Package: evolvability (via r-universe)

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Type Package

Title Calculation of Evolvability Parameters

Version 2.0.2

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)

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BugReports https://github.com/GHBolstad/evolvability/issues

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`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:	2.0.2
License:	GPL (>= 2)

Author(s)

Geir H. Bolstad <geir.bolstad@nina.no>

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

---

`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 because 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 symmetric variance matrix (see Details).
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). An error is given if G is not symmetric. If the variance matrix of the traits in condition_on cannot be inverted by solve(), a warning is issued and a matrix of NA is returned. A warning is also issued if G is not positive definite (it has negative eigenvalues); the result is then still calculated but may not be meaningful.

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

`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).

Usage

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

Arguments

`G`	A symmetric variance matrix (see Details).
`Beta`	Either a vector or a matrix of unit length selection gradients stacked column wise. A warning is issued if any gradient's Euclidean length differs from one by more than `sqrt(.Machine$double.eps)` or is not finite. Gradients are not automatically normalized.
`means`	An optional vector of trait means (for internal mean standardization).

Details

`G` must be symmetric, otherwise an error is given. If `solve(G)` fails because the matrix is singular or computationally singular, a warning is issued, the conditional evolvability, autonomy and integration are returned as `NA`, and the other parameters are still calculated. A warning is also issued if `G` is not positive definite (it has negative eigenvalues); the parameters are then still calculated but may not be meaningful.

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, 1, 0, 1, 2), 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. A warning is issued if any gradient's Euclidean length differs from one by more than sqrt(.Machine$double.eps) or is not finite. Gradients are not automatically normalized.
post.dist	logical: should the posterior distribution of the evolvability parameters be saved.

Details

An error is given if any draw in G_mcmc is not symmetric. If solve(G) fails for a posterior draw because the matrix is singular or computationally singular, a warning is issued. Conditional evolvability, autonomy and integration are NA for that draw, and their posterior summaries are NA; the other results are still calculated. A warning is also issued if draws are not positive definite (they have negative eigenvalues); the results are then still calculated but may not be meaningful for those draws.

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. A warning is issued if any gradient's Euclidean length differs from one by more than `sqrt(.Machine$double.eps)` or is not finite. Gradients are not automatically normalized.
`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.

Details

An error is given if any draw in `G_mcmc` is not symmetric. If `solve(G)` fails for a posterior draw because the matrix is singular or computationally singular, a warning is issued. Conditional evolvability, autonomy and integration are `NA` for that draw, and their posterior summaries are `NA`; the other results are still calculated. A warning is also issued if draws are not positive definite (they have negative eigenvalues); the results are then still calculated but may not be meaningful for those draws.

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 symmetric variance matrix (see Details).
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 `evolvabilityBetaMCMC` 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. `G` must be symmetric, otherwise an error is given. If `solve(G)` fails because the matrix is singular or computationally singular, a warning is issued, the conditional evolvability, autonomy and integration are `NA`, and the other parameters are still calculated. A warning is also issued if `G` is not positive definite (it has negative eigenvalues); the parameters are then still calculated but may not be meaningful.

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

`evolvabilityMeansMCMC` 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 `evolvabilityBetaMCMC` 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. An error is given if any draw of `G_mcmc` is not symmetric. If `solve(G)` fails for a draw because the matrix is singular or computationally singular, a warning is issued, and the conditional evolvability, autonomy and integration are `NA` for that draw and in their posterior summaries; the other parameters are still calculated. A warning is also issued if draws are not positive definite (they have negative eigenvalues); the parameters are then still calculated but may not be meaningful for those draws.

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. The first column must be the intercept (a column of ones), which is used for the total sum of squares and hence the R-squared.
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 symmetric variance matrix. An error is given if it is not symmetric.
means	A vector of trait means.

Details

An error is given if G is not symmetric, or if the length of means differs from the dimension of G.

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.

Details

An error is given if any draw in `G_mcmc` is not symmetric, or if the dimensions of `G_mcmc` and `means_mcmc` do not match.

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. (2021) 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 report the parameter estimates and convergence score for each iteration (reported with message).

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. (2021) and vignette("Analyzing_rates_of_evolution") 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

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

Usage

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

Arguments

G1	A symmetric variance matrix (see Details).
G2	A symmetric variance matrix (see Details).
Beta	Either a vector or a matrix of unit length selection gradients stacked column wise. A warning is issued if any gradient's Euclidean length differs from one by more than sqrt(.Machine$double.eps) or is not finite. Gradients are not automatically normalized.
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

G1 and G2 must be symmetric, otherwise an error is given. A warning is issued if either is not positive definite (it has negative eigenvalues); the response difference is then still calculated but may not be meaningful.

Value

An object of class 'responsediffBeta', 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, 1, 0, 1, 2), ncol = 3) / 10
G2 <- matrix(c(2, 1, 0, 1, 2, 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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