

Package ‘BBMV’

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Type Package

Title Macroevolutionary Models for Continuous Traits Evolving in
Adaptive Landscapes of any Shape

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Depends R (>= 3.1.0), ape

Suggests coda, geiger

Description This package provides a set of functions to fit general macroevolutionary models for continuous traits evolving in adaptive landscapes of any shape. The model is based on bounded Brownian motion (BBM), in which a continuous trait evolves along a phylogenetic tree under constant-rate diffusion between two reflective bounds. In addition to this random component, the trait evolves in a potential and is thus subject to a force that pulls it towards specific values - this force can be of any shape.

License GPL-2

NeedsCompilation no

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Description

This package provides a set of functions to fit general macroevolutionary models for continuous traits evolving in adaptive landscapes of any shape. The model is based on bounded Brownian motion (BBM), in which a continuous trait evolves along a phylogenetic tree under constant-rate diffusion between two reflective bounds. In addition to this random component, the trait evolves in a potential and is thus subject to a force that pulls it towards specific values - this force can be of any shape.

Details

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```

Author(s)

Florian C. Boucher Maintainer: Florian C. Boucher <floboucher@gmail.com>

References

Inferring bounded evolution in phenotypic characters from phylogenetic comparative data. F.C. Boucher and V. Demery. Systematic Biology, 65, 651-661, 2016

A general model for estimating macroevolutionary landscapes from phylogenetic comparative data. F.C. Boucher, V. Demery, E. Conti, L. J. Harmon and J. Uyeda. Submitted

charac_time	<i>Characteristic time measurement</i>
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Description

Calculate the characteristic time it takes for the BBM+V process to reach its stationary distribution.

Usage

```
charac_time(Npts, model)
```

Arguments

Npts	The number of points used in the discretization procedure.
model	A BBM+V model fit, as returned by fit_BBMV .

Value

The function returns the characteristic time of the process as a numeric value.

Author(s)

F. C. Boucher

Examples

```

# Simulate data: tree + continuous trait
library(geiger)
tree=sim.bdtree(stop='taxa',n=10) # tree with few tips for quick tests
tree$edge.length=100*tree$edge.length/max(branching.times(tree)) # rescale the tree
# Simulate trait evolving on the tree with a linear trend towards small values
TRAIT= Sim_BBMV(tree,x0=0,V=seq(from=0,to=5,length.out=50),sigma=10,bounds=c(-5, 5))
# fit a model with a linear potential:
BBM_x=fit_BBMV(tree,TRAIT,Npts=20,method='Nelder-Mead',verbose=TRUE,V_shape='linear')

# measure time to reach stationarity

```

```

charac_time(Npts=20, BBM_x)

# compare it with tree depth
max(branching.times(tree))

```

ConvProp_bounds	<i>Convolution of the diffusion matrix with the trait density vector.</i>
-----------------	---

Description

Internal function used for likelihood calculation and simulation.

Usage

```
ConvProp_bounds(X, t, prep_mat)
```

Arguments

X	A trait density vector.
t	The time over which to do the convolution (usually the length of one branch).
prep_mat	The diagonalized diffusion matrix.

Author(s)

F. C. Boucher

DiffMat_backwards	<i>Diffusion matrix building</i>
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Description

Internal function that builds the discretized diffusion matrix of the BBM+V process going backwards in time (for likelihood calculations)

Usage

```
DiffMat_backwards(V)
```

Arguments

V	A vector giving the values of the evolutionary potential (V) at each point in the gridded trait interval.
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Author(s)

F. C. Boucher

DiffMat_forward	<i>Diffusion matrix building</i>
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Description

Internal function that builds the discretized diffusion matrix of the BBM+V process going forward in time (for simulations)

Usage

```
DiffMat_forward(V)
```

Arguments

V	A vector giving the values of the evolutionary potential (V) at each point in the gridded trait interval.
---	---

Author(s)

F.C. Boucher

fit_BBMV	<i>Main function to fit the BBM+V model</i>
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Description

Fits various forms of the BBM+V model to trait data and a phylogeny, using maximum likelihood.

Usage

```
fit_BBMV(tree, trait, Npts = 50, method = "Nelder-Mead", verbose = T, V_shape, bounds = "estimate",
```

Arguments

tree	A phylogenetic tree in phylo format
trait	A named vector of trait values for the tips of the tree. It should match tip labels in the phylogeny.
Npts	The number of points used in the discretization procedure.
method	The optimization routine used.
verbose	If TRUE, prints progress to the screen.
V_shape	The shape of the evolutionary potential. This should be one of 'flat', 'linear', 'quadratic', or 'full'. Alternatively, a given potential can be specified using a vector of values for V, along with bounds.
bounds	Describes how to treat the bounds. If set to 'estimate' (the default), bounds will be estimated along with other parameters. Alternatively, you can fix two bounds by specifying a numeric vector containing the minimum and maximum bound of the trait interval as the first and second element, respectively.
init.optim	A parameter combination from which to start the optimization procedure, specified as a numeric vector. Default to NULL should work in most of the cases.

Details

Only 'Nelder-Mead' (the default, which we found to be more reliable) and 'L-BFGS-B' are supported as optimization methods. For further details on both methods see the help of the [optim](#) function.

The different values for `V_shape` refer to the following shapes of the evolutionary potential: (1) 'flat' is a flat potential as in BBM, i.e. $V(x) = 0$; (2) 'linear' is a linear potential, i.e. $V(x) = c.x$; (3) 'quadratic' is a quadratic potential, i.e. $V(x) = b.x^2 + c.x$; (4) 'full' is a potential with three polynomial terms, i.e. $V(x) = a.x^4 + b.x^2 + c.x$.

Value

A list with the following elements:

<code>par</code>	The ML estimates of model parameters: the two bounds of the trait interval (<code>\$bounds</code>), the diffusion rate (<code>\$sigsq</code>), the coefficients of the evolutionary potential (<code>\$a</code> , <code>\$b</code> , and <code>\$c</code> , depending on the shape fitted), and the value of the trait at the root of the tree (<code>\$root_value</code>).
<code>lnL</code>	The log-likelihood of the model.
<code>k</code>	The number of parameters of the model.
<code>aic</code>	The AIC of the model.
<code>aicc</code>	The AICc of the model.
<code>method</code>	The optimization method used to fit the model.
<code>convergence</code>	Convergence code returned by <code>optim</code> . 0 indicates successful convergence. For other values see the help of the optim function.
<code>message</code>	Convergence message returned by <code>optim</code> . See the help of the optim function.
<code>root_density</code>	A vector giving the density of probability of the trait at the root of the tree. Each element corresponds to one point in the discretized trait grid, from left (lower bound) to right (upper bound).
<code>ACE</code>	A list of tables, one for each node of the phylogeny. Each table has the position of the points in the trait grid as its first column, and their associated probabilities in the second column.

Author(s)

F. C. Boucher

Examples

```
# Simulate data: tree + continuous trait
library(geiger)
tree=sim.bdtree(stop='taxa',n=10) # tree with few tips for quick tests
tree$edge.length=100*tree$edge.length/max(branching.times(tree)) # rescale the tree
# Simulate trait evolving on the tree with a linear trend towards small values
TRAIT= Sim_BBMV(tree,x0=0,V=seq(from=0,to=5,length.out=50),sigma=10,bounds=c(-5, 5))
# fit a model with a linear potential:
BBM_x=fit_BBMV(tree,TRAIT,Npts=20,method='Nelder-Mead',verbose=TRUE,V_shape='linear')
```

FormatTree_bounds	<i>Tree formatting.</i>
-------------------	-------------------------

Description

Internal function used for likelihood calculation and simulation.

Usage

```
FormatTree_bounds(tree, trait, V, bounds)
```

Arguments

tree	A phylogenetic tree in phylo format.
trait	A vector of traits at the tips of the tree
V	A vector giving the evolutionary potential.
bounds	A vector of bounds of the trait interval.

Author(s)

F. C. Boucher

get.landscape.BBMV	<i>Plot macroevolutionary landscapes</i>
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Description

Plot the adaptive landscape estimated in a BBM+V model.

Usage

```
get.landscape.BBMV(model, Npts = 50, main = "Macroevolutionary landscape", ylab = "-V", xlab = "Trait")
get.multiple.landscapes.BBMV(models, Npts = 50, xlim = NULL, ylim = NULL, main = "Macroevolutionary landscapes")
```

Arguments

model	A BBM+V model fit, as returned by fit_BBMV .
models	A list of BBM+V model fits, as returned by fit_BBMV .
landscape	If TRUE (the default), plots the adaptive landscape. If FALSE, plots the evolutionary potential instead.
Npts	The number of points used to discretize the trait interval for plotting.
main	A title for the plot.
ylim	The upper limit of the plotting region when multiple adaptive landscapes are plotted together.
xlim	The limits of the x-axis.
ylab	Label of the y-axis.
xlab	Label of the x-axis.

Value

A plot of the adaptive landscape (or alternatively the evolutionary potential) across the trait interval.

Author(s)

F. C. Boucher

Examples

```
# Simulate data: tree + continuous trait
library(geiger)
tree=sim.bdtree(stop='taxa',n=10) # tree with few tips for quick tests
tree$edge.length=100*tree$edge.length/max(branching.times(tree)) # rescale the tree
# Simulate trait evolving on the tree with a linear trend towards small values
TRAIT= Sim_BBMV(tree,x0=0,V=seq(from=0,to=5,length.out=50),sigma=10,bounds=c(-5, 5))

# fit a model with a linear potential:
BBM_x=fit_BBMV(tree,TRAIT,Npts=20,method='Nelder-Mead',verbose=TRUE,V_shape='linear')

# plot the macroevolutionary landscape
get.landscape.BBMV(model=BBM_x,Npts=100)
```

LogLik_bounds

Likelihood calculations for the BBM+V model

Description

Internal functions that calculate the log-likelihood of various versions of the BBM+V model, used in ML and MCMC estimation.

Usage

```
LogLik_bounds(tree_formatted, dCoeff, dMat, bounds)
LogLik_bounds_est(tree, trait, dCoeff, V, bounds)
LogLik_bounds_est_root(tree, trait, dCoeff, V, x0_pos, bounds)
bBM_loglik_0_flex_points(tree, trait, Npts)
bBM_loglik_bounds(tree_formatted, dMat, bounds)
bBM_loglik_linear_bounds(tree_formatted, Npts = 100, bounds)
bBM_loglik_quadra_bounds(tree_formatted, Npts = 100, bounds)
bBM_loglik_x_flex_points(tree, trait, Npts)
bBM_loglik_x2x_flex_points(tree, trait, Npts)
bBM_loglik_x4x2x_bounds(tree_formatted, Npts = 100, bounds)
bBM_loglik_x4x2x_flex_pts(tree, trait, Npts)
```

Arguments

tree_formatted	A formatted tree as returned by FormatTree_bounds .
dCoeff	The diffusion coefficient.
dMat	The discretized diffusion matrix.
V	A numeric vector giving the value of the evolutionary potential in each point of the trait grid.

bounds	A vector giving the bounds of the trait interval.
x0_pos	The value of the trait at the root of the tree.
tree	A phylogenetic tree in phylo format.
trait	A trait vector for tip taxa.
Npts	The number of points used for discretizing the trait interval.

Author(s)

F. C. Boucher

log_prior_7pars_root_bounds
Prior function.

Description

Internal function that calculates the log prior, used in MCMC estimation of the BBM+V model.

Usage

```
log_prior_7pars_root_bounds(type = c(rep("Normal", 4), rep("Uniform", 3)),
  shape = list(c(0, 10), c(0, 10), c(0, 10), c(0, 10), NA, 10, 10),
  pars, Npts_int, trait)
```

Arguments

type	A vector giving the type of prior for each parameter.
shape	A list giving the shape of the prior for each parameter.
pars	The parameter values at which the prior should be evaluated.
Npts_int	The number of points on the grid between min(trait) and max(trait).
trait	A named vector of trait values for the tips of the tree.

Author(s)

F. C. Boucher

MH_MCMC_V_ax4bx2cx_root_bounds

MCMC estimation

Description

The function estimates the parameters of the BBM+V model using an MCMC chain with the Metropolis Hastings algorithm and a Gibbs sampler.

Usage

```
MH_MCMC_V_ax4bx2cx_root_bounds(tree, trait, Nsteps = 5e+05, record_every = 100,
plot_every = 500, Npts_int = 50, pars_init = c(0, 0, 0, 0, 25, -10, 10),
prob_update = c(0.25, 0.2, 0.2, 0.2, 0.05, 0.05, 0.05), verbose = TRUE,
plot = TRUE, save_to = "testMCMC.Rdata", save_every = 10000,
type_priors = c(rep("Normal", 4), rep("Uniform", 3)),
shape_priors = list(c(0, 10), c(0, 10), c(0, 10), c(0, 10), NA, 10, 10),
proposal_type = "Uniform", proposal_sensitivity = c(0.1, 0.1, 0.1, 0.1, 1, 1, 1),
prior.only = F)
```

Arguments

tree	A phylogenetic tree in phylo format.
trait	A named vector of trait values for the tips of the tree. It should match tip labels in the phylogeny.
Nsteps	The number of generations in the MCMC chain.
record_every	The frequency used for sampling the MCMC chain.
plot_every	The frequency at which the chain is plotted (if plot=TRUE).
Npts_int	The number of points on the grid between min(trait) and max(trait).
pars_init	A vector giving the initial parameters for starting the algorithm, which correspond to the following: $c(\log(\text{sig}^2/2), a, b, c, x_0, B_{\min}, B_{\max})$.
prob_update	A vector giving the relative frequencies of update of the different parameters of the model.
verbose	If TRUE, will print some generations of the chain to the screen.
plot	If TRUE, the chain is plotted from time to time.
save_to	The path to the file where the chain is saved (can be useful in case the chain crashes).
save_every	Sets how often the chain is saved.
type_priors	A character vector specifying the type of priors used. Either 'Uniform' or 'Normal'. See Details.
shape_priors	A list that gives the shape for each prior. See Details.
proposal_type	The type of proposal function, only 'Uniform' is available (the default).
proposal_sensitivity	A numeric vector specifying the width of the uniform proposal for each parameter. See Details.
prior.only	Default to FALSE for estimation of the posterior. If TRUE, the likelihood is not evaluated: this is mostly useful for internal test of the Gibbs sampler.

Details

When specifying initial parameters yourself, be careful since x_0 is actually the index of the point on the grid (between 1 and N_{pts_int}), not the actual root value. Also the first parameter ($\log(\sigma^2/2)$) is the diffusion coefficient, not the evolutionary rate (σ^2). Finally, be careful that the initial bounds you propose actually contain all trait values in your dataset.

Priors can be either 'Normal' (preferred) or 'Uniform' for $\log(\sigma^2/2)$, a , b and c . The only option for bounds and x_0 is discrete uniform priors, specified by 'Uniform'.

Each element of the `shape_priors` list should be a vector giving $c(\text{mean}, \text{sd})$ for normal priors and $c(\text{min}, \text{max})$ for continuous uniform priors. The shape is not specified for the root prior (it is set as 'NA' by default), since it is fixed to be discrete uniform on the grid. Values for the priors on the bounds (forced to be discrete uniform) are a single numeric value giving the maximum number of points that can be added on the trait grid outside of the observed trait interval, with a default value of 10 points.

Elements of the `proposal_sensitivity` vector can be any positive number for continuously varying parameters: $c(\log(\sigma^2/2), a, b, c)$. Default values should often be a good start. Only integer numbers are possible for x_0 , B_{min} , and B_{max} and give how many steps at a time can be travelled on the trait grid when updating these parameters. It is recommended to keep it to 1, as it is by default.

Value

A matrix of numeric values giving values of all parameters, the likelihood, prior and posterior at each generation sampled in the MCMC chain (one row per sample taken). The matrix has the following columns:

<code>step</code>	The number of the generation sampled.
<code>sigsq</code>	The evolutionary rate.
<code>a</code>	The coefficient of the x^4 term of the evolutionary potential.
<code>b</code>	The coefficient of the x^2 term of the evolutionary potential.
<code>c</code>	The coefficient of the x term of the evolutionary potential.
<code>root</code>	The value of the trait at the root of the tree.
<code>bmin</code>	The value of the lower bound of the trait interval.
<code>bmax</code>	The value of the upper bound of the trait interval.
<code>lnprior</code>	The logarithm of the prior.
<code>lnlik</code>	The logarithm of the likelihood.
<code>quasi-lnpost</code>	The logarithm of the (unnormalized) posterior.
<code>Acceptance</code>	Whether the proposed MCMC move was accepted (1) or not (0).
<code>Par_updated</code>	Which parameter was updated in this generation.

Author(s)

F. C. Boucher

Optim_bBM_0_flex_pts_multiple_starts

Maximum-likelihood estimation

Description

Set of internal functions that are used for ML optimization of various forms of the BBM+v model.

Usage

```
Optim_bBM_0_flex_pts_multiple_starts(tree, trait, Npts = 50, method = "Nelder-Mead", verbose = T)
Optim_bBM_x4x2x(tree, trait, Npts = 100, bounds = NULL, method = "L-BFGS-B", init.optim = NULL)
Optim_bBM_x4x2x_flex_pts_start(tree, trait, Npts = 50, method = "Nelder-Mead",
start.point=c(log(var(trait))/(2*max(branching.times(tree)))),0,0,0,
min(trait)-0.5*(max(trait) - min(trait)),
max(trait)+0.5*(max(trait) - min(trait))))
Optim_bBM_x4x2x_flex_pts_multiple_starts(tree, trait, Npts = 50,
method = "Nelder-Mead", verbose = T)
Optim_bBM_x2x_flex_pts_start(tree, trait, Npts = 50, method = "Nelder-Mead",
start.point = c(log(var(trait))/(2 * max(branching.times(tree)))), 0, 0,
min(trait)-0.5*(max(trait)-min(trait)),max(trait)+0.5*(max(trait)-min(trait))))
Optim_bBM_x2x_flex_pts_multiple_starts(tree, trait, Npts = 50,
method = "Nelder-Mead", verbose = T)
Optim_bBM_x_flex_pts_start(tree, trait, Npts = 50, method = "Nelder-Mead",
start.point = c(log(var(trait))/(2 * max(branching.times(tree)))), 0,
min(trait)-0.5*(max(trait)-min(trait)),max(trait)+0.5*(max(trait)-min(trait))))
Optim_bBM_x_flex_pts_multiple_starts(tree, trait, Npts = 50,
method = "Nelder-Mead", verbose = T)
Optim_bBM_quadratic(tree, trait, Npts = 100, bounds = NULL, method = "L-BFGS-B", init.optim = NULL)
Optim_bBM_linear(tree, trait, Npts = 100, bounds = NULL, method = "L-BFGS-B", init.optim = NULL)
Optim_bBM_bounds_fixed_potential(tree, trait, V, bounds = NULL, init.optim = NULL)
Optim_bBM_0_flex_pts_start(tree, trait, Npts = 50, method = "Nelder-Mead",
start.point = c(log(var(trait))/(2 * max(branching.times(tree)))),
min(trait)-0.5*(max(trait)-min(trait)),max(trait)+0.5*(max(trait)-min(trait))))
```

Arguments

tree	A phylogenetic tree in phylo format
trait	A named vector of trait values for the tips of the tree. It should match tip labels in the phylogeny.
Npts	The number of points used in the discretization procedure.
method	The optimization routine used.
verbose	If TRUE, prints progress to the screen.
bounds	A vector giving the bounds of the trait interval.
init.optim	A parameter combination from which to start the optimization procedure, specified as a numeric vector. Default to NULL should work in most of the cases.
start.point	A parameter combination from which to start the optimization procedure, specified as a numeric vector.
V	A numeric vector giving the potential.

Author(s)

F. C. Boucher

```
prep_mat_exp
```

Matrix exponential.

Description

Internal function used for likelihood calculation and simulation.

Usage

```
prep_mat_exp(dCoeff, dMat, bounds)
```

Arguments

dCoeff	The diffusion coefficient.
dMat	The diffusion matrix.
bounds	A vector of bounds of the trait interval.

Author(s)

F. C. Boucher

```
proposal_7pars_root_bounds
```

Parameter update

Description

Internal function that proposes parameter updates used in MCMC estimation of the BBM+V model.

Usage

```
proposal_7pars_root_bounds(type = "Uniform", sensitivity, pars, trait, Npts_int)
```

Arguments

type	The type of proposal function, only 'Uniform' is available (the default).
sensitivity	A numeric vector specifying the width of the uniform proposal for each parameter.
pars	The current parameters in the MCMC chain.
trait	A named vector of trait values for the tips of the tree. It should match tip labels in the phylogeny.
Npts_int	The number of points on the grid between min(trait) and max(trait).

Author(s)

F. C. Boucher

Sim_BBMV

*Simulation of the BBM+V process.***Description**

The function simulates a continuous trait evolving according to the BBM+V process along the branches of a phylogenetic tree.

Usage

```
Sim_BBMV(tree, x0 = 0, V = rep(0, 100), sigma, bounds)
```

Arguments

tree	A phylogenetic tree in phylo format.
x0	The value of the trait at the root of the tree.
V	A vector giving the values of the evolutionary potential at each point of the discretized trait grid. Default is a flat potential, i.e. bounded Brownian Motion.
sigma	The square root of the diffusion rate.
bounds	A vector giving the values of the bounds of the trait interval.

Value

A numeric vector with values of the trait at the tips of the tree. Names correspond to tip labels in the tree.

Author(s)

F. C. Boucher

Examples

```
# Simulate data: tree + continuous trait
library(geiger)
tree=sim.bdtree(stop='taxa',n=20) # tree with few tips for quick tests
tree$edge.length=100*tree$edge.length/max(branching.times(tree)) # rescale the tree

# Simulate a trait evolving on the tree with a linear trend towards small values
TRAIT= Sim_BBMV(tree,x0=0,V=seq(from=0,to=5,length.out=50),sigma=10,bounds=c(-5, 5))
hist(TRAIT)
```

Uncertainty_BBMV	<i>Measure uncertainty in parameter estimation</i>
------------------	--

Description

This function measures the uncertainty associated with ML parameter estimates, returning plots as well as confidence intervals

Usage

```
Uncertainty_BBMV(model, tree, trait, Npts = 50, effort_uncertainty = 100)
```

Arguments

<code>model</code>	A BBM+V model fit, as returned by fit_BBMV .
<code>tree</code>	A phylogenetic tree, in phylo format.
<code>trait</code>	A named vector of trait values for the tips of the tree. It should match tip labels in the phylogeny.
<code>Npts</code>	The number of points used to discretize the trait interval.
<code>effort_uncertainty</code>	The number of values of each parameter that should be tried to assess uncertainty.

Author(s)

F. C. Boucher

Examples

```
# Simulate data: tree + continuous trait
library(geiger)
tree=sim.bdtree(stop='taxa',n=10) # tree with few tips for quick tests
tree$edge.length=100*tree$edge.length/max(branching.times(tree)) # rescale the tree
# Simulate trait evolving on the tree with a linear trend towards small values
TRAIT= Sim_BBMV(tree,x0=0,V=seq(from=0,to=5,length.out=50),sigma=10,bounds=c(-5, 5))
# fit a model with a linear potential:
BBM_x=fit_BBMV(tree,TRAIT,Npts=20,method='Nelder-Mead',verbose=TRUE,V_shape='linear')
# Measure uncertainty around ML estimates of parameters
Uncertainty_BBMV(BBM_x,tree,trait= TRAIT,Npts=20,effort_uncertainty= 50)
```

VectorPos_bounds	<i>Discretization of a continuous trait value into a probability vector.</i>
------------------	--

Description

Internal function used for likelihood calculation and simulation.

Usage

```
VectorPos_bounds(x, V, bounds)
```

Arguments

x	A numeric value of the trait.
V	The evolutionary potential used
bounds	A vector with the values of both bounds.

Author(s)

F. C. Boucher

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