Package: evolvability (via r-universe)

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Type Package

Title Calculation of Evolvability Parameters

Version 2.0.0

Description Provides tools for calculating evolvability parameters from estimated G-matrices as defined in Hansen and Houle (2008) <doi:10.1111/j.1420-9101.2008.01573.x> and fits phylogenetic comparative models that link the rate of evolution of a trait to the state of another evolving trait (see Hansen et al. 2021 Systematic Biology <doi:10.1093/sysbio/syab079>). The package was released with Bolstad et al. (2014) <doi:10.1098/rstb.2013.0255>, which contains some examples of use.

License GPL (>= 2)

Imports coda, Matrix, ape, lme4, stats

RoxygenNote 7.2.3

Encoding UTF-8

Suggests knitr, rmarkdown

VignetteBuilder knitr

Repository https://ghbolstad.r-universe.dev

RemoteUrl https://github.com/ghbolstad/evolvability

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Contents

`evolvability-package` *Calculation of Evolvability Parameters*

Description

This package calculates evolvability parameters from estimated G-matrices as defined in Hansen and Houle (2008) <doi:10.1111/j.1420-9101.2008.01573.x>. It can use both point estimates and posterior/bootstrap distributions of the G-matrices. This package was released with Bolstad et al. (2014) <doi:10.1098/rstb.2013.0255>, which contains some examples of use.

Details

Package:	evolvability
Type:	Package
Version:	1.1.0
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License:	GPL (>= 2)

Author(s)

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References

Bolstad G. H., Hansen T. F., Pelabon C. Falahati-Anabaran M., Perez-Barrales R. & Armbruster W. S. 2014. Genetic constraints predict evolutionary divergence in Dalechampia blossoms. Phil. Trans. R. Soc. B. 369:20130255. doi:10.1098/rstb.2013.0255

Hansen T. F. & Houle D. (2008) Measuring and comparing evolvability and constraint in multivariate characters. J. Evol. Biol. 21:1201-1219. doi:10.1111/j.1420-9101.2008.01573.x

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`Almer` *Linear mixed model with correlated random effects structure*

Description

`Almer` fits a univariate linear mixed model incorporating a correlated random effects structure. Can be used to fit phylogenetic mixed models and animal models. The function is based on the `lme4` package and is very similar to `lmer`, apart from the A argument.

Usage

```
Almer(
  formula,
  data = NULL,
  A = list(),
  REML = TRUE,
 control = lme4::lmerControl(check.nobs.vs.nlev = "ignore", check.nobs.vs.rankZ =
    "ignore", check.nobs.vs.nRE = "ignore"),
  start = NULL,
  verbose = 0L,
  weights = NULL,
  na.action = "na.omit",
  offset = NULL,
  contrasts = NULL,
  devFunOnly = FALSE,
  ...
)
```

Arguments

`formula`	as in `lmer`.
`data`	as in `lmer`.
`A`	an optional named list of sparse matrices. The names must correspond to the names of the random effects in the formula argument. All levels of the random effect should appear as row and column names for the matrices.

`REML`	as in `lmer`.
`control`	as in `lmer`.
`start`	as in `lmer`.
`verbose`	as in `lmer`.
`weights`	as in `lmer`.
`na.action`	as in `lmer`.
`offset`	as in `lmer`.
`contrasts`	as in `lmer`.
`devFunOnly`	as in `lmer`.
`...`	as in `lmer`.

Value

`Almer` an object of class `merMod`.

Author(s)

Geir H. Bolstad

Examples

```
# See the vignette 'Phylogenetic mixed model'.
```

`Almer_boot` *Parametric bootstrap on* `Almer` *model fit*

Description

`Almer_boot` performs a parametric bootstrap from an `Almer` model fit

Usage

```
Almer_boot(mod, nsim = 1000)
```

Arguments

`mod`	A fitted object from `Almer`
`nsim`	The number of simulations.

Value

`Almer_boot` a list with entries fixef, vcov, fixef_distribution and vcov_distribution, where the two first entries includes the means, standard deviations, and quantiles of the fixed effects means and (co)variances, respectively, and the two latter includes the complete bootstrap distribution.

Author(s)

Geir H. Bolstad

Examples

```
# See the vignette 'Phylogenetic mixed model'.
```

`Almer_SE` *Linear mixed model for response variables with uncertainty*

Description

`Almer_SE` Linear mixed model for response variables with uncertainty

Usage

```
Almer_SE(
  formula,
  SE = NULL,
  maxiter = 100,
 control = lme4::lmerControl(check.nobs.vs.nlev = "ignore", check.nobs.vs.rankZ =
    "ignore", check.nobs.vs.nRE = "ignore"),
  ...
)
```

Arguments

`formula`	as in `lmer`.
`SE`	A vector of standard errors associated with the response variable. NB! Must have column name "SE" in the data.
`maxiter`	The maximum number of iterations.
`control`	as in `lmer`.
`...`	Further optional arguments, see `Almer`.

Value

`Almer_SE` returns an object of class `merMod`.

Author(s)

Geir H. Bolstad

Examples

```
# See the vignette 'Phylogenetic mixed model'.
```

`Almer_sim` *Simulate responses from `Almer` fit*

Description

`Almer_sim` Simulate responses from an `Almer` model fit.

Usage

```
Almer_sim(mod, nsim = 1000)
```

Arguments

`mod`	A fitted object from `Almer`
`nsim`	The number of simulations.

Details

This function is only included as the `simulate.merMod` function did not seem to work properly when the number of random effect levels equal the number of observations.

Value

`Almer_sim` a matrix of simulated responses, columns correspond to each simulations.

Author(s)

Geir H. Bolstad

Examples

```
# See the vignette 'Phylogenetic mixed model'.
```

`conditionalG` *Computing a conditional sub-matrix of G*

Description

`conditinoalG` calculates a conditional variance matrix.

Usage

```
conditionalG(G, condition_on = NULL)
```

Arguments

`G`	A variance matrix (must be symmetric and positive definite).
`condition_on`	Either an integer with the column number indicating which trait to condition on or a vector with several column numbers (integers).

Details

The function calculates a sub-matrix of `G` conditional on the traits defined by the the `condition_on` vector. The function is based on equation 3 in Hansen et al. (2003).

Value

A matrix that is a sub-matrix of the input matrix conditional on the non-included traits.

Author(s)

Geir H. Bolstad

References

Hansen TF, Armbruster WS, Carlsson ML & Pélabon C. 2003. Evolvability and genetic constraint in Dalechampia blossoms: genetic correlations and conditional evolvability. J. Exp. Zool. 296B:23-39.

Examples

```
# Constructing a G-matrix:
G <- matrix(c(
  1, 1, 0, 1,
  1, 2, 1, 1,
  0, 1, 2, 1,
  1, 1, 1, 3
), ncol = 4)

# Computing a conditional 2x2 sub-matrix by conditioning on
# trait 3 and 4:
G_sub_conditional <- conditionalG(G, condition_on = c(3, 4))
G_sub_conditional

# The average evolvabilities of this matrix can then be
# compared can than be compared to the average evolvabilities
# of the corresponding unconditional sub-matrix of G:
evolvabilityMeans(G_sub_conditional)
evolvabilityMeans(G[-c(3, 4), -c(3, 4)])
```

`evolvabilityBeta` *Calculate evolvability parameters along a set of selection gradients*

Description

`G` needs to be symmetric and positive definite.

Usage

```
evolvabilityBeta(G, Beta, means = 1)
```

Arguments

`G`	A variance matrix.
`Beta`	Either a vector or a matrix of unit length selection gradients stacked column wise.
`means`	An optional vector of trait means (for internal mean standardization).

Details

`evolvabilityBeta` calculates (unconditional) evolvability (e), respondability (r), conditional evolvability (c), autonomy (a) and integration (i) along selection gradients given an additive-genetic variance matrix as described in Hansen and Houle (2008).

Value

An object of `class 'evolvabilityBeta'`, which is a list with the following components:

`Beta`	The matrix of selection gradients.
`e`	The evolvability of each selection gradient.
`r`	The respondability of each selection gradient.
`c`	The conditional evolvability of each selection gradient.
`a`	The autonomy of each selection gradient.
`i`	The integration of each selection gradient.

Author(s)

Geir H. Bolstad

References

Hansen, T. F. & Houle, D. (2008) Measuring and comparing evolvability and constraint in multivariate characters. J. Evol. Biol. 21:1201-1219.

Examples

```
G <- matrix(c(1, 1, 0, 1, 2, 2, 0, 2, 3), ncol = 3) / 10
Beta <- randomBeta(5, 3)
X <- evolvabilityBeta(G, Beta)
summary(X)
```

`evolvabilityBetaMCMC` *Calculate posterior distribution of evolvability parameters from a set of selection gradients*

Description

`evolvabilityBetaMCMC` calculates (unconditional) evolvability (e), respondability (r), conditional evolvability (c), autonomy (a) and integration (i) from selection gradients given the posterior distribution of an additive-genetic variance matrix. These measures and their meanings are described in Hansen and Houle (2008).

Usage

```
evolvabilityBetaMCMC(G_mcmc, Beta, post.dist = FALSE)
```

Arguments

`G_mcmc`	posterior distribution of a variance matrix in the form of a table. Each row in the table must be one iteration of the posterior distribution (or bootstrap distribution). Each iteration of the matrix must be on the form as given by `c(x)`, where `x` is a matrix. A posterior distribution of a matrix in the slot `VCV` of a object of class `MCMCglmm` is by default on this form.
`Beta`	either a vector or a matrix of unit length selection gradients stacked column wise.
`post.dist`	logical: should the posterior distribution of the evolvability parameters be saved.

Value

An object of `class 'evolvabilityBetaMCMC'`, which is a list with the following components:

`eB`	The posterior median and highest posterior density interval of evolvability for each selection gradient.
`rB`	The posterior median and highest posterior density interval of respondability for each selection gradien
`cB`	The posterior median and highest posterior density interval of conditional evolvability for each selectio
`aB`	The posterior median and highest posterior density interval of autonomy for each selection gradient.
`iB`	The posterior median and highest posterior density interval of integration for each selection gradient.
`Beta`	The matrix of selection gradients.
`summary`	The means of evolvability parameters across all selection gradients.
`post.dist`	The full posterior distribution.

Author(s)

Geir H. Bolstad

References

Hansen, T. F. & Houle, D. (2008) Measuring and comparing evolvability and constraint in multivariate characters. J. Evol. Biol. 21:1201-1219.

Examples

```
# Simulating a posterior distribution
# (or bootstrap distribution) of a G-matrix:
G <- matrix(c(1, 1, 0, 1, 4, 1, 0, 1, 2), ncol = 3)
G_mcmc <- sapply(c(G), function(x) rnorm(10, x, 0.01))
G_mcmc <- t(apply(G_mcmc, 1, function(x) {
  G <- matrix(x, ncol = sqrt(length(x)))
  G[lower.tri(G)] <- t(G)[lower.tri(G)]
  c(G)
}))

# Simulating a posterior distribution
# (or bootstrap distribution) of trait means:
means <- c(1, 1.4, 2.1)
means_mcmc <- sapply(means, function(x) rnorm(10, x, 0.01))

# Mean standardizing the G-matrix:
G_mcmc <- meanStdGMCMC(G_mcmc, means_mcmc)

# Generating selection gradients in five random directions:
Beta <- randomBeta(5, 3)

# Calculating evolvability parameters:
x <- evolvabilityBetaMCMC(G_mcmc, Beta, post.dist = TRUE)
summary(x)
```

`evolvabilityBetaMCMC2` *Calculate posterior distribution of evolvability parameters from a selection gradient estimated with uncertainty*

Description

`evolvabilityBetaMCMC2` calculates (unconditional) evolvability (e), respondability (r), conditional evolvability (c), autonomy (a) and integration (i) along a selection gradient estimate with uncertainty.

Usage

```
evolvabilityBetaMCMC2(G_mcmc, Beta_mcmc, post.dist = FALSE)
```

Arguments

`G_mcmc`	A posterior distribution of a variance matrix in the form of a table. Each row in the table must be one iteration of the posterior distribution (or bootstrap distribution). Each iteration of the matrix must be on the form as given by `c(x)`, where `x` is a matrix. A posterior distribution of a matrix in the slot `VCV` of a object of class `MCMCglmm` is by default on this form.
`Beta_mcmc`	A posterior distribution of a unit length selection gradient where iterations are given row wise.
`post.dist`	logical: should the posterior distribution of the evolvability parameters be saved.

`Beta.median`	posterior median and highest posterior density interval of the selection gradient.
`summary`	The posterior median and highest posterior density interval of evolvability parameters.
`post.dist`	The full posterior distributions of the evolvability parameters.

Author(s)

Geir H. Bolstad

References

Hansen, T. F. & Houle, D. (2008) Measuring and comparing evolvability and constraint in multivariate characters. J. Evol. Biol. 21:1201-1219.

Examples

```
{
  # Simulating a posterior distribution
  # (or bootstrap distribution) of a G-matrix:
  G <- matrix(c(1, 1, 0, 1, 4, 1, 0, 1, 2), ncol = 3)
  G_mcmc <- sapply(c(G), function(x) rnorm(10, x, 0.01))
  G_mcmc <- t(apply(G_mcmc, 1, function(x) {
    G <- matrix(x, ncol = sqrt(length(x)))
    G[lower.tri(G)] <- t(G)[lower.tri(G)]
    c(G)
  }))

  # Simulating a posterior distribution
  # (or bootstrap distribution) of trait means:
  means <- c(1, 1.4, 2.1)
  means_mcmc <- sapply(means, function(x) rnorm(10, x, 0.01))

  # Mean standardizing the G-matrix:
  G_mcmc <- meanStdGMCMC(G_mcmc, means_mcmc)

  # Simulating a posterior distribution (or bootstrap distribution)
  # of a unit length selection gradient:
  Beta <- randomBeta(1, 3)
  Beta.mcmc <- sapply(c(Beta), function(x) rnorm(10, x, 0.01))
  Beta.mcmc <- t(apply(Beta.mcmc, 1, function(x) x / sqrt(sum(x^2))))
```

```
  # Running the model:
  evolvabilityBetaMCMC2(G_mcmc, Beta_mcmc = Beta.mcmc, post.dist = TRUE)
}
```

`evolvabilityMeans` *Calculate average evolvability parameters of a G-matrix*

Description

`evolvabilityMeans` calculates the average (unconditional) evolvability (e), respondability (r), conditional evolvability (c), autonomy (a) and integration (i) of a additive-genetic variance matrix using the approximation formulas described in Hansen and Houle (2008, 2009).

Usage

```
evolvabilityMeans(G, means = 1)
```

Arguments

`G`	A variance matrix (must be symmetric and positive definite).
`means`	An optional vector of trait means, for mean standardization.

Details

The equations for calculating the evolvability parameters are approximations, except for the minimum, maximum and unconditional evolvability which are exact. The bias of the approximations depends on the dimensionality of the G-matrix, with higher bias for few dimensions (see Hansen and Houle 2008). For low dimensional G-matrices, we recommend estimating the averages of the evolvability parameters using `evolavbilityBetaMCMC` over many random selection gradients (`randomBeta`). The maximum and minimum evolvability, which are also the maximum and minimum respondability and conditional evolvability, equals the largest and smallest eigenvalue of the G-matrix, respectively.

Value

A vector with the following components:

`e_mean`	The average (unconditional) evolvability.
`e_min`	The minimum evolvability.
`e_max`	The maximum evolvability.
`r_mean`	The average respondability.
`c_mean`	The average conditional evolvability.
`a_mean`	The average autonomy.
`i_mean`	The average integration.

Author(s)

Geir H. Bolstad

References

Hansen, T. F. & Houle, D. (2008) Measuring and comparing evolvability and constraint in multivariate characters. J. Evol. Biol. 21:1201-1219.
Hansen, T. F. & Houle, D. (2009) Corrigendum. J. Evol. Biol. 22:913-915.

Examples

```
G <- matrix(c(1, 1, 0, 1, 2, 1, 0, 1, 2), ncol = 3)
evolvabilityMeans(G)
```

`evolvabilityMeansMCMC` *Calculate posterior distribution of average evolvability parameters of a G-matrix*

Description

`evolvabilityMeans` calculates the average (unconditional) evolvability (e), respondability (r), conditional evolvability (c), autonomy (a) and integration (i) given the posterior distribution of a additive-genetic variance matrix using the approximation formulas described in Hansen and Houle (2008, 2009).

Usage

```
evolvabilityMeansMCMC(G_mcmc)
```

Arguments

`G_mcmc`	the posterior distribution of a variance matrix in the form of a table. Each row in the table must be one iteration of the posterior distribution (or bootstrap distribution). Each iteration of the matrix must be on the form as given by `c(x)`, where `x` is a matrix. A posterior distribution of a matrix in the slot `VCV` of a object of class `MCMCglmm` is by default on this form.

Details

The equations for calculating the evolvability parameters are approximations, except for the minimum, maximum and unconditional evolvability which are exact. The bias of the approximations depends on the dimensionality of the G-matrix, with higher bias for few dimensions (see Hansen and Houle 2008). For low dimensional G-matrices, we recommend estimating the averages of the evolvability parameters using `evolavbilityBetaMCMC` over many random selection gradients (`randomBeta`). The maximum and minimum evolvability, which are also the maximum and minimum respondability and conditional evolvability, equals the largest and smallest eigenvalue of the G-matrix, respectively.

Value

An object of `class 'evolvabilityMeansMCMC'`, which is a list with the following components:

`post.dist`	The posterior distribution of the average evolvability parameters.
`post.medians`	The posterior medians and HPD interval of the average evolvability parameters.

Author(s)

Geir H. Bolstad

References

Hansen, T. F. & Houle, D. (2008) Measuring and comparing evolvability and constraint in multivariate characters. J. Evol. Biol. 21:1201-1219.
Hansen, T. F. & Houle, D. (2009) Corrigendum. J. Evol. Biol. 22:913-915.

Examples

```
# Simulating a posterior distribution
# (or bootstrap distribution) of a G-matrix:
G <- matrix(c(1, 1, 0, 1, 4, 1, 0, 1, 2), ncol = 3)
G_mcmc <- sapply(c(G), function(x) rnorm(10, x, 0.01))
G_mcmc <- t(apply(G_mcmc, 1, function(x) {
  G <- matrix(x, ncol = sqrt(length(x)))
  G[lower.tri(G)] <- t(G)[lower.tri(G)]
  c(G)
}))

# Simulating a posterior distribution
# (or bootstrap distribution) of trait means:
means <- c(1, 1.4, 2.1)
means_mcmc <- sapply(means, function(x) rnorm(10, x, 0.01))

# Mean standardizing the G-matrix:
G_mcmc <- meanStdGMCMC(G_mcmc, means_mcmc)

# Estimating average evolvability paramters:
evolvabilityMeansMCMC(G_mcmc)
```

`GLS` *Generalized least square*

Description

`GLS` utilizes `lm.fit` and Cholesky decomposition to fit a generalized least squares regression

Usage

```
GLS(y, X, R = NULL, L = NULL, coef_only = FALSE)
```

Arguments

`y`	response variable
`X`	design matrix
`R`	residual covariance or correlation matrix (can be sparse), ignored if `L` is provided.
`L`	lower triangular matrix of the Cholesky decomposition of `R` (optional).
`coef_only`	reduces the output of the model to the estimated coefficients (and the generalized residual sums of squares) only.

Details

Note that the size of `R` does not matter (i.e. if `R` is multiplied by a scalar, the results don't change). Note also that the R-squared is estimated as 1-GSSE/GSST, where GSSE is the generalized residual sum of squares (i.e. the objective function score of the model) and GSST is the generalized total sum of squares (i.e. the objective function score of the model when only the intercept is included in the model)

Value

`GLS` a `list` of

- `coef`: a table of estimates and standard errors
- `R2`: the R-squared of the model fit
- `sigma2`: the residual variance
- `GSSE`: the generalized residual sum of squares (objective function score)
- `coef_vcov`: the error variance matrix of the estimates

Author(s)

Geir H. Bolstad

`macro_pred` *Macroevolutionary predictions*

Description

`macro_pred` Macroevolutionary predictions

Usage

```
macro_pred(y, V, useLFO = TRUE)
```

Arguments

`y`	vector of species means
`V`	phylogenetic variance matrix, must have same order as `y`
`useLFO`	excludes the focal species when calculating the corresponding species' mean. The correct way is to use TRUE, but in practice it has little effect and FALSE will speed up the model fit.

Details

`macro_pred` Gives a vector of macroevolutionary predictions for each species based on the other species given the phylogeny and a phylogenetic variance matrix.

Value

`macro_pred` returns a of macroevolutionary predictions at the tips.

Author(s)

Geir H. Bolstad

Examples

```
# Trait values
y <- rnorm(3)

# A variance matrix (the diagonal must be the same order as y).
V <- matrix(c(1.0, 0.5, 0.2, 0.5, 1.0, 0.4, 0.2, 0.4, 1.0), ncol = 3)

# Macroevolutionary predictions (output in the same order as y).
macro_pred(y, V)
```

`meanStdG` *Mean standardize a variance matrix*

Description

`meanStdG` mean standardizes a variance matrix (e.g. a G-matrix).

Usage

```
meanStdG(G, means)
```

Arguments

`G`	A variance matrix.
`means`	A vector of trait means.

Value

A mean standardized variance matrix.

Author(s)

Geir H. Bolstad

Examples

```
G <- matrix(c(1, 1, 0, 1, 4, 1, 0, 1, 2), ncol = 3)
means <- c(1, 1.4, 2.1)
meanStdG(G, means)
```

`meanStdGMCMC` *Mean standardize the posterior distribution of a G-matrix*

Description

`meanStdGMCMC` mean standardizes the posterior distribution of a variance matrix (e.g. a G-matrix)

Usage

```
meanStdGMCMC(G_mcmc, means_mcmc)
```

Arguments

`G_mcmc`	A posterior distribution of a variance matrix in the form of a table. Each row in the table must be one iteration of the posterior distribution (or bootstrap distribution). Each iteration of the matrix must be on the form as given by `c(x)`, where `x` is a matrix. A posterior distribution of a matrix in the slot `VCV` of a object of class `MCMCglmm` is by default on this form.
`means_mcmc`	A posterior distribution of a vector of means in the form of a table. Each row in the table must be one iteration of the posterior distribution (or bootstrap distribution). A posterior distribution of a mean vector in the slot `Sol` of an object of class `MCMCglmm` is by default on this form.

Value

The posterior distribution of a mean standardized variance matrix.

Author(s)

Geir H. Bolstad

Examples

```
# Simulating a posterior distribution
# (or bootstrap distribution) of a G-matrix:
G <- matrix(c(1, 1, 0, 1, 4, 1, 0, 1, 2), ncol = 3)
G_mcmc <- sapply(c(G), function(x) rnorm(10, x, 0.01))
G_mcmc <- t(apply(G_mcmc, 1, function(x) {
  G <- matrix(x, ncol = sqrt(length(x)))
  G[lower.tri(G)] <- t(G)[lower.tri(G)]
  c(G)
}))

# Simulating a posterior distribution
# (or bootstrap distribution) of trait means:
means <- c(1, 1.4, 2.1)
means_mcmc <- sapply(means, function(x) rnorm(10, x, 0.01))

# Mean standardizing the G-matrix:
meanStdGMCMC(G_mcmc, means_mcmc)
```

`phylH` *Phylogenetic heritability*

Description

`phylH` calculates the phylogenetic heritability from an `Almer` model fit and provides associated uncertainty using parametric bootstrapping.

Usage

```
phylH(mod, numerator, residual = "Residual", nsim = 10)
```

Arguments

`mod`	An object of class `'merMod'`
`numerator`	The name of phylogenetic effect level
`residual`	name of the residual effect level
`nsim`	number of bootstraps

Value

`phylH` returns a list with the REML estimate, the 95% confidence interval from the parametric bootstrap, and the bootstrap samples.

Author(s)

Geir H. Bolstad

Examples

```
# See the vignette 'Phylogenetic mixed model'.
```

`plot.rate_gls` *Plot of rate_gls object*

Description

`plot` method for class `'rate_gls'`.

Usage

```
## S3 method for class 'rate_gls'
plot(
  x,
  scale = "SD",
  print_param = TRUE,
  digits_param = 2,
  digits_rsquared = 1,
  main = "GLS regression",
  xlab = "x",
  ylab = "Response",
  col = "grey",
  cex.legend = 1,
  ...
)
```

Arguments

`x`	An object of class `'rate_gls'`.
`scale`	The scale of the y-axis, either the variance scale ('VAR'), that is y^2, or the standard deviation scale ('SD'), that is abs(y).
`print_param`	logical: if parameter estimates should be printed in the plot or not.
`digits_param`	The number of significant digits displayed for the parameters in the plots.
`digits_rsquared`	The number of decimal places displayed for the r-squared.
`main`	as in `plot`.
`xlab`	as in `plot`.
`ylab`	as in `plot`.
`col`	as in `plot`.
`cex.legend`	A character expansion factor relative to current par("cex") for the printed parameters.
`...`	Additional arguments passed to `plot`.

Details

Plots the gls rate regression fitted by the `rate_gls` function. The regression line gives the expected variance or standard deviation (depending on scale). The regression is linear on the variance scale.

Value

`plot` returns a plot of the gls rate regression

Author(s)

Geir H. Bolstad

Examples

```
# See the vignette 'Analyzing rates of evolution'.
```

`plot.simulate_rate` *Plot of simulate_rate object*

Description

`plot` method for class `'simulate_rate'`.

Usage

```
## S3 method for class 'simulate_rate'
plot(
  x,
  response = "rate_y",
  xlab = "Simulation timesteps",
  ylab = "Evolutionary rate of y",
  ...
)
```

Arguments

`x`	An object of class `'simulate_rate'`.
`response`	The variable for the y-axis of the plot, can be 'rate_y', 'y', or 'x'.
`xlab`	A label for the x axis.
`ylab`	A label for the y axis.
`...`	Additional arguments passed to `plot`.

Details

No plot is returned if model = 'recent_evol'.

Value

`plot` A plot of the evolution of the traits x or y, or the evolution of the evolutionary rate of y (i.e. $\sqrt{a+bx}$) in the simulation.

Author(s)

Geir H. Bolstad

Examples

```
# See the vignette 'Analyzing rates of evolution'.
```

---

randomBeta *Generating selection gradients/vectors in random directions.*

Description

`randomBeta` generates unit length vectors (selection gradients) uniformly distributed in a k-dimensional hypersphere.

Usage

```
randomBeta(n = 1, k = 2)
```

Arguments

`n`	Number of selection gradients/vectors.
`k`	Number of dimensions.

Details

`randomBeta` exploits the spherical symmetry of a multidimensional Gaussian density function. Each element of each vector is randomly sampled from a univariate Gaussian distribution with zero mean and unit variance. The vector is then divided by its norm to standardize it to unit length.

Value

`randomBeta` returns a matrix where the vectors are stacked column wise.

Author(s)

Geir H. Bolstad

Examples

```
# Two vectors of dimension 3:
randomBeta(n = 2, k = 3)
```

`rate_gls` *Generalized least squares rate model*

Description

`rate_gls` fits a generalized least squares model to estimate parameters of an evolutionary model of two traits x and y, where the evolutionary rate of y depends on the value of x. Three models are implemented. In the two first, 'predictor_BM' and 'predictor_gBM', the evolution of y follows a Brownian motion with variance linear in x, while the evolution of x either follows a Brownian motion or a geometric Brownian motion, respectively. In the third model, 'recent_evol', the residuals of the macroevolutionary predictions of y have variance linear in x. It is highly recommended to read Hansen et al. (in review) and `vignette("Analyzing_rates_of_evolution")` before fitting these models.

Usage

```
rate_gls(
  x,
  y,
  species,
  tree,
  model = "predictor_BM",
  startv = list(a = NULL, b = NULL),
  maxiter = 100,
  silent = FALSE,
  useLFO = TRUE,
  tol = 0.001
)
```

Arguments

`x`	The explanatory variable, which must be equal to the length of `y` and tips on the tree.
`y`	The trait values of response variable. Note that the algorithm mean centers y.
`species`	A vector with the names of the species, must be equal in length and in the same order as `x` and `y`.
`tree`	An object of class `phylo`, needs to be ultrametric and with total length of unit, tips must have the same names as in `species`.
`model`	The acronym of the evolutionary model to be fitted. There are three options: 'predictor_BM', 'predictor_gBM' or 'recent_evol' (see details).
`startv`	A vector of optional starting values for the a and b parameters.
`maxiter`	The maximum number of iterations for updating the GLS.
`silent`	logical: if the function should not print the generalized sum of squares for each iteration.

`useLFO`	logical: whether the focal species should be left out when calculating the corresponding species' means. Note that this is only relevant for the 'recent_evol' model. The most correct is to use `TRUE`, but in practice it has little effect and `FALSE` will speed up the model fit (particularly useful when bootstrapping). LFO is an acronym for 'Leave the Focal species Out'.
`tol`	tolerance for convergence. If the change in 'a' and 'b' is below this limit between the two last iteration, convergence is reached. The change is measured in proportion to the standard deviation of the response for 'a' and the ratio of the standard deviation of the response to the standard deviation of the predictor for 'b'.

Details

`rate_gls` is an iterative generalized least squares (GLS) model fitting a regression where the response variable is a vector of squared mean-centered `y`-values for the 'predictor_BM' and 'predictor_gBM' models and squared deviation from the evolutionary predictions (see `macro_pred`) for the 'recent_evol' model. Note that the algorithm mean centers `x` in the 'predictor_BM' and 'recent_evol' analyses, while it mean standardized `x` (i.e. divided `x` by its mean) in the 'predictor_gBM'. The evolutionary parameters a and b are inferred from the intercept and the slope of the GLS fit. Again, it is highly recommended to read Hansen et al. (in review) and `vignette("Analyzing_rates_of_evolutio` before fitting these models. In Hansen et al. (2021) the three models 'predictor_BM', 'predictor_gBM' and 'recent_evol' are referred to as 'Model 1', 'Model 2' and 'Model 3', respectively.

Value

An object of `class 'rate_gls'`, which is a list with the following components:

`model`	The name of the model ('predictor_BM', 'predictor_gBM' or 'recent_evolution').
`param`	The focal parameter estimates and their standard errors, where 'a' and 'b' are parameters of th
`Rsquared`	The generalized R squared of the GLS model fit.
`a_all_iterations`	The values for the parameter a in all iterations.
`b_all_iterations`	The values for the parameter b in all iterations.
`R`	The residual variance matrix.
`Beta`	The intercept and slope of GLS regression (response is y2 and explanatory variable is x).
`Beta_vcov`	The error variance matrix of `Beta`.
`tree`	The phylogenetic tree.
`data`	The data used in the GLS regression.
`convergence`	Whether the algorithm converged or not.
`additional_param`	Some additional parameter estimates.
`call`	The function call.

Author(s)

Geir H. Bolstad

References

Hansen TF, Bolstad GH, Tsuboi M. 2021. Analyzing disparity and rates of morphological evolution with model-based phylogenetic comparative methods. *Systematic Biology*. syab079. doi:10.1093/sysbio/syab079

Examples

```
# Also see vignette("Analyzing_rates_of_evolution").
## Not run:
# Generating a tree with 500 species
set.seed(102)
tree <- ape::rtree(n = 500)
tree <- ape::chronopl(tree, lambda = 1, age.min = 1)

### model = 'predictor_BM' ###
sim_data <- simulate_rate(tree,
  startv_x = 0, sigma_x = 0.25, a = 1, b = 1, model =
    "predictor_BM"
)
head(sim_data$tips)
gls_mod <- rate_gls(
  x = sim_data$tips$x, y = sim_data$tips$y,
  species = sim_data$tips$species, tree, model = "predictor_BM"
)
gls_mod$param
par(mfrow = c(1, 2))
# Response shown on the standard deviation scale (default):
plot(gls_mod, scale = "SD", cex.legend = 0.8)
# Response shown on the variance scale, where the regression is linear:
plot(gls_mod, scale = "VAR", cex.legend = 0.8)
par(mfrow = c(1, 1))
# Parametric bootstrapping to get the uncertainty of the parameter estimates
# taking the complete process into account.
# (this takes some minutes)
gls_mod_boot <- rate_gls_boot(gls_mod, n = 1000)
gls_mod_boot$summary

### model = 'predictor_gBM' ###
sim_data <- simulate_rate(tree,
  startv_x = 1, sigma_x = 1, a = 1, b = 1,
  model = "predictor_gBM"
)
head(sim_data$tips)
gls_mod <- rate_gls(
  x = sim_data$tips$x, y = sim_data$tips$y, species = sim_data$tips$species,
  tree, model = "predictor_gBM"
)
gls_mod$param
plot(gls_mod)
par(mfrow = c(1, 2))
# Response shown on the standard deviation scale (default):
plot(gls_mod, scale = "SD", cex.legend = 0.8)
# Response shown on the variance scale, where the regression is linear:
plot(gls_mod, scale = "VAR", cex.legend = 0.8)
# is linear.
par(mfrow = c(1, 1))

# Parametric bootstrapping to get the uncertainty of the parameter estimates
```

```
# taking the complete process into account. (This takes some minutes.)
gls_mod_boot <- rate_gls_boot(gls_mod, n = 1000)
gls_mod_boot$summary

### model = 'recent_evol' ###
sim_data <- simulate_rate(tree,
  startv_x = 0, sigma_x = 1, a = 1, b = 1, sigma_y = 1,
  model = "recent_evol"
)
head(sim_data$tips)
gls_mod <- rate_gls(
  x = sim_data$tips$x, y = sim_data$tips$y, species = sim_data$tips$species,
  tree, model = "recent_evol", useLFO = FALSE
)
# useLFO = TRUE is somewhat slower, and although more correct it should give
# very similar estimates in most situations.
gls_mod$param
par(mfrow = c(1, 2))
# Response shown on the standard deviation scale (default):
plot(gls_mod, scale = "SD", cex.legend = 0.8)
# Response shown on the variance scale, where the regression is linear:
plot(gls_mod, scale = "VAR", cex.legend = 0.8)
# linear.
par(mfrow = c(1, 1))

# Parametric bootstrapping to get the uncertainty of the parameter estimates
# taking the complete process into account. Note that x is considered as
# fixed effect. (This takes a long time.)
gls_mod_boot <- rate_gls_boot(gls_mod, n = 1000, useLFO = FALSE)
gls_mod_boot$summary

## End(Not run)
```

`rate_gls_boot` *Bootstrap of the `rate_gls` model fit*

Description

`rate_gls_boot` performs a parametric bootstrap of a `rate_gls` model fit.

Usage

```
rate_gls_boot(
  object,
  n = 10,
  useLFO = TRUE,
  silent = FALSE,
  maxiter = 100,
  tol = 0.001
)
```

Arguments

`object`	The output from `rate_gls`.
`n`	The number of bootstrap samples
`useLFO`	logical: when calculating the mean vector of the traits in the 'recent_evol' analysis, should the focal species be left out when calculating the corresponding species' mean. The correct way is to use TRUE, but in practice it has little effect and FALSE will speed up the model fit (particularly useful when bootstrapping).
`silent`	logical: whether or not the bootstrap iterations should be printed.
`maxiter`	The maximum number of iterations for updating the GLS.
`tol`	tolerance for convergence. If the change in 'a' and 'b' is below this limit between the two last iteration, convergence is reached. The change is measured in proportion to the standard deviation of the response for 'a' and the ratio of the standard deviation of the response to the standard deviation of the predictor for 'b'.

Value

A list where the first slot is a table with the original estimates and SE from the GLS fit in the two first columns followed by the bootstrap estimate of the SE and the 2.5%, 50% and 97.5% quantiles of the bootstrap distribution. The second slot contains the complete distribution.

Author(s)

Geir H. Bolstad

Examples

```
# See the vignette 'Analyzing rates of evolution' and in the help
# page of rate_gls.
```

`rate_gls_sim` *Simulate responses from `rate_gls` fit*

Description

`rate_gls_sim` responses from the models defined by an object of class `'rate_gls'`.

Usage

```
rate_gls_sim(object, nsim = 10)
```

Arguments

`object`	The fitted object from `rate_gls`
`nsim`	The number of simulations.

Details

`rate_gls_sim` simply passes the estimates in an object of class `'rate_gls'` to the function `simulate_rate` for simulating responses of the evolutionary process. It is mainly intended for internal use in `rate_gls_boot`.

Value

An object of `class 'simulate_rate'`, which is a list with the following components:

`tips`	A data frame of x and y values for the tips.
`percent_negative_roots`	The percent of iterations with negative roots in the rates of y (not given for model = 're
`compl_dynamics`	A list with the output of the complete dynamics (not given for model = 'recent_evol').

Author(s)

Geir H. Bolstad

Examples

```
# See the vignette 'Analyzing rates of evolution'.
```

`responsediffBeta` *Calculate response differences along a set of selection gradients*

Description

`G1` and `G2` need to be symmetric and positive definite.

Usage

```
responsediffBeta(G1, G2, Beta, means1 = 1, means2 = 1)
```

Arguments

`G1`	A variance matrix.
`G2`	A variance matrix.
`Beta`	Either a vector or a matrix of unit length selection gradients stacked column wise.
`means1`	An optional vector of trait means of G1 (for internal mean standardization).
`means2`	An optional vector of trait means of G2 (for internal mean standardization).

Details

`responsdiffBeta` calculates the response difference along selection gradients between two additive-genetic variance matrices as described in Hansen and Houle (2008).

Value

An object of `class 'responsdiffBeta'`, which is a list with the following components:

`Beta`	The matrix of selection gradients.
`d`	The response difference of each selection gradient.

Author(s)

Geir H. Bolstad

References

Hansen, T. F. & Houle, D. (2008) Measuring and comparing evolvability and constraint in multivariate characters. J. Evol. Biol. 21:1201-1219.

Examples

```
G1 <- matrix(c(1, 1, 0, 1, 2, 2, 0, 2, 3), ncol = 3) / 10
G2 <- matrix(c(1, 2, 0,2, 1, 1,0, 1, 3), ncol = 3)
Beta <- randomBeta(5, 3)
X <- responsediffBeta(G1, G2, Beta)
summary(X)
```

`round_and_format` *Rounds and formats in the same function*

Description

`round_and_format` rounds and formats a numeric vector. This is useful for providing output for tables or plots in a standardized format.

Usage

```
round_and_format(
  x,
  digits = 2,
  sign_digits = NULL,
  scientific = FALSE,
  trim = TRUE
)
```

Arguments

`x`	A numeric vector.
`digits`	Number of decimal places.
`sign_digits`	Number of significant digits (if given this overrides `digits`).
`scientific`	logical: whether encoding should be in scientific notation or not.
`trim`	logical: if leading blanks for justification to common width should be excluded or not.

Value

Rounded and formatted values as characters.

Author(s)

Geir H. Bolstad

`simulate_rate` *Simulating evolutionary rate model*

Description

`simulate_rate` Simulates three different evolutionary rates models. In the two first, 'predictor_BM' and 'predictor_gBM', the evolution of y follows a Brownian motion with variance linear in x, while the evolution of x either follows a Brownian motion or a geometric Brownian motion, respectively. In the third model, 'recent_evol', the residuals of the macroevolutionary predictions of y have variance linear in x.

Usage

```
simulate_rate(
  tree,
  startv_x = NULL,
  sigma_x = NULL,
  a,
  b,
  sigma_y = NULL,
  x = NULL,
  model = "predictor_BM"
)
```

Arguments

`tree`	A `phylo` object. Must be ultrametric and scaled to unit length.
`startv_x`	The starting value for x (usually 0 for 'predictor_BM' and 'recent_evol', and 1 for 'predictor_gBM').
`sigma_x`	The evolutionary rate of x.
`a`	A parameter of the evolutionary rate of y.
`b`	A parameter of the evolutionary rate of y.
`sigma_y`	The evolutionary rate for the macroevolution of y (Brownian motion process) used in the 'recent_evolution' model.
`x`	Optional fixed values of x (only for the 'recent_evol' model), must equal number of tips in the phylogeny, must correspond to the order of the tip labels.
`model`	Either a Brownian motion model of x 'predictor_BM', geometric Brownian motion model of x 'predictor_gBM', or 'recent_evol'.

Details

See the vignette ’Analyzing rates of evolution’ for an explanation of the evolutionary models. The data of the tips can be analyzed with the function `rate_gls`. Note that a large part of parameter space will cause negative roots in the rates of y (i.e. negative a+bx). In these cases the rates are set to 0. A warning message is given if the number of such instances is larger than 0.1%. For model 1 and 2, it is possible to set ‘a=’scaleme’‘, if this chosen then ‘a‘ will be given the lowest possible value constrained by a+bx>0.

Value

An object of `class 'simulate_rate'`, which is a list with the following components:

`tips`	A data frame of x and y values for the tips.
`percent_negative_roots`	The percent of iterations with negative roots in the rates of y (not given for model = ’re
`compl_dynamics`	A list with the output of the complete dynamics (not given for model = ’recent_evol’).

Author(s)

Geir H. Bolstad

Examples

```
# Also see the vignette 'Analyzing rates of evolution'.
## Not run:
# Generating a tree with 50 species
set.seed(102)
tree <- ape::rtree(n = 50)
tree <- ape::chronopl(tree, lambda = 1, age.min = 1)

### model = 'predictor_BM' ###
sim_data <- simulate_rate(tree, startv_x = 0, sigma_x = 0.25, a = 1, b = 1,
model = "predictor_BM")
head(sim_data$tips)
par(mfrow = c(1, 3))
plot(sim_data)
plot(sim_data, response = "y")
plot(sim_data, response = "x")
par(mfrow = c(1, 1))

### model = 'predictor_gBM' ###
sim_data <- simulate_rate(tree, startv_x = 1, sigma_x = 1, a = 1, b = 0.1,
model = "predictor_gBM")
head(sim_data$tips)
par(mfrow = c(1, 3))
plot(sim_data)
plot(sim_data, response = "y")
plot(sim_data, response = "x")
par(mfrow = c(1, 1))

### model = 'recent_evol' ###
sim_data <- simulate_rate(tree,
```

```
  startv_x = 0, sigma_x = 1, a = 1, b = 1, sigma_y = 1,
  model = "recent_evol"
)
head(sim_data$tips)

## End(Not run)
```

`summary.evolvabilityBeta` *Summarizing evolvability parameters over a set of selection gradients*

Description

`summary` method for class `'evolvabilityBeta'`.

Usage

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

Arguments

`object`	An object of class `'evolvabilityBeta'`.
`...`	Additional arguments.

Value

A list with the following components:

`Averages`	The averages of the evolvability parameters over all selection gradients.
`Minimum`	The minimum of the evolvability parameters over all selection gradients.
`Maximum`	The maximum of the evolvability parameters over all selection gradients.

Author(s)

Geir H. Bolstad

See Also

`evolvabilityBeta`

`summary.evolvabilityBetaMCMC`

Summarizing posterior distribution of evolvability parameters over a set of selection gradients

---

Description

`summary` method for class `'evolvabilityBetaMCMC'`.

Usage

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

Arguments

`object`	an object of class `'evolvabilityBetaMCMC'`.
`...`	additional arguments affecting the summary produced.

Value

A list with the following components:

`Averages`	The averages of the evolvability parameters over all selection gradients.
`Minimum`	The minimum (given by the posterior median) of the evolvability parameters over all selection gradients.
`Maximum`	The maximum (given by the posterior median) of the evolvability parameters over all selection gradients.

Author(s)

Geir H. Bolstad

See Also

`evolvabilityBetaMCMC`

`summary.responsediffBeta`

Summarizing response differences over a set of selection gradients

---

Description

`summary` method for class `'responsediffBeta'`.

Usage

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

Arguments

`object`	An object of class `'responsediffBeta'`.
`...`	Additional arguments.

Value

A list with the following components:

`Averages`	The averages of the response differences over all selection gradients.
`Minimum`	The minimum of the response differences over all selection gradients.
`Maximum`	The maximum of the response differences over all selection gradients.

Author(s)

Geir H. Bolstad

See Also

`responsediffBeta`

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