeness, but error calculation is integrated in the function cxr\_pm\_fit.

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### Usage

```
cxr_pm_bootstrap(
  fitness_model,
  optimization_method,
  data,
  focal_column,
  covariates,
  init_par,
  lower_bounds,
  upper_bounds,
  fixed_parameters,
  bootstrap_samples
)
```

# **Arguments**

fitness\_model function returning a single value to minimize, given a set of parameters and a fitness metric

optimization\_method

numerical optimization method

data dataframe with observations in rows and two sets of columns:

dataframe with observations in rows and two sets of columns

• fitness: fitness metric for the focal individual

• neighbours: columns with user-defined names with number of neighbours

for each group

focal\_column optional integer value giving the position, or name, of the column with neigh-

bours from the same species as the focal one. This is necessary if "alpha\_intra"

is specified.

covariates optional matrix with observations in rows and covariates in columns. Each cell

is the value of a covariate in a given observation.

init\_par 1d vector of initial parameters

lower\_bounds 1d vector of lower bounds

upper\_bounds 1d vector of upper bounds

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "alpha\_intra", "alpha\_inter"

and "alpha\_cov".

bootstrap\_samples

how many bootstrap samples to compute.

# Value

1d vector, the standard error of each parameter in init\_par

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cxr\_pm\_fit

General optimization for population models

# **Description**

Estimates parameters of user-specified population dynamics models.

# Usage

```
cxr_pm_fit(
  data,
  focal_column = NULL,
  model_family,
  covariates = NULL,
 optimization_method = c("Nelder-Mead", "BFGS", "CG", "ucminf", "L-BFGS-B", "nlm",
   "nlminb", "Rcgmin", "Rvmmin", "spg", "bobyqa", "nmkb", "hjkb", "nloptr_CRS2_LM",
    "nloptr_ISRES", "nloptr_DIRECT_L_RAND", "DEoptimR", "GenSA"),
  alpha_form = c("none", "global", "pairwise"),
  lambda_cov_form = c("none", "global"),
alpha_cov_form = c("none", "global", "pairwise"),
 initial_values = list(lambda = 0, alpha_intra = 0, alpha_inter = 0, lambda_cov = 0,
    alpha_cov = 0),
  lower_bounds = NULL,
  upper_bounds = NULL,
  fixed_terms = NULL,
  bootstrap_samples = 0
)
```

# Arguments

data

dataframe with observations in rows and two sets of columns:

- fitness: fitness metric for the focal individual
- neighbours: numeric columns with user-defined names, giving number of neighbours for each group

focal\_column

optional integer or character giving the column with neighbours from the same species as the focal one. This field is necessary if "alpha\_intra" is specified in initial\_values, lower\_bounds, upper\_bounds, or fixed\_terms.

model\_family

family of model to use. Available families are BH (Beverton-Holt), LV (Lotka-Volterra), RK (Ricker), and LW (Law-Watkinson). Users may also define their own families and models (see vignette 4).

covariates

optional named matrix or dataframe with observations (rows) of any number of environmental covariates (columns).

optimization\_method

numerical optimization method.

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alpha\_form what form does the alpha parameter take? one of "none" (no alpha in the model), "global" (a single alpha for all pairwise interactions), or "pairwise" (one alpha value for every interaction).

lambda\_cov\_form

form of the covariate effects on lambda. Either "none" (no covariate effects) or "global" (one estimate per covariate).

alpha\_cov\_form form of the covariate effects on alpha. One of "none" (no covariate effects),

"global" (one estimate per covariate on every alpha), or "pairwise" (one estimate
per covariate and pairwise alpha)

initial\_values list with components "lambda", "alpha\_intra", "alpha\_inter", "lambda\_cov", "alpha\_cov", specifying the initial values for numerical optimization. Single values are allowed.

lower\_bounds optional list with single values for "lambda", "alpha\_intra", "alpha\_inter", "lambda\_cov", "alpha\_cov".

upper\_bounds optional list with single values for "lambda", "alpha\_intra", "alpha\_inter", "lambda\_cov", "alpha\_cov".

fixed\_terms optional list of numeric vectors specifying the value of fixed model parameters, among "lambda", "alpha\_intra", "alpha\_inter", "lambda\_cov", and "alpha\_cov".

bootstrap\_samples

number of bootstrap samples for error calculation. Defaults to 0, i.e. no error is calculated.

# Value

an object of class 'cxr\_pm\_fit' which is a list with the following components:

- model\_name: string with the name of the fitness model
- · model: model function
- data: data supplied
- focal\_ID: name/ID of the focal taxa, if provided in 'focal\_column'
- covariates: covariate data supplied
- optimization\_method: optimization method used
- initial values: list with initial values
- fixed terms: list with fixed terms
- lambda: fitted value for lambda, or NULL if fixed
- alpha\_intra: fitted value for intraspecific alpha, or NULL if fixed
- alpha\_inter: fitted value for interspecific alpha, or NULL if fixed
- lambda\_cov: fitted value(s) for lambda\_cov, or NULL if fixed.
- alpha\_cov: fitted value(s) for alpha\_cov, or NULL if fixed. These are structured as a list with one element for each covariate.
- lambda\_standard\_error: standard error for lambda, if computed
- alpha\_intra\_standard\_error: standard error for intraspecific alpha, if computed

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- alpha\_inter\_standard\_error: standard error for interspecific alpha, if computed
- lambda\_cov\_standard\_error: standard error for lambda\_cov, if computed
- alpha\_cov\_standard\_error: standard error for alpha\_cov, if computed
- log\_likelihood: log-likelihood of the fit

#### **Examples**

```
data("neigh_list")
my.sp <- "BEMA"
# data for a single species, keep only fitness and neighbours columns
sp_data <- neigh_list[[my.sp]][2:ncol(neigh_list[[1]])]</pre>
 sp_fit <- cxr_pm_fit(data = sp_data,</pre>
                       focal_column = my.sp,
                       optimization_method = "bobyqa",
                       model_family = "BH",
                       alpha_form = "pairwise"
                       lambda_cov_form = "none",
                       alpha_cov_form = "none",
                    initial_values = list(lambda = 1,alpha_intra = 0.1,alpha_inter = 0.1),
                       lower_bounds = list(lambda = 0,alpha_intra = 0,alpha_inter = 0),
                       upper_bounds = list(lambda = 100,alpha_intra = 1,alpha_inter = 1),
                       bootstrap_samples = 3)
 summary(sp_fit)
```

cxr\_pm\_multifit

Multi-species parameter optimization

# **Description**

This function is a wrapper for estimating parameters for several focal species, instead of making separate calls to cxr\_pm\_fit.

# Usage

```
cxr_pm_multifit(
  data,
  model_family = c("BH"),
  focal_column = NULL,
  covariates = NULL,
  optimization_method = c("BFGS", "CG", "Nelder-Mead", "ucminf", "L-BFGS-B", "nlm",
    "nlminb", "Rcgmin", "Rvmmin", "spg", "bobyqa", "nmkb", "hjkb", "nloptr_CRS2_LM",
    "nloptr_ISRES", "nloptr_DIRECT_L_RAND", "DEoptimR", "GenSA"),
  alpha_form = c("none", "global", "pairwise"),
  lambda_cov_form = c("none", "global"),
  alpha_cov_form = c("none", "global", "pairwise"),
```

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```
initial_values = NULL,
lower_bounds = NULL,
upper_bounds = NULL,
fixed_terms = NULL,
bootstrap_samples = 0
)
```

#### **Arguments**

data named list in which each component is a dataframe with a fitness column and a

number of columns representing neighbours

model\_family family of model to use. Available families are BH (Beverton-Holt), LV (Lotka-

Volterra), RK (Ricker), and LW (Law-Watkinson). Users may also define their

own families and models (see vignette 4).

focal\_column character vector with the same length as data, giving the names of the columns

representing intraspecific observations for each species, or numeric vector giv-

ing the position of such columns.

covariates optional named list in which each component is a dataframe with values of each

covariate for each observation. The ith component of covariates are the covariate values that correspond to the ith component of data, so they must have

the same number of observations.

optimization\_method

numerical optimization method.

alpha\_form what form does the alpha parameter take? one of "none" (no alpha in the model),

"global" (a single alpha for all pairwise interactions), or "pairwise" (one alpha

value for every interaction).

lambda\_cov\_form

form of the covariate effects on lambda. Either "none" (no covariate effects) or

"global" (one estimate per covariate).

alpha\_cov\_form form of the covariate effects on alpha. One of "none" (no covariate effects),

"global" (one estimate per covariate on every alpha), or "pairwise" (one estimate

per covariate and pairwise alpha)

initial\_values list with components "lambda", "alpha\_intra", "alpha\_inter", "lambda\_cov", "al-

pha\_cov", specifying the initial values for numerical optimization. Single values

are allowed.

lower\_bounds optional list with single values for "lambda", "alpha\_intra", "alpha\_inter", "lambda\_cov",

"alpha\_cov".

upper\_bounds optional list with single values for "lambda", "alpha\_intra", "alpha\_inter", "lambda\_cov",

"alpha\_cov".

fixed\_terms optional named list in which each component is itself a list containing fixed

terms for each focal species.

bootstrap\_samples

number of bootstrap samples for error calculation. Defaults to 0, i.e. no error is

calculated.

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#### Value

an object of class 'cxr\_pm\_multifit' which is a list with the following components:

- model\_name: string with the name of the fitness model
- model: model function
- data: data supplied
- · taxa: names of the taxa fitted
- covariates: covariate data supplied
- optimization\_method: optimization method used
- initial\_values: list with initial values
- fixed terms: list with fixed terms
- lambda: fitted values for lambda, or NULL if fixed
- alpha\_intra: fitted values for alpha\_intra, or NULL if fixed
- alpha\_inter: fitted values for alpha\_inter, or NULL if fixed
- lambda\_cov: fitted values for lambda\_cov, or NULL if fixed
- alpha\_cov: fitted values for alpha\_cov, or NULL if fixed
- lambda\_standard\_error: standard errors for lambda, if computed
- alpha\_standard\_error: standard errors for alpha, if computed
- lambda\_cov\_standard\_error: standard errors for lambda\_cov, if computed
- alpha\_cov\_standard\_error: standard errors for alpha\_cov, if computed
- log\_likelihood: log-likelihoods of the fits

### **Examples**

```
# fit three species at once
data("neigh_list")
data <- neigh_list[1:3]</pre>
# keep only fitness and neighbours columns
for(i in 1:length(data)){
 data[[i]] <- data[[i]][,2:length(data[[i]])]</pre>
# be explicit about the focal species
focal.sp <- names(data)</pre>
# covariates: salinity
data("salinity_list")
salinity <- salinity_list[1:3]</pre>
# keep only salinity column
for(i in 1:length(salinity)){
  salinity[[i]] <- data.frame(salinity = salinity[[i]][,2:length(salinity[[i]])])</pre>
 fit_3sp <- cxr_pm_multifit(data = data,</pre>
                               optimization_method = "bobyqa",
                               model_family = "BH",
                               focal_column = focal.sp,
```

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```
covariates = salinity,
                           alpha_form = "pairwise",
                            lambda_cov_form = "global",
                           alpha_cov_form = "global",
                            initial_values = list(lambda = 1,
                                                  alpha_intra = 0.1,
                                                  alpha_inter = 0.1,
                                                  lambda\_cov = 0.1,
                                                  alpha_cov = 0.1),
                           lower_bounds = list(lambda = 0.01,
                                                alpha_intra = 0,
                                                alpha_inter = 0,
                                                lambda\_cov = 0,
                                                alpha_cov = 0),
                           upper_bounds = list(lambda = 100,
                                                alpha_intra = 1,
                                                alpha_inter = 1,
                                                lambda\_cov = 1,
                                                alpha_cov = 1),
                           bootstrap_samples = 3)
# brief summary
summary(fit_3sp)
# interaction matrix
fit\_3sp\$alpha\_matrix
```

densities\_to\_df

Converts a densities list to a tidy dataframe

# Description

Converts a densities list to a tidy dataframe

# Usage

```
densities_to_df(densities)
```

# Arguments

densities

list, species (optionally x year) with each element holding a sites x stages matrix. This function assumes three life stages.

# Value

dataframe with columns species-stage-site(-year)-density

34 fill\_dispersal\_matrix

```
fill_demography_matrix
```

Fill the vec-permutation demography matrix

# **Description**

Fill for a given species, across all sites.

# Usage

```
fill_demography_matrix(focal.sp, vpm, transition_matrices)
```

# **Arguments**

focal.sp integer, focal species.

vpm data structure holding all vector-permutation matrices; see 'vec\_permutation\_matrices'.

If not in an appropriate format, it is likely to fail without warning.

transition\_matrices

nested list species x sites, in which each element holds a 3x3 transition matrix.

If not in that format, it is likely to fail without warning.

# Value

vec-permutation demography matrix for a given species across sites.

```
fill_dispersal_matrix Fill the vec-permutation dispersal matrix
```

# **Description**

Fill for a given species, all sites

# Usage

```
fill_dispersal_matrix(
  focal.sp,
  num.sites,
  param,
  vpm,
  env = NULL,
  current.densities
)
```

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# **Arguments**

focal.sp integer, focal species
num.sites integer, how many sites

param param nested list,see 'build\_param' function

vpm data structure holding all vector-permutation matrices; see 'vec\_permutation\_matrices'

env optional numeric, environmental forcing for a given timestep

current.densities

list of length sp, each element is a matrix sites\*stages

#### Value

dispersal matrix, stages\*sites

fill\_transition\_matrix

Fill a transition matrix

# **Description**

Calculates the elements of a site-specific transition matrix for a given sp. Note that here, and through all functions, we fix three life stages. Also note that 'param' and 'env' must match, as for the 'vital\_rate' function.

# Usage

```
fill_transition_matrix(focal.sp, site, param, env = NULL, current.densities)
```

# **Arguments**

focal.sp integer, species site integer, site

param structure (see 'build\_param' function)

env optional numeric, environmental forcing for a given timestep

current.densities

list of length sp, each element is a matrix site\*stages

#### Value

3x3 transition matrix

fitness\_ratio

Fitness ratio among two or more species

# Description

Fitness ratio among two or more species

# Usage

```
fitness_ratio(
  effect_response_fit = NULL,
  fitness_sp1 = NULL,
  fitness_sp2 = NULL
)
```

# **Arguments**

#### Value

either a matrix with fitness ratios for all pairs of fitted species, or a single numeric value. The matrix elements represent the ratios of species in columns over species in rows, and conversely, the numeric value represents the ratio of sp1 over sp2.

### **Examples**

```
fitness_ratio(fitness_sp1 = 0.6, fitness_sp2 = 0.3)
```

```
generate_vital_rate_coefs
```

Generate coefficients for obtaining vital rates

# **Description**

Any vital rate is a function of several parameters, potentially including interactions or environmental effects. This function generates the coefficients for these parameters, so that users do not have to introduce them all manually in a 'param' list. Coefficients can be generated from a random sampling of a normal distribution with specified mean and standard deviation, or they can be retrieved from a model object that accepts a 'tidy' function from the broom/broom.mixed packages. This is because coefficients for vital rates can be understood as coefficients from statistical regressions.

### Usage

```
generate_vital_rate_coefs(
  param,
  sp = NULL,
  sites = NULL,
  vital.rate = NULL,
  vr.coef = NULL,
  mean.coef = NULL,
  sd.coef = NULL,
  glm.object = NULL,
  glm.coef.equivalence = NULL)
```

#### **Arguments**

	param	the original list with the structure of species, sites, vital rates to calculate, and parameters affecting them. See the function 'build_param'
		-
	sp	number or character of the species to calculate coefficients for. If empty, all species are assumed.
	sites	number or character of the sites to calculate coefficients for. If empty, all sites are assumed.
	vital.rate	character giving the vital rate to calculate coefficients for. If empty, all vital rates are assumed.
	vr.coef	character giving a specific coefficient to calculate. If empty, all coefficients are assumed.
	mean.coef	optional numeric value, mean for sampling coefficient values
	sd.coef	optional numeric value, standard deviation for sampling coefficient values
	glm.object	optional model object/coef table
glm.coef.equivalence		
	-	'C - 1- 411 ' '111 - 1'4 1'6C - C 4- ( (- 144 - 44 - 44 - 44 -

if a glm table is provided and its names differ from the 'param' data structure, you can include a named list in which names are the names from 'param' and its elements are the equivalent names from the glm table

### **Details**

In the current version, we assume that the model coefficients come from a logistic regression with binomial family. Otherwise, the function will probably not fail, but the coefficients will not be interpretable and the results in terms of obtaining the actual vital rates from these will be meaningless.

Also note that you need to take care manually of the signs of the coefficients, if entered through mean/sd pairs.

# Value

the updated parameter list

glm\_example\_coefs Generalized linear model coefficients

### **Description**

A table with coefficients from a GLM to serve as an example for importing into the data structure of the metapopulation model.

# Usage

```
data(glm_example_coefs)
```

#### **Format**

A named numerical matrix of 8 rows and 4 columns

```
LV_er_lambdacov_global_effectcov_global_responsecov_global

Effect response Lotka-Volterra model with covariate effects on lambda, effect, and response
```

# **Description**

Note that, as e and r are not pair-specific, all species parameters are fit in the same function.

# Usage

```
LV_er_lambdacov_global_effectcov_global_responsecov_global(
   par,
   fitness,
   target,
   density,
   covariates,
   fixed_parameters
)
```

# **Arguments**

density

par	1d vector with initial parameters in the order: lambda,lambda_cov,effect,effect_cov,response,response_co
fitness	1d vector with fitness observations
target	matrix with species in rows, observations in columns. Value is 1 if a species is focal for a given observation, 0 otherwise.

matrix with species in rows, observations in columns. Value is density of each

sp as neighbour for each observation.

covariates numeric dataframe or matrix with observations in rows and covariates in columns.

Each cell is the value of a covariate in a given observation

fixed\_parameters

 $optional\ list\ specifying\ values\ of\ fixed\ parameters,\ with\ components\ "lambda", "lambda\_cov", "effect", "e$ 

"response", "response\_cov".

#### Value

log-likelihood value

```
LV_er_lambdacov_none_effectcov_none_responsecov_none

*Effect response Lotka-Volterra model without covariate effects*
```

### **Description**

Note that, as e and r are not pair-specific, all species parameters are fit in the same function.

# Usage

```
LV_er_lambdacov_none_effectcov_none_responsecov_none(
    par,
    fitness,
    target,
    density,
    covariates,
    fixed_parameters
)
```

#### **Arguments**

par 1d vector with initial parameters in the order: lambda,effect,response,sigma.

fitness 1d vector with fitness observations.

target matrix with species in rows, observations in columns. Value is 1 if a species is

focal for a given observation, 0 otherwise.

density matrix with species in rows, observations in columns. Value is density of each

sp as neighbour for each observation.

covariates included for compatibility, not used in this model.

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "effect", "response".

#### Value

log-likelihood value

```
LV_pm_alpha_global_lambdacov_none_alphacov_none

Lotka-Volterra model with a global alpha and no covariate effects
```

# **Description**

Lotka-Volterra model with a global alpha and no covariate effects

#### Usage

```
LV_pm_alpha_global_lambdacov_none_alphacov_none(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

# **Arguments**

### Value

log-likelihood value

```
LV_pm_alpha_none_lambdacov_none_alphacov_none

Lotka-Volterra model with no alphas and no covariate effects
```

# **Description**

This model, in all families, is simply given by lambda.

#### Usage

```
LV_pm_alpha_none_lambdacov_none_alphacov_none(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

#### Arguments

#### Value

log-likelihood value

```
LV_pm_alpha_pairwise_lambdacov_global_alphacov_global

Lotka-Volterra model with pairwise alphas and global covariate effects on lambda and alpha
```

# **Description**

Lotka-Volterra model with pairwise alphas and global covariate effects on lambda and alpha

# Usage

```
LV_pm_alpha_pairwise_lambdacov_global_alphacov_global(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

#### **Arguments**

par 1d vector of initial parameters: lambda, lambda\_cov, alpha, alpha\_cov, and

sigma

fitness 1d vector of fitness observations, in log scale

neigh\_intra\_matrix

optional matrix of one column, number of intraspecific neighbours for each ob-

servation

neigh\_inter\_matrix

matrix of arbitrary columns, number of interspecific neighbours for each obser-

vation

covariates optional matrix with observations in rows and covariates in columns. Each cell

is the value of a covariate in a given observation

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "alpha\_intra", "alpha\_inter"

#### Value

log-likelihood value

```
LV_pm_alpha_pairwise_lambdacov_global_alphacov_pairwise
```

Lotka-Volterra model with pairwise alphas, covariate effects on lambda, and pairwise covariate effects on alpha

### Description

Lotka-Volterra model with pairwise alphas, covariate effects on lambda, and pairwise covariate effects on alpha

#### Usage

```
LV_pm_alpha_pairwise_lambdacov_global_alphacov_pairwise(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

### Arguments

par 1d vector of initial parameters: lambda, lambda\_cov, alpha, alpha\_cov, and

sigma

fitness 1d vector of fitness observations, in log scale

```
neigh_intra_matrix
```

optional matrix of one column, number of intraspecific neighbours for each ob-

servation

neigh\_inter\_matrix

matrix of arbitrary columns, number of interspecific neighbours for each obser-

vation

covariates

optional matrix with observations in rows and covariates in columns. Each cell

is the value of a covariate in a given observation

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "alpha\_intra", "alpha\_inter"

#### Value

log-likelihood value

LV\_pm\_alpha\_pairwise\_lambdacov\_none\_alphacov\_none

Lotka-Volterra model with pairwise alphas and no covariate effects

# Description

Lotka-Volterra model with pairwise alphas and no covariate effects

# Usage

```
LV_pm_alpha_pairwise_lambdacov_none_alphacov_none(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

#### Arguments

par 1d vector of initial parameters: 'lambda', 'alpha\_intra' (optional), 'alpha\_inter',

and 'sigma'

fitness 1d vector of fitness observations, in log scale

neigh\_intra\_matrix

optional matrix of one column, number of intraspecific neighbours for each ob-

servation

neigh\_inter\_matrix

matrix of arbitrary columns, number of interspecific neighbours for each obser-

vation

covariates included for compatibility, not used in this model

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "alpha\_intra", "alpha\_inter"

#### Value

log-likelihood value

```
LV_project_alpha_global_lambdacov_none_alphacov_none

Lotka-Volterra model for projecting abundances, with a global alpha
and no covariate effects
```

# Description

Lotka-Volterra model for projecting abundances, with a global alpha and no covariate effects

### Usage

```
LV_project_alpha_global_lambdacov_none_alphacov_none(
    lambda,
    alpha_intra,
    alpha_inter,
    lambda_cov,
    alpha_cov,
    abundance,
    covariates
)
```

### Arguments

lambda numeric lambda value.

alpha\_intra included for compatibility, not used in this model.

alpha\_inter single numeric value.

lambda\_cov included for compatibility, not used in this model.

alpha\_cov included for compatibility, not used in this model.

abundance named numeric vector of abundances in the previous timestep.

covariates included for compatibility, not used in this model.

# Value

numeric abundance projected one timestep

```
{\it LV\_project\_alpha\_none\_lambdacov\_none\_alphacov\_none} \\ Model~for~projecting~abundances,~with~no~alpha~and~no~covariate~effects
```

### **Description**

Model for projecting abundances, with no alpha and no covariate effects

#### Usage

```
LV_project_alpha_none_lambdacov_none_alphacov_none(
    lambda,
    alpha_intra,
    alpha_inter,
    lambda_cov,
    alpha_cov,
    abundance,
    covariates
)
```

# Arguments

```
lambda numeric lambda value.

alpha_intra included for compatibility, not used in this model.

alpha_inter included for compatibility, not used in this model.

lambda_cov included for compatibility, not used in this model.

alpha_cov included for compatibility, not used in this model.

alpha_cov included for compatibility, not used in this model.

abundance named numeric vector of abundances in the previous timestep.
```

covariates included for compatibility, not used in this model.

#### Value

numeric abundance projected one timestep

```
LV_project_alpha_pairwise_lambdacov_global_alphacov_global

Lotka-Volterra model for projecting abundances, with specific alpha

values and global covariate effects on alpha and lambda
```

#### **Description**

Lotka-Volterra model for projecting abundances, with specific alpha values and global covariate effects on alpha and lambda

#### Usage

```
LV_project_alpha_pairwise_lambdacov_global_alphacov_global(
    lambda,
    alpha_intra,
    alpha_inter,
    lambda_cov,
    alpha_cov,
    abundance,
    covariates
)
```

### Arguments

lambda numeric lambda value.

alpha\_intra single numeric value.

alpha\_inter numeric vector with interspecific alpha values.

lambda\_cov numeric vector with effects of covariates over lambda.

alpha\_cov named list of numeric values with effects of each covariate over alpha.

abundance named numeric vector of abundances in the previous timestep.

covariates matrix with observations in rows and covariates in columns. Each cell is the

value of a covariate in a given observation.

#### Value

numeric abundance projected one timestep

```
LV_project_alpha_pairwise_lambdacov_global_alphacov_pairwise

Lotka-Volterra model for projecting abundances, with specific alpha

values and global covariate effects on alpha and lambda
```

# **Description**

Lotka-Volterra model for projecting abundances, with specific alpha values and global covariate effects on alpha and lambda

### Usage

```
LV_project_alpha_pairwise_lambdacov_global_alphacov_pairwise(
  lambda,
  alpha_intra,
  alpha_inter,
  lambda_cov,
  alpha_cov,
  abundance,
  covariates
)
```

# Arguments

named numeric lambda value. lambda alpha\_intra single numeric value. alpha\_inter numeric vector with interspecific alpha values. lambda\_cov numeric vector with effects of covariates over lambda. alpha\_cov named list of named numeric vectors with effects of each covariate over alpha values. abundance named numeric vector of abundances in the previous timestep. covariates matrix with observations in rows and covariates in named columns. Each cell is the value of a covariate in a given observation.

#### Value

numeric abundance projected one timestep

```
LV_project_alpha_pairwise_lambdacov_none_alphacov_none

Lotka-Volterra model for projecting abundances, with specific alpha

values and no covariate effects
```

# Description

Lotka-Volterra model for projecting abundances, with specific alpha values and no covariate effects

# Usage

```
LV_project_alpha_pairwise_lambdacov_none_alphacov_none(
    lambda,
    alpha_intra,
    alpha_inter,
    lambda_cov,
    alpha_cov,
    abundance,
    covariates
)
```

#### **Arguments**

lambda	numeric lambda value.
alpha_intra	included for compatibility, not used in this model.
alpha_inter	single numeric value.
lambda_cov	included for compatibility, not used in this model.
alpha_cov	included for compatibility, not used in this model.
abundance	named numeric vector of abundances in the previous timestep.
covariates	included for compatibility, not used in this model.

#### Value

numeric abundance projected one timestep

```
LW_er_lambdacov_global_effectcov_global_responsecov_global

Effect response Law-Watkinson model with covariate effects on lambda, effect, and response
```

# Description

Note that, as e and r are not pair-specific, all species parameters are fit in the same function.

# Usage

```
LW_er_lambdacov_global_effectcov_global_responsecov_global(
  par,
  fitness,
  target,
  density,
  covariates,
  fixed_parameters
)
```

# **Arguments**

par	1d vector with initial parameters in the order: lambda,lambda_cov,effect,effect_cov,response,response_co
fitness	1d vector with fitness observations
target	matrix with species in rows, observations in columns. Value is 1 if a species is focal for a given observation, 0 otherwise.
density	matrix with species in rows, observations in columns. Value is density of each sp as neighbour for each observation.
covariates	numeric dataframe or matrix with observations in rows and covariates in columns. Each cell is the value of a covariate in a given observation

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "lambda\_cov", "effect", "eff "response", "response\_cov".

# Value

log-likelihood value

```
LW_er_lambdacov_none_effectcov_none_responsecov_none

Effect response Law-Watkinson model without covariate effects
```

# Description

Note that, as e and r are not pair-specific, all species parameters are fit in the same function.

#### Usage

```
LW_er_lambdacov_none_effectcov_none_responsecov_none(
  par,
  fitness,
  target,
  density,
  covariates,
  fixed_parameters
)
```

### **Arguments**

par 1d vector with initial parameters in the order: lambda,effect,response,sigma.

fitness 1d vector with fitness observations.

target matrix with species in rows, observations in columns. Value is 1 if a species is

focal for a given observation, 0 otherwise.

density matrix with species in rows, observations in columns. Value is density of each

sp as neighbour for each observation.

covariates included for compatibility, not used in this model.

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "effect", "response".

#### Value

log-likelihood value

```
LW_pm_alpha_global_lambdacov_none_alphacov_none

Law-Watkinson model with a global alpha and no covariate effects
```

# **Description**

Law-Watkinson model with a global alpha and no covariate effects

#### Usage

```
LW_pm_alpha_global_lambdacov_none_alphacov_none(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

#### Arguments

#### Value

log-likelihood value

```
LW_pm_alpha_none_lambdacov_none_alphacov_none

Law-Watkinson model with no alphas and no covariate effects
```

# **Description**

This model, in all families, is simply given by lambda.

# Usage

```
LW_pm_alpha_none_lambdacov_none_alphacov_none(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

#### **Arguments**

#### Value

log-likelihood value

```
LW_pm_alpha_pairwise_lambdacov_global_alphacov_global

Law-Watkinson model with pairwise alphas and global covariate effects on lambda and alpha
```

# **Description**

Law-Watkinson model with pairwise alphas and global covariate effects on lambda and alpha

#### Usage

```
LW_pm_alpha_pairwise_lambdacov_global_alphacov_global(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

# **Arguments**

par 1d vector of initial parameters: lambda, lambda\_cov, alpha, alpha\_cov, and

sigma

fitness 1d vector of fitness observations, in log scale

neigh\_intra\_matrix

optional matrix of one column, number of intraspecific neighbours for each ob-

servation

```
neigh_inter_matrix
```

matrix of arbitrary columns, number of interspecific neighbours for each obser-

vation

covariates

optional matrix with observations in rows and covariates in columns. Each cell

is the value of a covariate in a given observation

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "alpha\_intra", "alpha\_inter"

#### Value

log-likelihood value

```
LW_pm_alpha_pairwise_lambdacov_global_alphacov_pairwise
```

Law-Watkinson model with pairwise alphas, covariate effects on lambda, and pairwise covariate effects on alpha

### **Description**

Law-Watkinson model with pairwise alphas, covariate effects on lambda, and pairwise covariate effects on alpha

# Usage

```
LW_pm_alpha_pairwise_lambdacov_global_alphacov_pairwise(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

#### **Arguments**

par 1d vector of initial parameters: lambda, lambda\_cov, alpha, alpha\_cov, and

sigma

fitness 1d vector of fitness observations, in log scale

neigh\_intra\_matrix

optional matrix of one column, number of intraspecific neighbours for each ob-

servation

neigh\_inter\_matrix

matrix of arbitrary columns, number of interspecific neighbours for each obser-

vation

covariates optional matrix with observations in rows and covariates in columns. Each cell

is the value of a covariate in a given observation

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "alpha\_intra", "alpha\_inter"

# Value

log-likelihood value

```
LW_pm_alpha_pairwise_lambdacov_none_alphacov_none

Law-Watkinson model with pairwise alphas and no covariate effects
```

# **Description**

Law-Watkinson model with pairwise alphas and no covariate effects

# Usage

```
LW_pm_alpha_pairwise_lambdacov_none_alphacov_none(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

# **Arguments**

```
par 1d vector of initial parameters: 'lambda', 'alpha_intra' (optional), 'alpha_inter', and 'sigma'

fitness 1d vector of fitness observations, in log scale

neigh_intra_matrix optional matrix of one column, number of intraspecific neighbours for each observation

neigh_inter_matrix matrix of arbitrary columns, number of interspecific neighbours for each observation

covariates included for compatibility, not used in this model

fixed_parameters
```

optional list specifying values of fixed parameters, with components "lambda", "alpha\_intra", "alpha\_inter"

#### Value

log-likelihood value

# **Description**

Law-Watkinson model for projecting abundances, with a global alpha and no covariate effects

# Usage

```
LW_project_alpha_global_lambdacov_none_alphacov_none(
  lambda,
  alpha_intra,
  alpha_inter,
  lambda_cov,
  alpha_cov,
  abundance,
  covariates
)
```

#### **Arguments**

```
lambda numeric lambda value.

alpha_intra included for compatibility, not used in this model.

alpha_inter single numeric value.

lambda_cov included for compatibility, not used in this model.

alpha_cov included for compatibility, not used in this model.

abundance named numeric vector of abundances in the previous timestep.

covariates included for compatibility, not used in this model.
```

### Value

numeric abundance projected one timestep

```
LW_project_alpha_none_lambdacov_none_alphacov_none

Model for projecting abundances, with no alpha and no covariate effects
```

# **Description**

Model for projecting abundances, with no alpha and no covariate effects

### Usage

```
LW_project_alpha_none_lambdacov_none_alphacov_none(
  lambda,
  alpha_intra,
  alpha_inter,
  lambda_cov,
  alpha_cov,
  abundance,
  covariates
)
```

### Arguments

```
lambda numeric lambda value.

alpha_intra included for compatibility, not used in this model.

alpha_inter included for compatibility, not used in this model.

lambda_cov included for compatibility, not used in this model.

alpha_cov included for compatibility, not used in this model.

abundance named numeric vector of abundances in the previous timestep.

covariates included for compatibility, not used in this model.
```

#### Value

numeric abundance projected one timestep

```
LW_project_alpha_pairwise_lambdacov_global_alphacov_global

Law-Watkinson model for projecting abundances, with specific alpha

values and global covariate effects on alpha and lambda
```

# **Description**

Law-Watkinson model for projecting abundances, with specific alpha values and global covariate effects on alpha and lambda

### Usage

```
LW_project_alpha_pairwise_lambdacov_global_alphacov_global(
    lambda,
    alpha_intra,
    alpha_inter,
    lambda_cov,
    alpha_cov,
    abundance,
    covariates
)
```

### **Arguments**

lambda numeric lambda value.

alpha\_intra single numeric value.

alpha\_inter numeric vector with interspecific alpha values.

lambda\_cov numeric vector with effects of covariates over lambda.

alpha\_cov named list of numeric values with effects of each covariate over alpha.

abundance named numeric vector of abundances in the previous timestep.

covariates matrix with observations in rows and covariates in columns. Each cell is the

value of a covariate in a given observation.

#### Value

numeric abundance projected one timestep

```
LW_project_alpha_pairwise_lambdacov_global_alphacov_pairwise
```

Law-Watkinson model for projecting abundances, with specific alpha values and global covariate effects on alpha and lambda

# Description

Law-Watkinson model for projecting abundances, with specific alpha values and global covariate effects on alpha and lambda

#### **Usage**

```
LW_project_alpha_pairwise_lambdacov_global_alphacov_pairwise(
    lambda,
    alpha_intra,
    alpha_inter,
    lambda_cov,
    alpha_cov,
    abundance,
    covariates
)
```

# **Arguments**

lambda named numeric lambda value.

alpha\_intra single numeric value.

alpha\_inter numeric vector with interspecific alpha values.

lambda\_cov numeric vector with effects of covariates over lambda.

alpha\_cov named list of named numeric vectors with effects of each covariate over alpha

values.

abundance named numeric vector of abundances in the previous timestep.

covariates matrix with observations in rows and covariates in named columns. Each cell is

the value of a covariate in a given observation.

#### Value

numeric abundance projected one timestep

```
LW_project_alpha_pairwise_lambdacov_none_alphacov_none

Law-Watkinson model for projecting abundances, with specific alpha

values and no covariate effects
```

# **Description**

Law-Watkinson model for projecting abundances, with specific alpha values and no covariate effects

### Usage

```
LW_project_alpha_pairwise_lambdacov_none_alphacov_none(
    lambda,
    alpha_intra,
    alpha_inter,
    lambda_cov,
    alpha_cov,
    abundance,
    covariates
)
```

### **Arguments**

lambda numeric lambda value.

alpha\_intra included for compatibility, not used in this model.

alpha\_inter single numeric value.

lambda\_cov included for compatibility, not used in this model.

alpha\_cov included for compatibility, not used in this model.

abundance named numeric vector of abundances in the previous timestep.

covariates included for compatibility, not used in this model.

### Value

numeric abundance projected one timestep

58 neigh\_list

metapopulation\_example\_param

Metapopulation dynamics coefficients

# **Description**

A nested list containing vital rate coefficients for projecting metapopulation dynamics. The first level of the list has 3 elements, one for each species modelled. The second level of the list has 2 elements, one for each site modelled. For each combination species-site, there is a data.frame of eight rows - one per each vital rate, and eight columns - one per coefficient, that correspond to the coefficients of a GLM. These are named as alpha,beta1, etc, in the data.frame, and correspond to the intercept, environmental effect, effects of each of the three species' density, and environment:density interactions

### Usage

data(metapopulation\_example\_param)

#### **Format**

A nested list with 3x2 elements, each of which a dataframe of 8 rows and 8 numeric columns

neigh\_list

neighbours and fitness observations

# **Description**

A dataset containing fitness and neighbours for plant individuals of 17 species. The dataset is a named list with 16 elements, each of which is a dataframe with the following columns:

- obs\_ID: unique identifier for each observation
- fitness: number of viable seeds of the focal individual
- 17 columns indicating the number of neighbours from each plant sp. in a radius of 7.5 cm from the focal individual

### Usage

```
data(neigh_list)
```

#### **Format**

A list with 17 elements, each of which a dataframe of variable number of rows and 18 columns

### Note

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

niche\_overlap 59

niche\_overlap

Niche overlap between two species

# **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

```
niche_overlap(
  cxr_multifit = NULL,
  cxr_sp1 = NULL,
  cxr_sp2 = NULL,
  pair_matrix = NULL
)
```

# **Arguments**

```
cxr_multifit cxr_pm_multifit object, with parameters for a series of species.

cxr_sp1 cxr_pm_fit object giving the parameters from the first species.

cxr_sp2 cxr_pm_fit object giving the parameters from the second species.

2x2 matrix with intra and interspecific interaction coefficients between the two species.
```

#### **Details**

Niche overlap has a common functional form, in the context of Modern Coexistence Theory (MCT), for a series of models, including those specified in table A1 of Hart et al. (2018) Journal of Ecology 106, 1902-1909. Other model families may not adhere to the general definition.

Furthermore, the MCT definition only accounts for competitive interactions (i.e. positive alpha coefficients in these models). An alternative definition is given in Saavedra et al. (2017) Ecological Monographs 87,470-486. In this 'structural approach', positive interactions are allowed. Incidentally, both approaches yield qualitatively similar, but not equivalent, results for purely competitive matrices.

In all cases, these definitions only apply to models whose feasible equilibrium point can be described by a linear equation (see Saavedra et al. 2017, Hart et al. 2018 for details).

This function calculates niche overlap among two or more taxa, using both the MCT and the structural formulation. The function, as in avg\_fitness\_diff and competitive\_ability, accepts three different parameterizations:

A cxr\_pm\_multifit object, from which niche overlap will be computed across all species pairs.

- two cxr\_pm\_fit objects, one for each species.
- explicit lambda and alpha values, as well as the model family from which these parameters were obtained.

If negative interactions are present, the MCT niche overlap will be NA. The cxr objects may be calculated with user-defined model families. If this is the case, or if simply a 2x2 matrix is provided, the niche overlap metrics will be calculated and a warning will be raised.

#### Value

either a dataframe with as many rows as species, or a single named numeric vector, containing niche overlap values for the MCT (modern coexistence theory) and SA (structural approach) formulations.

# **Examples**

```
niche_overlap(pair_matrix = matrix(c(0.33,0.12,0.2,0.4),nrow = 2))
```

```
RK_er_lambdacov_global_effectcov_global_responsecov_global

*Effect response Beverton-Holt model with covariate effects on lambda, effect, and response
```

### **Description**

Note that, as e and r are not pair-specific, all species parameters are fit in the same function.

### Usage

```
RK_er_lambdacov_global_effectcov_global_responsecov_global(
  par,
  fitness,
  target,
  density,
  covariates,
  fixed_parameters
)
```

#### **Arguments**

par	1d vector with initial parameters in the order: lambda,lambda_cov,effect,effect_cov,response,response_co
fitness	1d vector with fitness observations
target	matrix with species in rows, observations in columns. Value is 1 if a species is focal for a given observation, 0 otherwise.
density	matrix with species in rows, observations in columns. Value is density of each

sp as neighbour for each observation.

covariates numeric dataframe or matrix with observations in rows and covariates in columns.

Each cell is the value of a covariate in a given observation

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "lambda\_cov", "effect", "eff "response", "response\_cov".

#### Value

log-likelihood value

```
RK_er_lambdacov_none_effectcov_none_responsecov_none

*Effect response Ricker model without covariate effects*
```

#### **Description**

Note that, as e and r are not pair-specific, all species parameters are fit in the same function.

### Usage

```
RK_er_lambdacov_none_effectcov_none_responsecov_none(
  par,
  fitness,
  target,
  density,
  covariates,
  fixed_parameters
)
```

#### **Arguments**

par 1d vector with initial parameters in the order: lambda,effect,response,sigma.

fitness 1d vector with fitness observations.

target matrix with species in rows, observations in columns. Value is 1 if a species is

focal for a given observation, 0 otherwise.

density matrix with species in rows, observations in columns. Value is density of each

sp as neighbour for each observation.

covariates included for compatibility, not used in this model.

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "effect", "response".

#### Value

log-likelihood value

```
RK_pm_alpha_global_lambdacov_none_alphacov_none

Ricker model with a global alpha and no covariate effects
```

# **Description**

Ricker model with a global alpha and no covariate effects

#### Usage

```
RK_pm_alpha_global_lambdacov_none_alphacov_none(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

# **Arguments**

### Value

log-likelihood value

```
RK_pm_alpha_none_lambdacov_none_alphacov_none

Ricker model with no alphas and no covariate effects
```

# **Description**

This model, in all families, is simply given by lambda.

### Usage

```
RK_pm_alpha_none_lambdacov_none_alphacov_none(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

#### Arguments

#### Value

log-likelihood value

```
RK_pm_alpha_pairwise_lambdacov_global_alphacov_global

Ricker model with pairwise alphas and global covariate effects on lambda and alpha
```

# **Description**

Ricker model with pairwise alphas and global covariate effects on lambda and alpha

# Usage

```
RK_pm_alpha_pairwise_lambdacov_global_alphacov_global(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

### Arguments

par 1d vector of initial parameters: lambda, lambda\_cov, alpha, alpha\_cov, and

sigma

fitness 1d vector of fitness observations, in log scale

neigh\_intra\_matrix

optional matrix of one column, number of intraspecific neighbours for each ob-

servation

neigh\_inter\_matrix

matrix of arbitrary columns, number of interspecific neighbours for each obser-

vation

covariates optional matrix with observations in rows and covariates in columns. Each cell

is the value of a covariate in a given observation

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "alpha\_intra", "alpha\_inter"

#### Value

log-likelihood value

```
RK_pm_alpha_pairwise_lambdacov_global_alphacov_pairwise
```

Ricker model with pairwise alphas, covariate effects on lambda, and pairwise covariate effects on alpha

# **Description**

Ricker model with pairwise alphas, covariate effects on lambda, and pairwise covariate effects on alpha

#### Usage

```
RK_pm_alpha_pairwise_lambdacov_global_alphacov_pairwise(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

# Arguments

par 1d vector of initial parameters: lambda, lambda\_cov, alpha, alpha\_cov, and

sigma

fitness 1d vector of fitness observations, in log scale

```
neigh_intra_matrix
```

optional matrix of one column, number of intraspecific neighbours for each ob-

servation

neigh\_inter\_matrix

matrix of arbitrary columns, number of interspecific neighbours for each obser-

vation

covariates

optional matrix with observations in rows and covariates in columns. Each cell

is the value of a covariate in a given observation

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "alpha\_intra", "alpha\_inter"

#### Value

log-likelihood value

RK\_pm\_alpha\_pairwise\_lambdacov\_none\_alphacov\_none

Ricker model with pairwise alphas and no covariate effects

# Description

Ricker model with pairwise alphas and no covariate effects

# Usage

```
RK_pm_alpha_pairwise_lambdacov_none_alphacov_none(
  par,
  fitness,
  neigh_intra_matrix = NULL,
  neigh_inter_matrix,
  covariates,
  fixed_parameters
)
```

#### Arguments

par 1d vector of initial parameters: 'lambda', 'alpha\_intra' (optional), 'alpha\_inter',

and 'sigma'

fitness 1d vector of fitness observations, in log scale

neigh\_intra\_matrix

optional matrix of one column, number of intraspecific neighbours for each ob-

servation

neigh\_inter\_matrix

matrix of arbitrary columns, number of interspecific neighbours for each obser-

vation

covariates included for compatibility, not used in this model

fixed\_parameters

optional list specifying values of fixed parameters, with components "lambda", "alpha\_intra", "alpha\_inter"

# Value

log-likelihood value

```
{\it RK\_project\_alpha\_global\_lambdacov\_none\_alphacov\_none} \\ {\it Ricker\ model\ for\ projecting\ abundances,\ with\ a\ global\ alpha\ and\ no\ covariate\ effects}
```

# Description

Ricker model for projecting abundances, with a global alpha and no covariate effects

### Usage

```
RK_project_alpha_global_lambdacov_none_alphacov_none(
  lambda,
  alpha_intra,
  alpha_inter,
  lambda_cov,
  alpha_cov,
  abundance,
  covariates
)
```

### **Arguments**

lambda numeric lambda value.

alpha\_intra included for compatibility, not used in this model.

alpha\_inter single numeric value.

lambda\_cov included for compatibility, not used in this model.

alpha\_cov included for compatibility, not used in this model.

abundance named numeric vector of abundances in the previous timestep.

covariates included for compatibility, not used in this model.

# Value

numeric abundance projected one timestep

```
{\it RK\_project\_alpha\_none\_lambdacov\_none\_alphacov\_none} \\ {\it Model for projecting abundances, with no alpha and no covariate effects}
```

### **Description**

Model for projecting abundances, with no alpha and no covariate effects

#### Usage

```
RK_project_alpha_none_lambdacov_none_alphacov_none(
  lambda,
  alpha_intra,
  alpha_inter,
  lambda_cov,
  alpha_cov,
  abundance,
  covariates
)
```

### **Arguments**

```
lambda numeric lambda value.

alpha_intra included for compatibility, not used in this model.

alpha_inter included for compatibility, not used in this model.

lambda_cov included for compatibility, not used in this model.

alpha_cov included for compatibility, not used in this model.

abundance named numeric vector of abundances in the previous timestep.

covariates included for compatibility, not used in this model.
```

#### Value

numeric abundance projected one timestep

```
RK_project_alpha_pairwise_lambdacov_global_alphacov_global

Ricker model for projecting abundances, with specific alpha values

and global covariate effects on alpha and lambda
```

#### **Description**

Ricker model for projecting abundances, with specific alpha values and global covariate effects on alpha and lambda

#### Usage

```
RK_project_alpha_pairwise_lambdacov_global_alphacov_global(
  lambda,
  alpha_intra,
  alpha_inter,
  lambda_cov,
  alpha_cov,
  abundance,
  covariates
)
```

### **Arguments**

lambda numeric lambda value.
alpha\_intra single numeric value.
alpha\_inter numeric vector with interspecific alpha values.
lambda\_cov numeric vector with effects of covariates over lambda.

alpha\_cov named list of numeric values with effects of each covariate over alpha.

abundance named numeric vector of abundances in the previous timestep.

covariates matrix with observations in rows and covariates in columns. Each cell is the

value of a covariate in a given observation.

#### Value

numeric abundance projected one timestep

```
RK_project_alpha_pairwise_lambdacov_global_alphacov_pairwise

Ricker model for projecting abundances, with specific alpha values

and global covariate effects on alpha and lambda
```

# **Description**

Ricker model for projecting abundances, with specific alpha values and global covariate effects on alpha and lambda

### Usage

```
RK_project_alpha_pairwise_lambdacov_global_alphacov_pairwise(
  lambda,
  alpha_intra,
  alpha_inter,
  lambda_cov,
  alpha_cov,
  abundance,
  covariates
)
```

### **Arguments**

lambda named numeric lambda value. alpha\_intra single numeric value. alpha\_inter numeric vector with interspecific alpha values. lambda\_cov numeric vector with effects of covariates over lambda. alpha\_cov named list of named numeric vectors with effects of each covariate over alpha values. abundance named numeric vector of abundances in the previous timestep. covariates matrix with observations in rows and covariates in named columns. Each cell is the value of a covariate in a given observation.

#### Value

numeric abundance projected one timestep

```
RK_project_alpha_pairwise_lambdacov_none_alphacov_none

Ricker model for projecting abundances, with specific alpha values

and no covariate effects
```

# **Description**

Ricker model for projecting abundances, with specific alpha values and no covariate effects

# Usage

```
RK_project_alpha_pairwise_lambdacov_none_alphacov_none(
    lambda,
    alpha_intra,
    alpha_inter,
    lambda_cov,
    alpha_cov,
    abundance,
    covariates
)
```

#### **Arguments**

lambda	numeric lambda value.
alpha_intra	included for compatibility, not used in this model.
alpha_inter	single numeric value.
lambda_cov	included for compatibility, not used in this model.
alpha_cov	included for compatibility, not used in this model.
abundance	named numeric vector of abundances in the previous timestep.
covariates	included for compatibility, not used in this model.

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#### Value

numeric abundance projected one timestep

salinity\_list

Salinity measurements

### **Description**

A list containing salinity values associated to the data from 'neigh\_list'. The list has 17 elements, one for each focal species considered. Each element of the list is a dataframe with 2 columns:

- obs\_ID: unique identifier of each observation
- salinity: salinity measurement for that observation, in accumulated microsiemens/m2

# Usage

```
data(salinity_list)
```

#### **Format**

A list with 17 elements, each of which a dataframe of variable number of rows and 2 numeric columns

#### Note

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

spatial\_sampling

spatial arrangement of the observations

# **Description**

A dataset giving the spatial arrangement of observations. The dataset is a list of 16 elements following the structure of 'neigh\_list'. Each list component is a dataframe with columns:

#### Usage

```
data(spatial_sampling)
```

#### **Format**

A list with 16 elements, each of which a dataframe of variable number of rows and 18 columns

species\_fitness 71

#### **Details**

- obs\_ID: unique identifier for each observation
- plot: one of 9 plots of 8.5 x 8.5 m
- subplot: one of 36 subplots of 1x1 m within each plot

#### Note

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

species\_fitness

Fitness of a species

## **Description**

Calculates the fitness of a species sensu Godoy et al. (2014). Note that its definition is model-specific, i.e. it depends on the model family from which interaction coefficients were estimated. The function given here assumes a community of n-species, so that species fitness is calculated according to a general competitive response (r) substituting the 2-sp denominator terms of table A1 of Hart et al. 2018. This competitive response can be calculated for a series of species with the function 'cxr\_er\_fit'.

#### Usage

```
species_fitness(
  effect_response_fit = NULL,
  lambda = NULL,
  competitive_response = NULL,
  model_family = NULL
)
```

# **Arguments**

#### **Details**

Thus, the function accepts two sets of parameters. First, a 'cxr\_er\_fit' object returned from that function. In this case, species fitness will be calculated for all focal taxa included in the 'cxr\_er\_fit' object.

Otherwise, users may enter a specification of the model to use, as well as lambda and competitive response parameters of a single species.

72 species\_rates

If no model family is provided, or a model family for which there is no associated 'XX\_species\_fitness' function, the function resorts to the standard Lotka-Volterra formulation (Hart et al. 2018). Overall, we strongly suggest that you use the standard formulation ONLY if you are completely confident that the model from which you obtained your parameters is consistent with it. Otherwise, you should include your own formulation of species fitness (see vignette 4).

# Value

single numeric value/vector, species fitness of one or several taxa

species\_rates

Species germination and survival rates

# Description

A dataset containing germination and survival rates for 17 plant species. It includes columns with the scientific names and their associated codes.

# Usage

```
data(species_rates)
```

#### **Format**

A data frame with 17 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.

summary.cxr\_er\_fit 73

summary.cxr\_er\_fit

CXR summary method for effect response model fits

# Description

CXR summary method for effect response model fits

# Usage

```
## S3 method for class 'cxr_er_fit'
summary(object, ...)
```

# Arguments

```
object a cxr_er_fit object, from the function with the same name ... other arguments, not used
```

#### Value

console output

summary.cxr\_pm\_fit

CXR summary method for population model fits

# Description

CXR summary method for population model fits

# Usage

```
## S3 method for class 'cxr_pm_fit'
summary(object, ...)
```

# **Arguments**

```
object a cxr_pm_fit object, from the function with the same name ... other arguments, not used
```

#### Value

console output

```
\verb"summary.cxr_pm_multifit"
```

CXR summary method for multispecies fits

#### **Description**

CXR summary method for multispecies fits

# Usage

```
## S3 method for class 'cxr_pm_multifit'
summary(object, ...)
```

# **Arguments**

object a cxr\_pm\_multifit object, from the function with the same name other arguments, not used

#### Value

console output

```
vec_permutation_matrices
```

Generate templates for dispersal, demography, and permutation matrices

# **Description**

this follows the vec-permutation approach as defined in: Hunter and Caswell 2005, doi:10.1016/j.ecolmodel.2005.05.002, Ozgul et al. 2009, doi: 10.1086/597225

### Usage

```
vec_permutation_matrices(num.sp, num.sites, num.stages)
```

# Arguments

num.sp integer, number of species
num.sites integer, number of sites
num.stages integer, number of stages

### Value

nested list, of the form 'list[[type]][[sp]]', where 'type' is demography, dispersal, or permutation.

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# **Examples**

```
# number of demographic stages - this should be always fixed to 3 for
# compatibility with other functions
num.stages <- 3
num.sp <- 4
num.sites <- 5
vpm <- vec_permutation_matrices(num.sp,num.sites,num.stages)</pre>
```

vital\_rate

Vital rate calculation

# **Description**

Calculates vital rates from their effect sizes and terms. This is equivalent to predicting from a binomial glm with given coefficients. In this version, the user needs to ensure that 'param' and 'env' match, i.e. that if the 'param' list is defined with environmental forcing, it is passed here, and viceversa. In future versions I may implement checks for that here, but for now, be aware that it will fail.

# Usage

```
vital_rate(vr, sp, site, param, env = NULL, densities)
```

# **Arguments**

vr	integer or char, vital rate to obtain, from the ones defined in 'param'. So far, valid names are "Sj", "Sn", "Sr", "Rn", "Rr", "D", "Ds, "O".
sp	integer or char, species
site	intger or char, site
param	param nested list (see 'build_param')
env	optional numeric, environmental forcing
densities	densities of all sp in the site, including individuals from all three life stages

# Value

numeric value

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RK_pm_alpha_pairwise_lambdacov_global_alphacov_pairwise,
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