# Package: evoTS (via r-universe)

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Title Analyses of Evolutionary Time-Series

Version 1.0.3

Description Facilitates univariate and multivariate analysis of evolutionary sequences of phenotypic change. The package extends the modeling framework available in the 'paleoTS' package. Please see <<https://klvoje.github.io/evoTS/index.html>> for information about the package and the implemented models.

License GPL  $(>= 2)$ 

Encoding UTF-8

Imports paleoTS (>= 0.4-4), mvtnorm, plotly, pracma, MASS, stats, utils

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LazyData true

Roxygen list(markdown = TRUE)

RoxygenNote 7.3.1

Suggests rmarkdown, knitr

**Depends**  $R (= 3.5.0)$ 

URL <https://klvoje.github.io/evoTS/index.html>

BugReports <https://github.com/klvoje/evoTS/issues>

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

RemoteUrl https://github.com/klvoje/evots

RemoteRef HEAD

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<span id="page-2-0"></span>as.evoTS.multi.BW.acceldecel.fit

*Class for fit to evolutionary sequence (time-series) models*

# Description

A function that combines useful information summarizing model fit.

# Usage

```
as.evoTS.multi.BW.acceldecel.fit(
 converge,
 modelName,
 logL,
  ancestral.values,
 SE.anc,
 r,
 SE.r,
 R,
 SE.R,
 method,
 K,
 n,
  iter
)
```
# Arguments



# <span id="page-3-0"></span>Details

This function is used by the model-fitting routines for the Unbiased Random Walk models with an accelerated and decelerated rate of evoluton to create standardized output

# Note

This function is not likely to be called directly by the user.

# Author(s)

Kjetil Lysne Voje

as.evoTS.multi.BW.fit *Class for fit to evolutionary sequence (time-series) models*

# Description

A function that combines useful information summarizing model fit.

## Usage

```
as.evoTS.multi.BW.fit(
 converge,
 modelName,
 logL,
  ancestral.values,
  SE.anc,
 R,
  SE.R,
  shift.point,
 method,
 K,
 n,
  iter
)
```
# Arguments



<span id="page-4-0"></span>

# Details

This function is used by the model-fitting routines for the multivariate Unbiased Random Walk models to create standardized output

# Note

This function is not likely to be called directly by the user.

# Author(s)

Kjetil Lysne Voje

as.evoTS.multi.OU.fit *Class for fit to evolutionary sequence (time-series) models*

# Description

A function that combines useful information summarizing model fit.

```
as.evoTS.multi.OU.fit(
  converge,
  logL,
  ancestral.values,
  SE.anc,
  optima,
  SE.optima,
  A,
  SE.A,
  half.life,
  R,
  SE.R,
  method,
  K,
  n,
  iter
\mathcal{E}
```
<span id="page-5-0"></span>

# Details

This function is used by the model-fitting routines for the multivariate Ornstein-Uhlenbeck models to create standardized output

# Note

This function is not likely to be called directly by the user.

# Author(s)

Kjetil Lysne Voje

as.evoTS.multi.URW.fit

*Class for fit to evolutionary sequence (time-series) models*

# Description

A function that combines useful information summarizing model fit.

# as.evoTS.multi.URW.fit 7

# Usage

```
as.evoTS.multi.URW.fit(
  converge,
 modelName,
 logL,
  ancestral.values,
  SE.anc,
 R,
  SE.R,
 method,
 K,
 n,
  iter
```
# Arguments

)



# Details

This function is used by the model-fitting routines for the multivariate Unbiased Random Walk models to create standardized output

# Note

This function is not likely to be called directly by the user.

# Author(s)

Kjetil Lysne Voje

```
as.evoTS.multi.URW.shift.fit
```
*Class for fit to evolutionary sequence (time-series) models*

# Description

A function that combines useful information summarizing model fit.

# Usage

```
as.evoTS.multi.URW.shift.fit(
  converge,
  modelName,
  logL,
  ancestral.values,
  SE.anc,
  R,
  SE.R,
  shift.point,
  method,
  K,
  n,
  iter
\mathcal{L}
```
# Arguments



## <span id="page-8-0"></span>as.evoTSfit.OUBM 9

## Details

This function is used by the model-fitting routines for the multivariate Unbiased Random Walk models to create standardized output

# Note

This function is not likely to be called directly by the user.

#### Author(s)

Kjetil Lysne Voje

as.evoTSfit.OUBM *Class for fit to evolutionary sequence (time-series) models*

#### Description

A function that combines useful information summarizing model fit.

# Usage

as.evoTSfit.OUBM(logL, parameters, modelName, method, K, n, iter, se)

## Arguments



#### Details

This function is used by the model-fitting routines for the univariate Ornstein-Uhlenbeck model where the optimum evolves as an Unbiased Random Walk to create standardized output

#### Note

This function is not likely to be called directly by the user.

# Author(s)

Kjetil Lysne Voje

```
diameter_S.yellowstonensis
```
*Evolutionary sequence (time-series) of phenotypic change in diameter in the lineage Stephanodiscus yellowstonensis*

#### Description

Phenotypic data (diameter) from a centric diatom lineage Stephanodiscus yellowstonensis. The time series spans about 14 000 years. The data set contains data on valve diameter (measured in micrometres). The data consists of an object of class paleoTS (diameter\_S.yellowstonensis). Objects of class paleoTS can be analyzed in evoTS. The object (trait data set) contains a vector of sample means (mm), sample variances (vv), sample sizes (nn) and sample ages (tt). The oldest sample is listed first. The data spans an interval of 13728 years.

# Usage

```
data(diameter_S.yellowstonensis)
```
#### Format

An object of class "paleoTS".

# References

Theriot et al. 2006. Late Quaternary rapid morphological evolution of an endemic diatom in Yellowstone Lake, Wyoming. Paleobiology 32:38-54

#### Examples

```
ln.diameter<-paleoTS::ln.paleoTS(diameter_S.yellowstonensis)
ln.diameter$tt<-ln.diameter$tt/(max(ln.diameter$tt))
opt.joint.decel(ln.diameter)
```
fit.all.univariate *Fit all univariate models to an evolutionary sequence (time-series).*

#### Description

Wrapper function to find maximum likelihood solutions for all univariate models (excluding models with mode shifts) to an evolutionary sequence (time-series).

#### Usage

fit.all.univariate(y, pool = TRUE)

#### <span id="page-10-0"></span>fit.mode.shift 11

#### Arguments



#### Value

The function returns a list of all investigated models and their highest log-likelihood (and their corresponding AICc and AICc weight).

#### Author(s)

Kjetil Lysne Voje

# References

Hunt, G. 2006. Fitting and comparing models of phyletic evolution: random walks and beyond. *Paleobiology* 32:578–601

Hunt, G., Bell, M. A. & Travis, M. P. Evolution towards a new adaptive optimum: Phenotypic evolution in a fossil stickleback lineage. *Evolution* 62:700–710 (2008)

#### Examples

```
## ##Generate a paleoTS object.
x <- paleoTS::sim.GRW(30)
```
## Fit univariate models to the data. fit.all.univariate(x, pool = TRUE)

fit.mode.shift *Fit two models to two separate segments to an evolutionary sequence (time-series).*

# Description

Wrapper function to find maximum likelihood solutions to two models to an evolutionary sequence.

```
fit.mode.shift(
  y,
 model1 = c("Stasis", "URW", "GRW", "OU"),
 model2 = c("Stasis", "URW", "GRW", "OU"),
  fit.al1 = FALSE,minb = 7,
  shift.point = NULL,
  pool = TRUE,
```

```
silent = FALSE,
  hess = FALSE
\lambda
```


## Value

the function returns a list of all investigated models and their highest log-likelihood (and their corresponding AICc and AICc weight).



In addition, if fit.all=TRUE the function also returns a list of all investigated models and their highest log-likelihood (and their corresponding AICc and AICc weight).

# Note

The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

## <span id="page-12-0"></span>Author(s)

Kjetil Lysne Voje

#### References

Hunt, G. 2006. Fitting and comparing models of phyletic evolution: random walks and beyond. *Paleobiology* 32:578–601

Hunt, G., Bell, M. A. & Travis, M. P. Evolution towards a new adaptive optimum: Phenotypic evolution in a fossil stickleback lineage. *Evolution* 62:700–710 (2008)

#### Examples

```
##Generate a paleoTS object.
x <- paleoTS::sim.GRW(30)
```
## Fit a mode-shift model without defining a shift point (the example may take > 5 seconds to run) fit.mode.shift(x, model1="URW", model2="Stasis")

fit.multivariate.OU *Fit predefined multivariate Ornstein-Uhlenbeck models to multivariate evolutionary sequence (time-series) data.*

# **Description**

Function to find maximum likelihood solutions to a large suite of predefined multivariate Ornstein-Uhlenbeck model fitted to multivariate evolutionary sequence (time-series) data.

```
fit.multivariate.OU(
 yy,
 A.matrix = "diag",R.matrix = "symmetric",
 method = "Nelder-Mead",
 hess = FALSE,
 pool = TRUE,trace = FALSE,iterations = NULL,
  iter.sd = NULL,
  user.init.diag.A = NULL,
  user.init.diag.R = NULL,
  user.init.off.diag.A = NULL,
  user.init.off.diag.R = NULL,
  user.init.theta = NULL,
  user.init.anc = NULL
)
```


# Details

A detailed explanation of the predefined models that can be fitted using the function is given in the online vignette (https://klvoje.github.io/evoTS/index.html), but a short summary is provided here. Note that this function provides the user with fixed options for how to parameterize the A and R matrices. For full flexibility, the user is allowed to customize the parameterization of the A and R matrix in the 'fit.multivariate.OU.user.defined' function. The type of trait dynamics is defined based on how the pull matrix (A) and drift matrix (R) are defined. The function allows testing four broad categories of models: 1 Independent evolution (A.matrix ="diag", R.matrix = "diag"); 2 Independent adaptation (A.matrix ="diag", R.matrix = "symmetric"); 3 Non-independent adaptation (A.matrix = "upper.tri"/"lower.tri"/full", R.matrix = "diagonal"); 4 Non-independent evolution (A.matrix = "upper.tri"/"lower.tri"/"full", R.matrix = "symmetric"). Setting the A.matrix to "diagonal" means the traits do not affect each others optimum (A matrix). A "diagonal" R matrix means the stochastic changes in the traits are assumed to be uncorrelated. A "symmetric" R matrix means the stochastic changes in the traits are assumed to be correlated, i.e. that they are non-independent. A "full" parameterization of A estimates the effect of each trait on the optima on the other traits. The "upper.tri" option parameterize the model in such a way that the first layer (first trait in the data set) adapts non-independently because its optimum is affected by all other traits included in the data set, while the bottom layer (the last trait in the data set) adapts independently (as an Ornstein Uhlenbeck process). Layers in between the upper- and lower layer (not the first or last trait in the data set (if there are more than two traits in the data set)) evolve non-independently as their optimum is affected by all layers/traits below themselves. The option "lower.tri" defines the causality the opposite way compared to "upper.tri". It is also possible to implement a model where the bottom layer (last trait in the data set) evolve as an Unbiased random walk (akin to a Brownian motion) which affects the optima for all other traits in the data set (i.e. all layers except the bottom layer). This model can be fitted by defining A.matrix ="OUBM", which will override how the R matrix is defined.

The function searches - using an optimization routine - for the maximum-likelihood solution for the chosen multivariate Ornstein-Uhlenbeck model. The argument 'method' is passed to the 'optim' function and is included for the convenience of users to better control the optimization routine. Note that the the default method (Nelder-Mead) seems to work for most evolutionary sequences. The method L-BFGS-B allows box-constraints on some parameters (e.g. non-negative variance parameters) and is faster than Nelder-Mead, but is less stable than the default method (Nelder-Mead).

Initial estimates to start the optimization come from maximum-likelihood estimates of the univariate Ornstein-Uhlenbeck model (from the paleoTS package) fitted to each time-series separately.

It is good practice to repeat any numerical optimization procedure from different starting points. This is especially important for complex models as the log-likelihood surface might contain more than one peak. The number of iterations is controlled by the argument 'iterations'. The function will report the model parameters from the iteration with the highest log-likelihood.

There is no guarantee that the likelihood can be computed with the initial parameters provided by the function. The starting values for fitting the multivariate OU model are based on maximum likelihood parameter estimates for the univariate OU model fitted to each trait separately, which seems to provide sensible (and working) initial parameter estimates for almost all tested data sets. However, the provided initial parameters may fail depending on the nature of the data. If an error message is returned saying "function cannot be evaluated at initial parameters", the user can try to start the optimization procedure from other initial parameter values using "user.init.diag.A", "user.init.diag.R", "user.init.off.diag.A", "user.init.off.diag.R", "user.init.theta", and "user.init.anc." It is usually the initial guess of the off-diagonal elements of the A and R matrices that prevents the optimization routine to work. It is therefore recommended to only try to change these initial values before experimenting with different starting values for the diagonal of the A and R matrices.

#### Value

First part of the output reports the log-likelihood of the model and its AICc score. The second part of the output is the maximum log-likelihood model parameters (ancestral.values, optima, A, and R). The half-life is also provided, which is the The last part of the output gives information about the number of parameters in the model  $(K)$ , number of samples in the data  $(n)$  and number of times the optimization routine was run (iter).

Note

The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

#### Author(s)

Kjetil Lysne Voje

#### References

Reitan, T., Schweder, T. & Henderiks, J. Phenotypic evolution studied by layered stochastic differential equations. *Ann Appl Statistics* 6, 1531–1551 (2012).

Bartoszek, K., Pienaar, J., Mostad, P., Andersson, S. & Hansen, T. F. A phylogenetic comparative method for studying multivariate adaptation. *J Theor Biol* 314, 204–215 (2012).

Clavel, J., Escarguel, G. & Merceron, G. mvmorph: an r package for fitting multivariate evolutionary models to morphometric data. *Methods Ecol Evol 6*, 1311–1319 (2015).

#### Examples

## Generate a evoTS object by simulating a multivariate dataset  $x \le -\sin.multi.0U(15)$ 

##Fit a multivariate Ornstein-Uhlenbeck model to the data. This example will run for a long time. fit.multivariate.OU(x, A.matrix="diag", R.matrix="symmetric")

fit.multivariate.OU.user.defined

*Fit user-defined multivariate Ornstein-Uhlenbeck models to multivariate evolutionary sequence (time-series) data.*

#### **Description**

Function to find maximum likelihood solutions to a multivariate Ornstein-Uhlenbeck model fitted using user-defined A and R matrices.

```
fit.multivariate.OU.user.defined(
 yy,
 A.user = NULL,
 R.user = NULL,method = "Nelder-Mead",
```
<span id="page-15-0"></span>

```
hess = FALSE,pool = TRUE,trace = FALSE,
  iterations = NULL,
  iter.sd = NULL,
 user.init.diag.A = NULL,
 user.init.upper.diag.A = NULL,
 user.init.lower.diag.A = NULL,
 user.init.diag.R = NULL,
 user.init.off.diag.R = NULL,
 user.init.theta = NULL,
 user.init.anc = NULL
\mathcal{L}
```


#### Details

This function provides users the flexibility to define their own A and R matrices. The possibility to define any A matrices enable detailed investigation of specific evolutionary hypotheses. The parameters to be estimated in the matrices are indicated by the value 1. All other entries in the matrix must be 0.

The function searches - using an optimization routine - for the maximum-likelihood solution for the chosen multivariate Ornstein-Uhlenbeck model. The argument 'method' is passed to the 'optim' function and is included for the convenience of users to better control the optimization routine. Note that the the default method (Nelder-Mead) seems to work for most evolutionary sequences. The method L-BFGS-B allows box-constraints on some parameters (e.g. non-negative variance parameters) and is faster than Nelder-Mead, but is less stable than the default method (Nelder-Mead).

Initial estimates to start the optimization come from maximum-likelihood estimates of the univariate Ornstein-Uhlenbeck model (from the paleoTS package) fitted to each time-series separately.

It is good practice to repeat any numerical optimization procedure from different starting points. This is especially important for complex models as the log-likelihood surface might contain more than one peak. The number of iterations is controlled by the argument 'iterations'. The function will report the model parameters from the iteration with the highest log-likelihood.

There is no guarantee that the likelihood can be computed with the initial parameters provided by the function. The starting values for fitting the multivariate OU model are based on maximum likelihood parameter estimates for the univariate OU model fitted to each trait separately, which seems to provide sensible (and working) initial parameter estimates for almost all tested data sets. However, the provided initial parameters may fail depending on the nature of the data. If an error message is returned saying "function cannot be evaluated at initial parameters", the user can try to start the optimization procedure from other initial parameter values using "user.init.diag.A", "user.init.upper.diag.A", "user.init.lower.diag.A", "user.init.diag.R", "user.init.off.diag.R", "user.init.theta", and "user.init.anc." It is usually the initial guess of the off-diagonal elements of the A and R matrices that prevents the optimization routine to work. It is therefore recommended to only try to change these initial values before experimenting with different starting values for the diagonal of the A and R matrices.

#### Value

First part of the output reports the log-likelihood of the model and its AICc score. The second part of the output is the maximum log-likelihood model parameters (ancestral.values, optima, A, and R). The half-life is also provided, which is the The last part of the output gives information about the number of parameters in the model  $(K)$ , number of samples in the data  $(n)$  and number of times the optimization routine was run (iter).

#### Note

The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

#### <span id="page-18-0"></span>Author(s)

Kjetil Lysne Voje

#### References

Reitan, T., Schweder, T. & Henderiks, J. Phenotypic evolution studied by layered stochastic differential equations. *Ann Appl Statistics* 6, 1531–1551 (2012).

Bartoszek, K., Pienaar, J., Mostad, P., Andersson, S. & Hansen, T. F. A phylogenetic comparative method for studying multivariate adaptation. *J Theor Biol* 314, 204–215 (2012).

Clavel, J., Escarguel, G. & Merceron, G. mvmorph: an r package for fitting multivariate evolutionary models to morphometric data. *Methods Ecol Evol 6*, 1311–1319 (2015).

#### Examples

```
## Generate a evoTS object by simulating a multivariate dataset
x \le -\sin.multi.0U(15)## Define an A matrix that is lower diagonal.
A \leq matrix(c(1,0,1,1), nrow=2, byrow=TRUE)
```

```
## Define a diagonal R matrix.
R \leq -\text{matrix}(c(1, 0, 0, 1), \text{nrow=2}, \text{byrow=TRUE})
```
## Fit the multivariate Ornstein-Uhlenbeck model to the data. This example will run for a long time. fit.multivariate.OU.user.defined(x, A.user=A, R.user=R, trace=TRUE)

fit.multivariate.URW *Fit multivariate Unbiased Random Walk models to multivariate evolutionary sequence (time-series) data.*

# **Description**

Function to find maximum likelihood solutions to a multivariate Unbiased Random Walk model.

```
fit.multivariate.URW(
  yy,
 R = "symmetric",r = "fixed",method = "L-BFGS-B",
  hess = FALSE,
 pool = TRUE,
  trace = FALSE,
  iterations = NULL,
  iter.sd = NULL
)
```


# **Details**

The function allows the users to test six variants of multivariate Unbiased Random Walk models. There are two options for the structure of the R matrix. A "diagonal" R matrix means the stochastic changes in the traits are assumed to be uncorrelated. A "symmetric" R matrix means the stochastic changes in the traits are assumed to be correlated, i.e. that they are non-independent.

There are three options for the 'r' parameter. The "fixed" option means there is no change in the rate of change across time  $(r = 0)$ . Setting r to "fixed" therefore fits a regular multivariate Unbiased Random Walk. The "decel" and "accel" options make the rate of change (the R matrix) decay (r < 0) and increase  $(r > 0)$  exponentially through time, respectively.

The function searches - using an optimization routine - for the maximum-likelihood solution for the chosen multivariate Unbiased Random Walk model. The argument 'method' is passed to the 'optim' function and is included for the convenience of users to better control the optimization routine. The the default method (L-BFGS-B) seems to work for most evolutionary sequences.

Initial estimates to start the optimization come from maximum-likelihood estimates of the univariate Unbiased Random Walk model (from the paleoTS package) fitted to each time-series separately.

It is good practice to repeat any numerical optimization procedure from different starting points. This is especially important for complex models as the log-likelihood surface might contain more than one peak. The number of iterations is controlled by the argument 'iterations'. The function will report the model parameters from the iteration with the highest log-likelihood.

#### Value

First part of the output reports the log-likelihood of the model and its AICc score. The second part of the output is the maximum log-likelihood model parameters (ancestral.values, R). The last part of the output gives information about the number of parameters in the model  $(K)$ , number of samples in the data (n) and number of times the optimization routine was run (iter).

#### <span id="page-20-0"></span>Note

The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

# Author(s)

Kjetil Lysne Voje

## References

Revell, L. J. & Harmon, L. Testing quantitative genetic hypotheses about the evolutionary rate matrix for continuous characters. *Evolutionary Ecology Research* 10, 311–331 (2008).

Voje, K. L. Testing eco-evolutionary predictions using fossil data: Phyletic evolution following ecological opportunity. *Evolution* 74, 188–200 (2020).

#### Examples

```
## Generate an evoTS object by simulating a multivariate dataset
x <- sim.multi.URW(30)
```
## Fit a multivariate Unbiased Random Walk model to the data, allowing for correlated changes. fit.multivariate.URW(x,  $R = "symmetric", r = "fixed")$ 

fit.multivariate.URW.shift

*Fit separate multivariate Unbiased Random Walk models to two different segments of a multivariate evolutionary sequence (time-series).*

#### Description

Function to find maximum likelihood solutions for multivariate Unbiased Random Walk models fitted to two different segments of a multivariate evolutionary sequence (time-series).

```
fit.multivariate.URW.shift(
  yy,
 minb = 10,
 hess = FALSE,
 pool = TRUE,
  shift.point = NULL,
  method = "L-BFGS-B",
  trace = FALSE,
```

```
iterations = NULL,
  iter.sd = NULL
)
```


## Details

The function searches - using an optimization routine - for the maximum-likelihood solution for a multivariate Unbiased Random Walk model ti two non-overlapping segments in the time series.

The argument 'method' is passed to the 'optim' function and is included for the convenience of users to better control the optimization routine. The the default method (L-BFGS-B) seems to work for most evolutionary sequences.

Initial estimates to start the optimization come from maximum-likelihood estimates of the univariate Unbiased Random Walk model (from the paleoTS package) fitted to each time-series separately.

It is good practice to repeat any numerical optimization procedure from different starting points. This is especially important for complex models as the log-likelihood surface might contain more than one peak. The number of iterations is controlled by the argument 'iterations'. The function will report the model parameters from the iteration with the highest log-likelihood.

#### Value

First part of the output reports the log-likelihood of the model and its AICc score. The second part of the output is the maximum log-likelihood model parameters (ancestral.values, R). The last part of the output gives information about the number of parameters in the model (K), number of samples in the data (n) and number of times the optimization routine was run (iter).

#### **Note**

The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of

<span id="page-22-0"></span>sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

#### Author(s)

Kjetil Lysne Voje

#### References

Revell, L. J. & Harmon, L. Testing quantitative genetic hypotheses about the evolutionary rate matrix for continuous characters. *Evolutionary Ecology Research* 10, 311–331 (2008).

#### Examples

```
## Generate an evoTS object by simulating a multivariate dataset
x <- sim.multi.URW(60)
```
## Fit two multivariate Unbiased Random Walk models to separate parts of the time-series. fit.multivariate.URW.shift $(x, \text{ shift.point} = 31)$ 

logL.joint.accel.decel.single.R

*Log-likelihoods for evolutionary models*

#### Description

Returns log-likelihood for a multivariate Unbiased Random Walk model with accelerating or decelerating rates of evolution through time.

## Usage

```
logL.joint.accel.decel.single.R(init.par, y, m, n, anc.values, yy)
```
## Arguments



#### Details

In general, users will not be access these functions directly, but instead use the optimization functions, which use these functions to find the best-supported parameter values.

# <span id="page-23-0"></span>Value

The log-likelihood of the parameter estimates, given the data.

# Author(s)

Kjetil Lysne Voje

logL.joint.accel.decel.single.R.zero.corr *Log-likelihoods for evolutionary models*

# Description

Returns log-likelihood for a multivariate Unbiased Random Walk model with uncorrelated changes and with accelerating or decelerating rates of evolution through time.

# Usage

logL.joint.accel.decel.single.R.zero.corr(init.par, y, m, n, anc.values, yy)

# Arguments



# Details

In general, users will not be access these functions directly, but instead use the optimization functions, which use these functions to find the best-supported parameter values.

# Value

The log-likelihood of the parameter estimates, given the data.

## Author(s)

Kjetil Lysne Voje

<span id="page-24-0"></span>logL.joint.accel\_decel

*Log-likelihoods for evolutionary models*

# Description

Returns log-likelihood for an Unbiased Random Walk with an accelerating or decelerating rate of change through time.

# Usage

logL.joint.accel\_decel(p, y)

# Arguments



# Details

In general, users will not be access these functions directly, but instead use the optimization functions, which use these functions to find the best-supported parameter values.

#### Value

The log-likelihood of the parameter estimates, given the data.

#### Author(s)

Kjetil Lysne Voje

logL.joint.multi.OUOU *Log-likelihoods for evolutionary models*

# Description

Returns log-likelihood for a multivariate Ornstein-Uhlenbeck model.

```
logL.joint.multi.OUOU(init.par, yy, A.matrix, R.matrix)
```
<span id="page-25-0"></span>

#### Details

In general, users will not be access these functions directly, but instead use the optimization functions, which use these functions to find the best-supported parameter values.

# Value

The log-likelihood of the parameter estimates, given the data.

#### Author(s)

Kjetil Lysne Voje

logL.joint.multi.OUOU.user

*Log-likelihoods for evolutionary models*

# Description

Returns log-likelihood for a multivariate Ornstein-Uhlenbeck model with used defined A and R matrices..

```
logL.joint.multi.OUOU.user(
  init.par,
  yy,
 A.user,
 R.user,
  locations.A,
  location.diag.A,
  location.upper.tri.A,
  location.lower.tri.A,
  locations.R,
  location.diag.R,
  location.upper.tri.R
)
```


# Details

In general, users will not be access these functions directly, but instead use the optimization functions, which use these functions to find the best-supported parameter values.

# Value

The log-likelihood of the parameter estimates, given the data.

# Author(s)

Kjetil Lysne Voje

<span id="page-27-0"></span>logL.joint.multi.R *Log-likelihoods for evolutionary models*

# Description

Returns log-likelihood for a multivariate Unbiased Random Walk model fitted to separate segments of a multivariate time series.

# Usage

logL.joint.multi.R(init.par, C, y, m, n, anc.values, yy)

# Arguments



# Details

In general, users will not be access these functions directly, but instead use the optimization functions, which use these functions to find the best-supported parameter values.

#### Value

The log-likelihood of the parameter estimates, given the data.

# Author(s)

Kjetil Lysne Voje

#### <span id="page-28-0"></span>Description

Returns log-likelihood for an Ornstein-Uhlenbeck model where the optimum evolves as a Unbiased Random Walk. The movement of the optimum is not parameterized based on separate data.

## Usage

logL.joint.OU.BM(p, y, opt.anc)

#### Arguments



# Details

In general, users will not be access these functions directly, but instead use the optimization functions, which use these functions to find the best-supported parameter values.

# Value

The log-likelihood of the parameter estimates, given the data.

# Author(s)

Kjetil Lysne Voje

#### References

Hansen, T. F., Pienaar, J. & Orzack, S. H. A Comparative Method for Studying Adaptation to a Randomly Evolving Environment. *Evolution* 62, 1965–1977 (2008).

<span id="page-29-0"></span>logL.joint.single.R *Log-likelihoods for evolutionary models*

# Description

Returns log-likelihood for a multivariate Unbiased Random Walk model.

#### Usage

```
logL.joint.single.R(init.par, C, y, m, n, anc.values, yy)
```
## Arguments



# Details

In general, users will not be access these functions directly, but instead use the optimization functions, which use these functions to find the best-supported parameter values.

# Value

The log-likelihood of the parameter estimates, given the data.

#### Author(s)

Kjetil Lysne Voje

<span id="page-30-0"></span>logL.joint.single.R.zero.corr

*Log-likelihoods for evolutionary models*

# Description

Returns log-likelihood for a multivariate Unbiased Random Walk model with uncorrelated changes.

# Usage

```
logL.joint.single.R.zero.corr(init.par, C, y, m, n, anc.values, yy)
```
# Arguments



# Details

In general, users will not be access these functions directly, but instead use the optimization functions, which use these functions to find the best-supported parameter values.

#### Value

The log-likelihood of the parameter estimates, given the data.

# Author(s)

Kjetil Lysne Voje

<span id="page-31-0"></span>logL.joint.Stasis.OU *Log-likelihoods for evolutionary models*

# Description

Returns log-likelihood for a model with stasis in the first segment and an Ornstein-Uhlenbeck process in the second segment. .

#### Usage

logL.joint.Stasis.OU(p, y, gg)

## Arguments



# Details

In general, users will not be access these functions directly, but instead use the optimization functions, which use these functions to find the best-supported parameter values.

# Value

The log-likelihood of the parameter estimates, given the data.

# Author(s)

Kjetil Lysne Voje

logL.joint.URW.URW *Log-likelihoods for evolutionary models*

## Description

Returns log-likelihood for a model with an Unbiased Random Walk in the first segment and an Unbiased Random Walk in the second segment.

#### Usage

logL.joint.URW.URW(p, y, gg)

<span id="page-32-0"></span>

#### Details

In general, users will not access these functions directly, but instead use the optimization functions, which use these functions to find the best-supported parameter values.

# Value

The log-likelihood of the parameter estimates, given the data.

# Author(s)

Kjetil Lysne Voje

loglik.surface.accel *Calculate the log-likelihood surface for a part of parameter space*

#### Description

Function to calculate the log-likelihood surface for a part of parameter space for an Unbiased Random Walk with an accelerated rate of evolution.

#### Usage

loglik.surface.accel(y, vstep.vec, r.vec, pool = TRUE)

#### Arguments



# Value

the function returns the range of parameter values that are within two log-likelihood units from the best (maximum) parameter estimate and a log-likelihood surface.

How fine-scaled the estimated log-likelihood surface is depends on the step size between the values in the input-vectors. The step-size therefore determines how accurate the representation of the support surface is, including the returned upper and lower estimates printed in the console. The range of the input vectors needs to be increased if the confidence interval includes the boundary of the input vector. Note also that it might be wise to include the maximum likelihood estimates as part of the input vectors. The computed support surface is conditional on the best estimates of the other model parameters that are not part of the support surface (e.g. the estimated ancestral trait value).

#### Author(s)

Kjetil Lysne Voje

#### Examples

```
## Generate a paleoTS objects
x <- sim.accel.decel(50)
```
## Fit the model to the data. x1<-opt.joint.accel(x)

```
## Create log-likelihood surface (the example may take > 5 seconds to run)
loglik.surface.accel(x, vstep.vec = seq(0,4,0.005), r.vec = seq(0.15,0.25,0.005))
```
loglik.surface.decel *Calculate the log-likelihood surface for a part of parameter space*

## Description

Function to calculate the log-likelihood surface for a part of parameter space for an Unbiased Random Walk with an decelerated rate of evolution.

# Usage

```
loglik.surface.decel(y, vstep.vec, r.vec, pool = TRUE)
```
## Arguments



<span id="page-33-0"></span>

# Note

## <span id="page-34-0"></span>Value

the function returns the range of parameter values that are within two log-likelihood units from the best (maximum) parameter estimate and a log-likelihood surface.

# Note

How fine-scaled the estimated log-likelihood surface is depends on the step size between the values in the input-vectors. The step-size therefore determines how accurate the representation of the support surface is, including the returned upper and lower estimates printed in the console. The range of the input vectors needs to be increased if the confidence interval includes the boundary of the input vector. Note also that it might be wise to include the maximum likelihood estimates as part of the input vectors. The computed support surface is conditional on the best estimates of the other model parameters that are not part of the support surface (e.g. the estimated ancestral trait value).

#### Author(s)

Kjetil Lysne Voje

#### Examples

```
## Generate a paleoTS objects
x <- sim.accel.decel(30, r=-0.5)
## Fit the model to the data.
x1<-opt.joint.decel(x)
```

```
## Create log-likelihood surface (the example may take > 5 seconds to run)
loglik.sumface.decel(x, vstep.vec = seq(0, 5, 0.1), r.vec = seq(-1, 0, 0.01))
```
loglik.surface.GRW *Calculate the log-likelihood surface for a part of parameter space*

#### Description

Function to calculate the log-likelihood surface for a part of parameter space for a General Random Walk.

```
loglik.surface.GRW(y, mstep.vec, vstep.vec, pool = TRUE)
```
<span id="page-35-0"></span>

#### Value

the function returns the range of parameter values that are within two log-likelihood units from the best (maximum) parameter estimate and a log-likelihood surface.

# Note

How fine-scaled the estimated log-likelihood surface is depends on the step size between the values in the input-vectors. The step-size therefore determines how accurate the representation of the support surface is, including the returned upper and lower estimates printed in the console. The range of the input vectors needs to be increased if the confidence interval includes the boundary of the input vector. Note also that it might be wise to include the maximum likelihood estimates as part of the input vectors. The computed support surface is conditional on the best estimates of the other model parameters that are not part of the support surface (e.g. the estimated ancestral trait value).

#### Author(s)

Kjetil Lysne Voje

#### Examples

```
## Generate a paleoTS objects
x <- paleoTS::sim.GRW(30)
## Fit the the model to the data.
x1<-paleoTS::opt.joint.GRW(x)
```

```
## Create log-likelihood surface (the example may take > 5 seconds to run)
loglik.surface.GRW(x, mstep.vec= seq(0, 0.3, 0.01), vstep.vec = seq(0, 0.3, 0.01))
```
loglik.surface.OU *Calculate the log-likelihood surface for a part of parameter space*

#### Description

Function to calculate the log-likelihood surface for a part of parameter space for a Ornstein-Uhlenbeck model.

loglik.surface.OU 37

#### Usage

```
loglik.surface.OU(
  y,
  stat.var.vec,
  h.vec,
  anc = NULL,theta = NULL,
  pool = TRUE
)
```
## Arguments



#### Value

the function returns the range of parameter values that are within two log-likelihood units from the best (maximum) parameter estimate and a log-likelihood surface.

# Note

How fine-scaled the estimated log-likelihood surface is depends on the step size between the values in the input-vectors. The step-size therefore determines how accurate the representation of the support surface is, including the returned upper and lower estimates printed in the console. The range of the input vectors needs to be increased if the confidence interval includes the boundary of the input vector. Note also that it might be wise to include the maximum likelihood estimates as part of the input vectors. The computed support surface is conditional on the best estimates of the other model parameters that are not part of the support surface (e.g. the estimated ancestral trait value).

## Author(s)

Kjetil Lysne Voje

## Examples

```
## Generate a paleoTS objects
x <- paleoTS::sim.OU(40)
## Fit the model to the data.
x1<-paleoTS::opt.joint.OU(x)
```
##calculate half-life from model output

```
log(2)/x1$parameters[4]
```

```
##calculate stationary variance from model output
x1$parameters[2]/(2*x1$parameters[4])
```

```
## Create log-likelihood surface (the example may take > 5 seconds to run)
loglik.surface.OU(x, stat.var.vec=seq(0.001,0.5,0.01), h.vec=seq(0.01,10, 0.1))
```
loglik.surface.OUBM *Calculate the log-likelihood surface for a part of parameter space*

# Description

Function to calculate the log-likelihood surface for a part of parameter space for a Ornstein-Uhlenbeck model where the optimum changes according to an Unbiased Random Walk.

#### Usage

```
loglik.surface.OUBM(
 y,
 stat.var.vec,
 h.vec,
  anc = NULL,
  theta.0 = NULL,
 vo = NULL,
 opt.anc = TRUE,
 pool = TRUE
)
```
#### Arguments



#### Value

the function returns the range of parameter values that are within two log-likelihood units from the best (maximum) parameter estimate and a log-likelihood surface.

## <span id="page-38-0"></span>Note

How fine-scaled the estimated log-likelihood surface is depends on the step size between the values in the input-vectors. The step-size therefore determines how accurate the representation of the support surface is, including the returned upper and lower estimates printed in the console. The range of the input vectors needs to be increased if the confidence interval includes the boundary of the input vector. Note also that it might be wise to include the maximum likelihood estimates as part of the input vectors. The computed support surface is conditional on the best estimates of the other model parameters that are not part of the support surface (e.g. the estimated ancestral trait value).

#### Author(s)

Kjetil Lysne Voje

#### Examples

```
## Generate a paleoTS objects
x \leftarrow \text{sim.} \text{OUBM}(40)## Fit the model.
x1<-opt.joint.OUBM(x)
##calculate half-life from model output
log(2)/x1$parameters[3]
##calculate stationary variance from model output
x1$parameters[2]/(2*x1$parameters[3])
```

```
## Create log-likelihood surface (the example may take > 5 seconds to run)
loglik.surface.OUBM(x, stat.var.vec=seq(0,4,0.01), h.vec=seq(0.0,5, 0.1))
```
loglik.surface.stasis *Calculate the log-likelihood surface for a part of parameter space*

#### Description

Function to calculate the log-likelihood surface for a part of parameter space for the Stasis model.

```
loglik.surface.stasis(y, theta.vec, omega.vec, pool = TRUE)
```
<span id="page-39-0"></span>

#### Value

the function returns the range of parameter values that are within two log-likelihood units from the best (maximum) parameter estimate and a log-likelihood surface.

# Note

How fine-scaled the estimated log-likelihood surface is depends on the step size between the values in the input-vectors. The step-size therefore determines how accurate the representation of the support surface is, including the returned upper and lower estimates printed in the console. The range of the input vectors needs to be increased if the confidence interval includes the boundary of the input vector. Note also that it might be wise to include the maximum likelihood estimates as part of the input vectors. The computed support surface is conditional on the best estimates of the other model parameters that are not part of the support surface (e.g. the estimated ancestral trait value).

#### Author(s)

Kjetil Lysne Voje

#### Examples

```
## Generate a paleoTS objects
x <- paleoTS::sim.Stasis(30)
## Fit the the model to the data.
x1<-paleoTS::opt.joint.Stasis(x)
```

```
## Create log-likelihood surface (the example may take > 5 seconds to run)
loglik.surface.stasis(x, theta.vec= seq(-0.15, 0.1, 0.001), omega.vec = seq(0, 0.1, 0.001))
```
loglik.surface.URW *Calculate the log-likelihood surface for a part of parameter space*

#### **Description**

Function to calculate the log-likelihood surface for a part of parameter space for a Unbiased Random Walk.

#### loglik.surface.URW 41

#### Usage

loglik.surface.URW(y, vstep.vec, pool = TRUE)

#### Arguments



# Value

the function returns the range of parameter values that are within two log-likelihood units from the best (maximum) parameter estimate and a log-likelihood surface.

## Note

How fine-scaled the estimated log-likelihood surface is depends on the step size between the values in the input-vectors. The step-size therefore determines how accurate the representation of the support surface is, including the returned upper and lower estimates printed in the console. The range of the input vectors needs to be increased if the confidence interval includes the boundary of the input vector. Note also that it might be wise to include the maximum likelihood estimates as part of the input vectors. The computed support surface is conditional on the best estimates of the other model parameters that are not part of the support surface (e.g. the estimated ancestral trait value).

# Author(s)

Kjetil Lysne Voje

#### Examples

```
## Generate a paleoTS objects
x <- paleoTS::sim.GRW(30)
```
## Fit a the model to the data by defining shift points. x1<-paleoTS::opt.joint.URW(x)

## Create log-likelihood surface (the example may take > 5 seconds to run) loglik.surface.URW(x, vstep.vec = seq(0,0.5,0.001))

# <span id="page-41-0"></span>Description

Function to make a multivariate data set consisting of two or more evolutionary sequences (timeseries).

# Usage

```
make.multivar.evoTS(
 evoTS.1 = NULL,evoTS.2 = NULL,evoTS.3 = NULL,
 evoTS.4 = NULL,evoTS.5 = NULL,evoTS.6 = NULL,evoTS.7 = NULL,evoTS.8 = NULL,evoTS.9 = NULL,evoTS.10 = NULL\mathcal{L}
```
# Arguments



## <span id="page-42-0"></span>Details

See the function as.paleoTS for details. See also read.paleoTS, which is often a more convenient way for getting the relevant data from text files.

## Value

a multivariate evoTS object that can be analysed with functions fitting multivariate models (e.g. fit.multivariate.OU, fit.multivariate.URW)

# Author(s)

Kjetil Lysne Voje

## Examples

```
## Generate two evolutionary sequences (time-series)
x1 <- paleoTS::sim.GRW(60)
x2 <- paleoTS::sim.GRW(60)
```

```
## Make a multivariate data set
x1_x2<-make.multivar.evoTS(x1, x2)
```


#### Description

Function to find maximum likelihood solution to a multivariate Unbiased Random Walk model with increasing (exponential accelerating) rate of change through time.

```
opt.accel.single.R(
  yy,
  method = "L-BFGS-B",
  hess = FALSE,
 pool = TRUE,trace = FALSE,
  iterations = NULL,
  iter.sd = NULL
)
```


#### Details

The function searches - using an optimization routine - for the maximum-likelihood solution for a multivariate Unbiased Random Walk model with increasing (exponential accelerating) rate of change through time.

The argument 'method' is passed to the 'optim' function and is included for the convenience of users to better control the optimization routine. The the default method (L-BFGS-B) seems to work for most evolutionary sequences.

Initial estimates to start the optimization come from maximum-likelihood estimates of the univariate Unbiased Random Walk model (from the paleoTS package) fitted to each time-series separately. The starting value for  $r = 1$ .

It is good practice to repeat any numerical optimization procedure from different starting points. This is especially important for complex models as the log-likelihood surface might contain more than one peak. The number of iterations is controlled by the argument 'iterations'. The function will report the model parameters from the iteration with the highest log-likelihood.

# Value

First part of the output reports the log-likelihood of the model and its AICc score. The second part of the output is the maximum log-likelihood model parameters (ancestral.values, R, r). The last part of the output gives information about the number of parameters in the model (K), number of samples in the data (n) and number of times the optimization routine was run (iter).

#### Note

The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

# Author(s)

Kjetil Lysne Voje

# <span id="page-44-0"></span>Examples

## Generate an evoTS object by simulating a multivariate dataset indata <- sim.multi.URW(60)

## Fit a multivariate Unbiased Random Walk with an increasing rate of change through time. opt.accel.single.R(indata)

opt.accel.single.R.zero.corr

*Fit multivariate Unbiased Random Walk model with uncorrelated trait changes and with increasing (exponential accelerating) rate of change through time.*

## Description

Function to find maximum likelihood solution to a multivariate Unbiased Random Walk model with uncorrelated trait changes and with increasing (exponential accelerating) rate of change through time.

# Usage

```
opt.accel.single.R.zero.corr(
  yy,
  method = "L-BFGS-B",
 hess = FALSE,
 pool = TRUE,trace = FALSE,
  iterations = NULL,
  iter.sd = NULL
)
```
## Arguments



# Details

The function searches - using an optimization routine - for the maximum-likelihood solution for a multivariate Unbiased Random Walk model with uncorrelated trait changes and with increasing (exponential accelerating) rate of change through time.

The argument 'method' is passed to the 'optim' function and is included for the convenience of users to better control the optimization routine. The the default method (L-BFGS-B) seems to work for most evolutionary sequences.

Initial estimates to start the optimization come from maximum-likelihood estimates of the univariate Unbiased Random Walk model (from the paleoTS package) fitted to each time-series separately. The starting value for  $r = 1$ .

It is good practice to repeat any numerical optimization procedure from different starting points. This is especially important for complex models as the log-likelihood surface might contain more than one peak. The number of iterations is controlled by the argument 'iterations'. The function will report the model parameters from the iteration with the highest log-likelihood.

# Value

First part of the output reports the log-likelihood of the model and its AICc score. The second part of the output is the maximum log-likelihood model parameters (ancestral.values, R, r). The last part of the output gives information about the number of parameters in the model (K), number of samples in the data (n) and number of times the optimization routine was run (iter).

# Note

The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

#### Author(s)

Kjetil Lysne Voje

#### Examples

```
## Generate an evoTS object by simulating a multivariate dataset
x <- sim.multi.URW(30)
```
## Fit a multivariate Unbiased Random Walk model with an increasing rate of change through time. opt.accel.single.R.zero.corr(x)

<span id="page-46-0"></span>opt.decel.single.R *Fit multivariate Unbiased Random Walk with decreasing (exponential decaying) rate of change through time.*

# Description

Function to find maximum likelihood solution to a multivariate Unbiased Random Walk model with decreasing (exponential decaying) rate of change through time.

#### Usage

```
opt.decel.single.R(
 yy,
 method = "L-BFGS-B",
 hess = FALSE,
  pool = TRUE,trace = FALSE,
  iterations = NULL,
  iter.sd = NULL
)
```
## Arguments



#### Details

The function searches - using an optimization routine - for the maximum-likelihood solution for a multivariate Unbiased Random Walk model with decreasing (exponential decaying) rate of change through time.

The argument 'method' is passed to the 'optim' function and is included for the convenience of users to better control the optimization routine. The the default method (L-BFGS-B) seems to work for most evolutionary sequences.

Initial estimates to start the optimization come from maximum-likelihood estimates of the univariate Unbiased Random Walk model (from the paleoTS package) fitted to each time-series separately. The starting value for  $r = -1$ .

<span id="page-47-0"></span>It is good practice to repeat any numerical optimization procedure from different starting points. This is especially important for complex models as the log-likelihood surface might contain more than one peak. The number of iterations is controlled by the argument 'iterations'. The function will report the model parameters from the iteration with the highest log-likelihood.

#### Value

First part of the output reports the log-likelihood of the model and its AICc score. The second part of the output is the maximum log-likelihood model parameters (ancestral.values, R, r). The last part of the output gives information about the number of parameters in the model (K), number of samples in the data (n) and number of times the optimization routine was run (iter).

#### Note

The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

#### Author(s)

Kjetil Lysne Voje

#### References

Voje, K. L. 2020. Testing eco-evolutionary predictions using fossil data: Phyletic evolution following ecological opportunity.*Evolution* 74:188–200.

#### Examples

## Generate an evoTS object by simulating a multivariate dataset indata <- sim.multi.URW(30)

## Fit a multivariate Unbiased Random Walk model with a decreasing rate of change through time. opt.accel.single.R(indata)

opt.decel.single.R.zero.corr

*Fit multivariate Unbiased Random Walk model with uncorrelated trait changes and with decreasing (exponential decaying) rate of change through time.*

#### **Description**

Function to find maximum likelihood solution to a multivariate Unbiased Random Walk model with uncorrelated trait changes and with decreasing (exponential decaying) rate of change through time.

## Usage

```
opt.decel.single.R.zero.corr(
  yy,
  method = "L-BFGS-B",
 hess = FALSE,
 pool = TRUE,
  trace = FALSE,
  iterations = NULL,
  iter.sd = NULL
```

```
)
```
#### Arguments



## Details

The function searches - using an optimization routine - for the maximum-likelihood solution for a multivariate Unbiased Random Walk model with uncorrelated trait changes and with increasing (exponential accelerating) rate of change through time.

The argument 'method' is passed to the 'optim' function and is included for the convenience of users to better control the optimization routine. The the default method (L-BFGS-B) seems to work for most evolutionary sequences.

Initial estimates to start the optimization come from maximum-likelihood estimates of the univariate Unbiased Random Walk model (from the paleoTS package) fitted to each time-series separately. The starting value for  $r = -1$ .

It is good practice to repeat any numerical optimization procedure from different starting points. This is especially important for complex models as the log-likelihood surface might contain more than one peak. The number of iterations is controlled by the argument 'iterations'. The function will report the model parameters from the iteration with the highest log-likelihood.

#### Value

First part of the output reports the log-likelihood of the model and its AICc score. The second part of the output is the maximum log-likelihood model parameters (ancestral.values, R, r). The last part of the output gives information about the number of parameters in the model (K), number of samples in the data (n) and number of times the optimization routine was run (iter).

The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

## Author(s)

Kjetil Lysne Voje

# References

Voje, K. L. 2020. Testing eco-evolutionary predictions using fossil data: Phyletic evolution following ecological opportunity.*Evolution* 74:188–200.

# Examples

```
## Generate an evoTS object by simulating a multivariate dataset.
indata <- sim.multi.URW(30)
```
## Fit a multivariate Unbiased Random Walk model with a decreasing rate of change through time. opt.decel.single.R.zero.corr(indata)



# Description

Function to find maximum likelihood solutions to a Unbiased Random Walk with an accelerating or decelerating rate of change through time.

# Usage

```
opt.joint.accel(y, pool = TRUE, meth = "L-BFGS-B", hess = FALSE)
```
#### Arguments



<span id="page-49-0"></span>

# Note

# <span id="page-50-0"></span>opt.joint.decel 51

#### Value



#### Note

The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

#### Author(s)

Kjetil Lysne Voje

#### Examples

```
## Generate a paleoTS object by simulating a univariate evolutionary sequence
y <- paleoTS::sim.GRW(30)
```
## Fit the model opt.joint.accel(y)



# Description

Function to find maximum likelihood solutions to a Unbiased Random Walk with an decelerating or decelerating rate of change through time.

```
opt.joint.decel(y, pool = TRUE, meth = "L-BFGS-B", hess = FALSE)
```


# Value



## Note

The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

#### Author(s)

Kjetil Lysne Voje

#### References

Voje, K. L. 2020. Testing eco-evolutionary predictions using fossil data: Phyletic evolution following ecological opportunity.*Evolution* 74:188–200.

# Examples

```
## Generate a paleoTS object by simulating a univariate evolutionary sequence
x <- paleoTS::sim.GRW(30)
## Fit the model
opt.joint.decel(x)
```
<span id="page-52-0"></span>opt.joint.OUBM *Fit an Ornstein-Uhlenbeck model with an optimum that evolves according to a Unbiased Random Walk.*

# Description

Function to find maximum likelihood solutions to an Ornstein-Uhlenbeck model with an optimum that evolves according to a Unbiased Random Walk.

# Usage

```
opt.joint.OUBM(
  y,
 pool = TRUE,meth = "L-BFGS-B",
 hess = FALSE,
  iterations = NULL,
  iter.sd = NULL,
  opt.anc = TRUE
)
```
# Arguments



#### Value



The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

#### Author(s)

Kjetil Lysne Voje

## References

Hansen, T. F., Pienaar, J. & Orzack, S. H. 2008. A Comparative Method for Studying Adaptation to a Randomly Evolving Environment. *Evolution* 62:1965–1977.

# Examples

## Generate a paleoTS object by simulating a univariate evolutionary sequence x <- paleoTS::sim.GRW(60)

## Fit the model opt.joint.OUBM(x)

opt.joint.URW.Stasis *Optimization and log-likelihoods for pairs of models.*

#### Description

A collections of functions that serves the function fit.mode.shift. See fit.mode.shift for info.

#### Usage

```
opt.joint.URW.Stasis(
 y,
  gg,
 cl = list(fnscale = -1),pool = TRUE,
 meth = "L-BFGS-B",hess = FALSE
)
```
<span id="page-53-0"></span>

# Note

# <span id="page-54-0"></span>opt.single.R 55

## Arguments



# Details

In general, users will not be access these functions directly, but instead use the wrapper function, which use these functions to find the best-supported parameter values.

## Note

This function is not likely to be called directly by the user.

# Author(s)

Kjetil Lysne Voje

opt.single.R *Fit multivariate Unbiased Random Walk model.*

# Description

Function to find maximum likelihood solution to a multivariate Unbiased Random Walk model.

```
opt.single.R(
  yy,
  method = "L-BFGS-B",
  hess = FALSE,
  pool = TRUE,trace = FALSE,
  iterations = NULL,
  iter.sd = NULL
\mathcal{E}
```


#### Details

The function searches - using an optimization routine - for the maximum-likelihood solution for a multivariate Unbiased Random Walk model.

The argument 'method' is passed to the 'optim' function and is included for the convenience of users to better control the optimization routine. The the default method (L-BFGS-B) seems to work for most evolutionary sequences.

Initial estimates to start the optimization come from maximum-likelihood estimates of the univariate Unbiased Random Walk model (from the paleoTS package) fitted to each time-series separately.

It is good practice to repeat any numerical optimization procedure from different starting points. This is especially important for complex models as the log-likelihood surface might contain more than one peak. The number of iterations is controlled by the argument 'iterations'. The function will report the model parameters from the iteration with the highest log-likelihood.

#### Value

First part of the output reports the log-likelihood of the model and its AICc score. The second part of the output is the maximum log-likelihood model parameters (ancestral.values, R). The last part of the output gives information about the number of parameters in the model (K), number of samples in the data (n) and number of times the optimization routine was run (iter).

#### Note

The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

# Author(s)

Kjetil Lysne Voje

# <span id="page-56-0"></span>opt.single.R.zero.corr 57

# References

Revell, L. J. & Harmon, L. Testing quantitative genetic hypotheses about the evolutionary rate matrix for continuous characters. *Evolutionary Ecology Research* 10, 311–331 (2008).

# Examples

```
## Generate an evoTS objects by simulating a multivariate dataset
x <- sim.multi.URW(30)
```

```
## Fit a multivariate Unbiased Random Walk model.
opt.single.R(x)
```

```
opt.single.R.zero.corr
```
*Fit multivariate Unbiased Random Walk model with uncorrelated trait changes.*

# Description

Function to find maximum likelihood solution to a multivariate Unbiased Random Walk model with uncorrelated trait changes.

## Usage

```
opt.single.R.zero.corr(
 yy,
 method = "L-BFGS-B",
 hess = FALSE,
 pool = TRUE,trace = FALSE,
  iterations = NULL,
  iter.sd = NULL
)
```
#### Arguments



#### Details

The function searches - using an optimization routine - for the maximum-likelihood solution for a multivariate Unbiased Random Walk model with uncorrelated trait changes.

The argument 'method' is passed to the 'optim' function and is included for the convenience of users to better control the optimization routine. The the default method (L-BFGS-B) seems to work for most evolutionary sequences.

Initial estimates to start the optimization come from maximum-likelihood estimates of the univariate Unbiased Random Walk model (from the paleoTS package) fitted to each time-series separately.

It is good practice to repeat any numerical optimization procedure from different starting points. This is especially important for complex models as the log-likelihood surface might contain more than one peak. The number of iterations is controlled by the argument 'iterations'. The function will report the model parameters from the iteration with the highest log-likelihood.

# Value

First part of the output reports the log-likelihood of the model and its AICc score. The second part of the output is the maximum log-likelihood model parameters (ancestral.values, R). The last part of the output gives information about the number of parameters in the model (K), number of samples in the data (n) and number of times the optimization routine was run (iter).

#### Note

The models have been implemented to be compatible with the joint parameterization routine in the package paleoTS. The optimization is therefore fit using the actual sample values, with the autocorrelation among samples accounted for in the log-likelihood function. The joint distribution of sample means is multivariate normal, with means and variance-covariances determined by evolutionary parameters and sampling errors.

# Author(s)

Kjetil Lysne Voje

#### References

Revell, L. J. & Harmon, L. Testing quantitative genetic hypotheses about the evolutionary rate matrix for continuous characters. *Evolutionary Ecology Research* 10, 311–331 (2008).

#### Examples

```
## Generate an evoTS object by simulating a multivariate dataset
x <- sim.multi.URW(30)
```

```
## Fit a multivariate Unbiased Random Walk model with uncorrelated trait changes.
opt.single.R.zero.corr(x)
```
<span id="page-58-0"></span>

# Description

Plot a paleoTS object (slightly modified version of the same function in paleoTS)

# Usage

```
plotevoTS(
 x,
 nse = 1,
 pool = FALSE,
  add = FALSE,
 modelFit = NULL,pch = 19,
 1wd = 1.5,
 ylim = NULL,
 xlab = NULL,
 ylab = NULL,
  ...
)
```
# Arguments



# Value

The results are plotted.

# Author(s)

Kjetil Lysne Voje

```
plotevoTS.multivariate
```
*Plots multivariate evolutionary sequence (time-series) data set*

# Description

Function to plot multivariate evolutionary sequence (time-series), showing trait means over time.

# Usage

```
plotevoTS.multivariate(
 yy,
 nse = 1,
 col = NULL,lty = NULL,
 lwd = NULL,pch = NULL,
 x.label = NULL,
 y.label = NULL,
 y_{min} = NULL,y_max = NULL,cex.axis = NULL,
 cex.lab = NULL,
 cex.main = NULL,
 axes = NULL)
```
# Arguments



<span id="page-60-0"></span>ribs\_S.yellowstonensis 61

# Value

The results are plotted.

# Author(s)

Kjetil Lysne Voje

# Examples

```
## Generate two evolutionary sequences (time-series)
x1 <- paleoTS::sim.Stasis(60, vp=1)
x2 <- paleoTS::sim.Stasis(60, vp=1)
## Make a multivariate data set
x1_x2<-make.multivar.evoTS(x1, x2)
## Plot the data
plotevoTS.multivariate(x1_x2, y_min=-1, y_max=1)
```
ribs\_S.yellowstonensis

*Evolutionary sequence (time-series) of phenotypic change in the number of ribs in the lineage Stephanodiscus yellowstonensis*

#### Description

Phenotypic data (ribs) from a centric diatom lineage Stephanodiscus yellowstonensis. The time series spans about 14 000 years. The data set contains data on the number of costae (ribs) per valve. The data consists of an objects of class paleoTS (ribs\_S.yellowstonensis). Objects of class paleoTS can be analyzed in evoTS. The object (trait data set) contains a vector of sample means (mm), sample variances (vv), sample sizes (nn) and sample ages (tt). The oldest sample is listed first. The data spans an interval of 13728 years.

## Usage

```
data(ribs_S.yellowstonensis)
```
#### Format

An object of class "paleoTS".

#### References

Theriot et al. 2006. Late Quaternary rapid morphological evolution of an endemic diatom in Yellowstone Lake, Wyoming. Paleobiology 32:38-54

# Examples

```
ln.ribs<-paleoTS::ln.paleoTS(ribs_S.yellowstonensis)
ln.ribs$tt<-ln.ribs$tt/(max(ln.ribs$tt))
opt.joint.decel(ln.ribs)
```
sim.accel.decel *Simulate an Unbiased Random Walk with an accelerating or decelerating rate of change through time.*

# Description

Function to simulate an evolutionary sequence data set according to an Unbiased Random Walk with an accelerating or decelerating rate of change through time.

# Usage

```
sim.accel.decel(
 ns = 20,
 vs = 0.5,
 r = 0.2,
 vp = 0.2,
 nn = rep(20, ns),tt = 0:(ns - 1))
```
# Arguments



# Value

An evolutionary sequence (time-series) data set (a paleoTS object)

#### Author(s)

Kjetil Lysne Voje

<span id="page-61-0"></span>

## <span id="page-62-0"></span>sim.multi.OU 63

# Examples

```
##Simulate an unbiased random walk where the rate decelerates through time.
x<-sim.accel.decel(40, r=-0.5)
```
## Plot the data plotevoTS(x)



# Description

Function to simulate a multivariate Ornstein-Uhlenbeck evolutionary sequence data set.

# Usage

```
sim.multi.OU(
 ns = 30,anc = c(\emptyset, \emptyset),
 optima = c(3, 2),A = matrix(c(7, 0, 0, 6), nrow = 2, byrow = TRUE),R = matrix(c(0.05, 0, 0, 0.05), nrow = 2, byrow = TRUE),vp = 0.1,nn = rep(30, ns),
 tt = 0:(ns - 1))
```
# Arguments



## Value

A multivariate evolutionary sequence (time-series) data set.

The Ornstein Uhlenbeck model is reduced to an Unbiased Random Walk when the alpha parameter is zero. It is therefore possible to let a trait evolve as an Unbiased Random Walk by setting the diagonal element for that trait to a value close to zero (e.g. 1e-07). Elements in the diagonal of A cannot be exactly zero as this will result in a singular variance-covariance matrix.

## Author(s)

Kjetil Lysne Voje

#### Examples

##Define the A and R matrices

```
A_matrix<-matrix(c(4,-2,0,3), nrow=2, byrow = TRUE)
R_matrix <- matrix(c(4, 0.2, 0.2, 4), nrow=2, byrow = TRUE)
```
## Generate an evoTS object by simulating a multivariate dataset data\_set<-sim.multi.OU(40, optima =  $c(1.5,2)$ , A=A\_matrix , R = R\_matrix)

## plot the data plotevoTS.multivariate(data\_set)

sim.multi.URW *Simulate multivariate evolutionary sequence data that evolve according to an Unbiased Random Walk*

#### Description

Function to simulate multivariate evolutionary sequence data that evolve according to an Unbiased Random Walk

#### Usage

```
sim.multi.URW(
  ns = 30,anc = c(\theta, \theta),
 R = matrix(c(0.5, 0, 0, 0.5), nrow = 2, byrow = TRUE),vp = 0.1,
 nn = rep(30, ns),tt = 0:(ns - 1))
```
<span id="page-63-0"></span>

# Note

#### <span id="page-64-0"></span>sim.OUBM 65

## Arguments



# Value

A multivariate evolutionary sequence (time-series) data set.

# Author(s)

Kjetil Lysne Voje

# Examples

```
## Create a multivariate dataset
data_set \leq -sim.multi.URW(40, R = matrix(c(0.2, 0.1, 0.1, 0.3), nrow=2, byrow = TRUE))## plot the data
plotevoTS.multivariate(data_set)
```


# Description

Function to simulate an Ornstein-Uhlenbeck evolutionary sequence data set with an optimum moving according to an unbiased random walk.

```
sim.OUBM(
  ns = 20,
  anc = \theta,
  theta.0 = 1,
  alpha = 0.3,
  vstep.trait = 0.1,
  vstep,opt = 0.1,
  vp = 1,nn = rep(20, ns),tt = 0:(ns - 1)\mathcal{E}
```


# Value

An evolutionary sequence (time-series) data set (a paleoTS object)

# Author(s)

Kjetil Lysne Voje

# Examples

##Create data  $x < -sin.0$  UBM(50, theta.0 = 5, alpha = 0.6, vstep.opt = 0.5)

## plot the data plot(x)

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