

Package ‘BBMV’

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Type Package

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

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Author Florian C. Boucher

Maintainer Florian C. Boucher <flobfloboucher@gmail.com>

Depends R (>= 3.1.0), ape

Suggests coda, geiger

Description Provides a set of functions to fit general macroevolutionary models for continuous traits evolving in adaptive landscapes of any shape. This package implements the Fokker-Planck-Kolmogorov model (FPK), in which the trait evolves under random diffusion but is also subject to a force that pulls it towards specific values - this force can be of any shape. FPK has a version in which hard reflective bounds exist at the extremes of the trait interval: this second model is called BBM+V.

License GPL-2

NeedsCompilation no

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BBMV-package	<i>Models for Continuous Traits Evolving in Macroevo- lutionary Landscapes of any Shape</i>
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Description

Provides a set of functions to fit general macroevolutionary models for continuous traits evolving in adaptive landscapes of any shape. This package implements the Fokker-Planck-Kolmogorov model (FPK), in which the trait evolves under random diffusion but is also subject to a force that pulls it towards specific values - this force can be of any shape. FPK has a version in which hard reflective bounds exist at the extremes of the trait interval: this second model is called BBM+V.

Details

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Author(s)

Florian C. Boucher Maintainer: Florian C. Boucher <floboboucher@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

ACE_FPK

Ancestral Character Estimation

Description

Function to perform Ancestral Character Estimation under the FPK (or BBM+V) model

Usage

```
ACE_FPK(fit, specific.point = NULL)
```

Arguments

fit	An FPK model fit, as returned by find.mle_FPK .
specific.point	If set to NULL (the default), then the function will produce an ACE at all internal nodes in the tree. Alternatively, specific.point can be used to ask for an ACE at any specific point in the tree (i.e., not a node): specific.point must then be a vector with three elements: c(parent_node,child_node,time_from_start_of_branch).

Value

For each internal node, the function returns a table giving the probability density of the trait. The first column gives all possible trait values on the discretized trait grid, and the second the probability density at each of these points. If only a specific.point was asked, the function only returns one such table.

Author(s)

F. C. Boucher

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

Calculate the characteristic time it takes for the FPK process to reach its stationary distribution.

Usage

```
charac_time(Npts, fit)
```

Arguments

Npts	The number of points used in the discretization procedure.
fit	A FPK model fit, as returned by find.mle_FPK .

Value

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

Author(s)

F. C. Boucher

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

Description

Internal function that builds the discretized diffusion matrix of the FPK 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

find.mle_FPK	<i>Maximum-likelihood estimation</i>
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Description

Find the maximum-likelihood estimate of the FPK model.

Usage

```
find.mle_FPK(model, method = "Nelder-Mead", init.optim = NULL, safe = F)
```

Arguments

model	An FPK or BBM+V model, as generated by lnL_FPK or lnL_BBMV .
method	The optimization routine to be used: can be either "Nelder-Mead" (the default) or "L-BFGS-B". See the documentation of the optim function for more details. From our experience, "Nelder-Mead" seems to produce better results.
init.optim	A vector of initial values for model parameters to start the optimization algorithm. If left NULL (as is by default), the function chooses a reasonable starting point, but you might want to play around with it.
safe	If safe is set to TRUE, the function runs three different optimizations starting with different values of the rate of evolution (sigma). This can prove useful in difficult cases. Default to FALSE for a single optimization (which is quicker).

Value

A list with the following elements:

lnL	the log-likelihood of the model
aic	the Akaike Information Criterion of the model
k	the number of parameters of the model
par	a list of the MLEs of model parameters
par_fixed	a list with the parameters that were fixed. This includes the bounds use to discretize the model and eventually some of the parameters describing the shape of the macroevolutionary landscape.
root	A table giving the probability density of the trait at the root of the tree. The first column gives all possible trait values on the discretized trait grid, and the second the probability density at each of these points.
convergence	Convergence code returned by optim. 0 indicates successful convergence. For other values see the help of the optim function.
message	Convergence message returned by optim. See the help of the optim function.
tree	the tree used as input
trait	the trait vector used as input
Npts	the number of points used to discretize trait space.

Author(s)

F. C. Boucher

Examples

```
## Not run:
# 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 a macroevolutionary landscape with two peaks of equal heights
x=seq(from=-1.5,to=1.5,length.out=100)
bounds=c(min(x),max(x)) # the bounds we use for simulating
# they are just here for technical purposes but are not reached
V6=10*(x^4-0.5*(x^2)+0.*x) # this is the evolutionary potential: it has two wells
TRAIT= Sim_FPK(tree,x0=0,V=V6,sigma=10,bounds=c(-5, 5))
# fit the FPK model:
ll_FPK4=lnL_FPK(tree,TRAIT,Npts=25,a=NULL,b=NULL,c=NULL) # the full model
fit4=find.mle_FPK(model=ll_FPK4)

## End(Not run)
```

FormatTree_bounds	<i>Tree formatting.</i>
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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

FPK_sim_traitgram	<i>Simulations with traitgram</i>
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Description

Simulates a trait evolving according to the FPK model and also plots evolution along branches of this tree using a traitgram.

Usage

```
FPK_sim_traitgram(tree, x0, a, b, c, bounds, sigsq, time_step, res.x = 200
, ylim.plot = NULL, return.trait = FALSE)
```

Arguments

tree	The phylogenetic tree on which to simulate the trait evolving.
x0	The initial value of the trait (at the root of the tree).
a	The coefficient for the x^4 term of the potential.
b	The coefficient for the quadratic term of the potential.
c	The coefficient for the linear term of the potential.
bounds	The bounds on the trait interval.
sigsq	The evolutionary rate.
time_step	The time step for incremental simulations (should be smaller than the shortest branch in the tree).
res.x	The number of points to use for discretizing the trait interval.
ylim.plot	The y limits of the plot. If left to NULL, the bounds of the trait interval will be used, but you might want to zoom in a bit more if the bounds are not reached.
return.trait	If set to TRUE, the function returns a named vector of trait values at the tips of the tree.

Details

The function is slower than [Sim_FPK](#) since it simulates step by step along branches. It should be used to visualize trait evolution, but [Sim_FPK](#) should be preferred for quick simulations.

Value

The function is mainly designed to produce a plot, but eventually returns a named vector of trait values at the tips of the tree.

Author(s)

F. C. Boucher

See Also

[Sim_FPK](#)

get.landscape.FPK	<i>Plot macroevolutionary landscapes estimated by the FPK or BBM+V models</i>
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Description

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

Usage

```
get.landscape.FPK(fit, Npts = 100, main = "Macroevoolutionary landscape"
, ylab = "N.exp(-V)", xlab = "Trait", xlim = NULL, ylim = NULL)
```

Arguments

fit	An FPK model fit, as returned by find.mle_FPK .
Npts	The number of points used to discretize the trait interval for plotting.
main	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 across the trait interval.

Author(s)

F. C. Boucher

Examples

```
## Not run:
# 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 a macroevolutionary landscape with two peaks of equal heights
x=seq(from=-1.5,to=1.5,length.out=100)
bounds=c(min(x),max(x)) # the bounds we use for simulating
V6=10*(x^4-0.5*(x^2)+0.*x) # this is the evolutionary potential: it has two wells
TRAIT= Sim_FPK(tree,x0=0,V=V6,sigma=10,bounds=c(-5, 5))
# fit the FPK model:
ll_FPK4=lnL_FPK(tree,TRAIT,Npts=25,a=NULL,b=NULL,c=NULL) # the full model
fit4=find.mle_FPK(model=ll_FPK4)
# Plot the landscape estimated
get.landscape.FPK(fit=fit4)

## End(Not run)
```

lnL_FPK

*Creation of the likelihood function***Description**

Functions that builds the likelihood function of the FPK or BBM+V model

Usage

```
lnL_FPK(tree, trait, a = NULL, b = NULL, c = NULL, Npts)
lnL_BBMV(tree, trait, bounds, a = NULL, b = NULL, c = NULL, Npts)
```

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.
bounds	The two bounds that constrain trait values when fitting the BBM+V model. Specified by a numeric vector containing the minimum and maximum bound of the trait interval as the first and second element, respectively.
a	The value of the x^4 term in the evolutionary potential. If set to NULL (the default), this parameter will be estimated. If a numeric value is provided, this parameter will be fixed to the value specified.
b	The value of the quadratic term in the evolutionary potential. If set to NULL (the default), this parameter will be estimated. If a numeric value is provided, this parameter will be fixed to the value specified.
c	The value of the linear term in the evolutionary potential. If set to NULL (the default), this parameter will be estimated. If a numeric value is provided, this parameter will be fixed to the value specified.
Npts	The number of points used in the discretization procedure.

Value

A list of several items, including the data and model call, but most importantly the likelihood function (\$fun element).

Author(s)

F.C. Boucher

See Also

[find.mle_FPK](#)

Examples

```
## Not run:
# 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 a macroevolutionary landscape with two peaks of equal heights
x=seq(from=-1.5,to=1.5,length.out=100)
bounds=c(min(x),max(x)) # the bounds we use for simulating
V6=10*(x^4-0.5*(x^2)+0.*x) # this is the evolutionary potential: it has two wells
TRAIT= Sim_FPK(tree,x0=0,V=V6,sigma=10,bounds=c(-5, 5))
# create a likelihood function for the FPK model:
ll_FPK4=lnL_FPK(tree,TRAIT,Npts=25,a=NULL,b=NULL,c=NULL) # the full model

## End(Not run)
```

LogLik_bounds

*Likelihood of the FPK model***Description**

Internal functions use to calculate the likelihood of the FPK model, used in ML and MCMC estimation.

Usage

```
LogLik_bounds(tree_formatted, dCoeff, dMat, bounds)
LogLik_bounds_est_root(tree, trait, dCoeff, V, x0_pos, bounds)
```

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.

Author(s)

F. C. Boucher

log_prior_5pars_root_bounds
Prior function.

Description

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

Usage

```
log_prior_5pars_root_bounds(type = c(rep("Normal", 4), "Uniform"), shape =
  list(c(0, 10), c(0, 10), c(0, 10), c(0, 10), NA), pars, Npts, trait, bounds)
```

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	The number of points on the grid.
trait	A named vector of trait values for the tips of the tree.
bounds	The bounds on the trait interval.

Author(s)

F. C. Boucher

MH_MCMC_FPK	<i>MCMC estimation</i>
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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_FPK(tree, trait, bounds, Nsteps = 5e+05, record_every = 100, plot_every = 500,
  Npts = 50, pars_init = c(0, 0, 0, 0, 25), prob_update = c(0.2, 0.2, 0.2, 0.2, 0.2),
  verbose = TRUE, plot = TRUE, save_to = "MCMC_FPK_test.Rdata", save_every = 10000,
  type_priors = c(rep("Normal", 4), "Uniform"),
  shape_priors = list(c(0, 10), c(0, 10), c(0, 10), c(0, 10), NA), proposal_type = "Uniform",
  proposal_sensitivity = c(0.1, 0.1, 0.1, 0.1, 1), prior.only = F, burnin.plot = 0.1)
```

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.
bounds	A vector with two elements giving the bounds on the trait interval.
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	The number of points on the grid between the bounds.
pars_init	A vector giving the initial parameters for starting the algorithm, which correspond to the following: $c(\log(\sigma^2/2), a, b, c, x_0)$.
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.
burnin.plot	The percentage of samples considered as burnin and thus not shown on the trace plot that the function produces.

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 bounds you propose must 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 x_0 is a discrete uniform prior, 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.

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 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:

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

Author(s)

F. C. Boucher

Examples

```
## Not run:
# 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 a macroevolutionary landscape with two peaks of equal heights
x=seq(from=-1.5,to=1.5,length.out=100)
bounds=c(min(x),max(x)) # the bounds we use for simulating: for technical purposes only
V6=10*(x^4-0.5*(x^2)+0.*x) # this is the evolutionary potential: it has two wells
TRAIT= Sim_FPK(tree,x0=0,V=V6,sigma=10,bounds=c(-5, 5))
# Run a MCMC chain to fit the FPK model
MCMC=MH_MCMC_FPK(tree,trait=TRAIT,bounds=c(-1.5,1.5),Nsteps=10000,record_every=100,
  plot_every=100,Npts=20,pars_init=c(0,-4,-4,0,1),prob_update=c(0.2,0.25,0.25,0.25,0.05),
  verbose=TRUE,plot=TRUE,save_to='MCMC_FPK_test.Rdata',save_every=100,
  type_priors=c(rep('Normal',4),'Uniform'),
  shape_priors=list(c(0,10),c(0,10),c(0,10),c(0,10),NA),proposal_type='Uniform',
  proposal_sensitivity=c(0.1,0.1,0.1,0.1,1),prior.only=F)

## End(Not run)
```

prep_mat_exp	<i>Matrix exponential.</i>
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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_5pars_root_bounds	<i>Parameter update for the MCMC function</i>
----------------------------	---

Description

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

Usage

```
proposal_5pars_root_bounds(type = "Uniform", sensitivity, pars, trait)
```

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.

Author(s)

F. C. Boucher

Sim_FPK

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

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

Usage

```
Sim_FPK(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_FPK(tree,x0=0,V=seq(from=0,to=5,length.out=50),sigma=10,bounds=c(-5, 5))
```

trans_from_fixed

*Linear transformations***Description**

Internal function used to convert back and forth between the actual trait interval and [-1.5;1.5]

Usage

```
trans_from_fixed(x, bounds)
trans_to_fixed(x, bounds)
```


Arguments

x	A single value or vector of trait values.
bounds	The actual bounds on the trait interval

Value

A single value or vector of trait values transformed to the other interval.

Author(s)

F. C. Boucher

Uncertainty_FPK	<i>Parameter uncertainty</i>
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Description

This function plots likelihood profiles around the MLEs of parameters and returns 95% confidence intervals.

Usage

```
Uncertainty_FPK(fit, tree, trait, Npts = 50, effort_uncertainty = 100,
  scope_a = c(-10, 10), scope_b = c(-10, 10), scope_c = c(-10, 10))
```

Arguments

fit	An FPK model fit, as returned by find.mle_FPK .
tree	The phylogenetic tree.
trait	The named trait vector
Npts	The number of points used to discretize the trait interval.
effort_uncertainty	Determines the number of values at which the likelihood should be calculated for each parameter.
scope_a	Extreme values that should be investigated for parameter a.
scope_b	Extreme values that should be investigated for parameter b.
scope_c	Extreme values that should be investigated for parameter c.

Value

A list with 95% confidence intervals for all parameters.

Author(s)

F. C. Boucher

Examples

```
## Not run:
# 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 a macroevolutionary landscape with two peaks of equal heights
x=seq(from=-1.5,to=1.5,length.out=100)
bounds=c(min(x),max(x)) # the bounds we use for simulating: for technical purposes only
V6=10*(x^4-0.5*(x^2)+0.*x) # this is the evolutionary potential: it has two wells
TRAIT= Sim_FPK(tree,x0=0,V=V6,sigma=10,bounds=c(-5, 5))
# fit the FPK model:
ll_FPK4=lnL_FPK(tree,TRAIT,Npts=25,a=NULL,b=NULL,c=NULL) # the full model
fit4=find.mle_FPK(model=ll_FPK4)
# Measure uncertainty on model parameters
Uncertainty_FPK(fit=fit4,tree,trait=TRAIT,Npts=25,effort_uncertainty= 100,
  scope_a=c(-1,10),scope_b=c(-5,5),scope_c=c(-2,2))

## End(Not run)
```

VectorPos_bounds

Discretization of a continuous trait value into a probability vector.

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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*Topic **phylogenetic comparative
methods ; evolution ;
adaptation ; FPK model**

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