Package 'PBD'

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PBD-package

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PBD-package

Protracted Birth-Death Model of Diversification

Description

This package computes the (maximum) likelihood of the protracted speciation model for a given set of branching times This package is a likelihood-based statistical package to estimate parameters under the protracted speciation model.

First version: 0.8 New in version 0.9

- Bug fix for stem age

New in version 0.91

- Reports loglik = -Inf on an error in the deSolve package (function ode)

New in version 0.92

- Correcting order of parameters of pbd_sim

New in version 0.93

- pbd_sim produces a tree, a matrix containing all events in the simulation, and a tree with one sample per species.

New in version 1.0

- Conditioning is also possible on a range of values of the number of species.

New in version 1.1

- Simulation of the protracted speciation tree has more features.

New in version 1.2

- Optimization can make use of subplex (default) and simplex (older versions).

New in version 1.3

- Contains a function to carry out a bootstrap likelihood ratio test.
- Vignette and test added.
- Reports an error if exteq = TRUE and initparsopt contains 4 parameters.
- Option to limit a simulation to a certain maximum number of species; if exceeded, the simulation is ignored.

New in version 1.4:

- Includes all special cases in pbd_durspec_mean
- Fixes a bug in conditioning on a range of values of the number of species

Details

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Package: PBD
Type: Package
Version: 1.4
Date: 2017-5-4
License: GPL-2

pbd_loglik computes the likelihood of the protracted birth-death model of diversification, given a set of parameters and a data set of phylogenetic branching times.

pbd_ML finds the parameters that maximizes the likelihood computed by pbd_loglik.

pbd_bootstrap performs a maximum likelihood analysis and simulates with the maximum likelihood parameters. The ML parameters of the simulated data sets are then estimated, providing an uncertainty distribution for the original ML estimate on the original data.

Author(s)

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References

- Etienne, R.S. & J. Rosindell 2012. Systematic Biology 61: 204-213.
- Lambert, A., H. Morlon & R.S. Etienne 2014. Journal of Mathmematical Biology 70: 367-397. doi:10.1007/s00285-014-0767-x
- Etienne, R.S., H. Morlon & A. Lambert 2014. Evolution 68: 2430-2440, doi:10.1111/evo.12433
- . Etienne, R.S., A.L. Pigot & A.B. Phillimore 2016. Methods in Ecology & Evolution 7: 1092-1099, doi: 10.1111/2041-210X.12565

See Also

DDD

pbd_bootstrap	Bootstrap analysis under protracted birth-death model of diversifica-
	tion

Description

Likelihood maximization for protracted birth-death model of diversification followed by simulations of the model using the maximum likelihood parameter estimates to compute an estimate of the error in these estimates and to assess the goodness-of-fit of the model by comparing maximum likelihoods of the simulated data sets to the maximum likelihood of the real data set.

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Usage

```
pbd_bootstrap(
  brts,
   initparsopt = c(0.2, 0.1, 1),
   idparsopt = 1:length(initparsopt),
   idparsfix = NULL,
   parsfix = NULL,
   exteq = (length(initparsopt) < 4),</pre>
   parsfunc = c(function(t,pars) {pars[1]},function(t,pars) {pars[2]},
function(t,pars) {pars[3]}, function(t,pars) {pars[4]}),
   missnumspec = 0,
   cond = 1,
   btorph = 0,
   soc = 2,
   plotltt = 1,
   methode = "lsoda",
  n_low = 0,
   n_up = 0,
   tol = c(1E-4, 1E-4, 1E-6),
   maxiter = 1000 * round((1.25)^length(idparsopt)),
   endmc = 100,
   seed = 42
)
```

Arguments

brts	A set of branching times of a phylogeny, all positive
initparsopt	The initial values of the parameters that must be optimized
idparsopt	The ids of the parameters that must be optimized, e.g. 1:4 for all parameters. The ids are defined as follows: id == 1 corresponds to b (speciation-initiation rate) id == 2 corresponds to mu_1 (extinction rate of good species) id == 3 corresponds to la_1 (speciation-completion rate) id == 4 corresponds to mu_2 (extinction rate of incipient species)
idparsfix	The ids of the parameters that should not be optimized, e.g. $c(2,4)$ if mu_1 and mu_2 should not be optimized, but only b and la_1. In that case idparsopt must be $c(1,3)$.
parsfix	The values of the parameters that should not be optimized
exteq	Sets whether incipient species have the same (1) or different (0) extinction rate as good species. If exteq = 0, then idparsfix and idparsopt should together have all parameters 1:4
parsfunc	Specifies functions how the rates depend on time, default functions are constant functions
missnumspec	The number of species that are in the clade but missing in the phylogeny

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cond Conditioning:

cond == 0: conditioning on stem or crown age

cond == 1: conditioning on stem or crown age and non-extinction of the phy-

logeny

btorph Sets whether the likelihood is for the branching times (0) or the phylogeny (1) soc Sets whether the first element of the branching times is the stem (1) or the crown

(2) age

plotltt Sets whether the lineage-through-time plot should be plotted (1) or not (0)

methode Sets which method should be used in the ode-solver. Default is 'Isoda'. See

package deSolve for details.

n_low Sets the lower bound of the number of species on which conditioning should

be done when cond = 2. Set this to 0 when conditioning should be done on

precisely the number of species (default)

n_up Sets the upper bound of the number of species on which conditioning should

be done when cond = 2. Set this to 0 when conditioning should be done on

precisely the number of species (default)

tol Sets the tolerances in the optimization. Consists of:

reltolx = relative tolerance of parameter values in optimization reltolf = relative tolerance of function value in optimization abstolx = absolute tolerance of parameter values in optimization

maxiter Sets the maximum number of iterations in the optimization

endmc Sets the number of simulations for the bootstrap seed Sets the seed for the simulations of the bootstrap

Value

A list of three dataframes. The first dataframe contains the maximum likelihood results of the real data set, the second contains the simulated trees, and the third dataframe, with number of rows equal to endmc, contain the maximum likelihood results for the simulated data. The columns of both frames contains the following elements for each simulated data set:

ntips gives the number of tips

b gives the maximum likelihood estimate of b
mu_1 gives the maximum likelihood estimate of mu_1
la_1 gives the maximum likelihood estimate of la_1
mu_2 gives the maximum likelihood estimate of mu_2

loglik gives the maximum loglikelihood

df gives the number of estimated parameters, i.e. degrees of feedom

conv gives a message on convergence of optimization; conv = 0 means convergence

exp_durspec gives the expected duration of speciation median_durspec gives the median duration of speciation

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Author(s)

Rampal S. Etienne

See Also

pbd_ML

pbd_brts_density

Node depth probbaility density for protracted birth-death model of diversification

Description

pbd_brts_density computes the probability density of node depths under the protracted speciation model given a set of parameters

Usage

```
pbd_brts_density(
    pars1,
    pars1f = c(function(t,pars) {pars[1]},function(t,pars) {pars[2]},
function(t,pars) {pars[3]}, function(t,pars) {pars[4]}),
    methode = "lsoda",
    brts
)
```

Arguments

pars1 Vector of parameters:

pars1[1] corresponds to b (= la_1 in Etienne & Rosindell R2012) = speciation initiation rate

pars1[2] corresponds to mu_1 (= mu_g in Etienne & Rosindell 2012) = extinction rate of good species

pars1[3] corresponds to la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate

pars1[4] corresponds to mu_2 (= mu_i in ER2012) = extinction rate of incipient species

When rates depend on time this time dependence should be specified in pars1f and pars1 then becomes the parameters used in pars1f

pars1f

Vector of functions how the rates depend on time, default functions are constant functions of the parameters in pars1:

pars1f[1] corresponds to time-dependence of b (= la_1 in Etienne & Rosindell R2012) = speciation initiation rate

pars1f[2] corresponds to time-dependence of mu_1 (= mu_g in Etienne & Rosindell 2012) = extinction rate of good species

pars1f[3] corresponds to tiem-dependence of la_1 (= la_2 in Etienne & Rosin-dell 2012) = speciation completion rate

pars1f[4] corresponds to time-dependence of mu_2 (= mu_i in ER2012) = extinction rate of incipient species

methode

sets which method should be used in the ode-solver. Default is 'lsoda'. See package deSolve for details.

brts

A set of branching times of a phylogeny, all positive, for which the density must be computed

Value

The probability density for all branching times

Author(s)

Rampal S. Etienne

See Also

pbd_ML

Examples

```
pbd_brts_density(pars1 = c(0.2,0.1,1,0.1), methode = "lsoda", brts = 1:10)
```

pbd_durspec_cumdensity

Cumulative density of duration of speciation under protracted birthdeath model of diversification

Description

pbd_durspec_cumdensity computes the cumulative density of the duration of speciation under the protracted speciation model for a given set of parameters

```
pbd_durspec_cumdensity(
    pars,
    tau
)
```

Arguments

pars[1] corresponds to b (= la_3 in Etienne & Rosindell R2012) = speciation initiation rate

pars[2] corresponds to la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate

pars[3] corresponds to mu_2 (= mu_i in ER2012) = extinction rate of incipient species

tau

Value of the duration of speciation at which the cumulative density must be computed

Value

The cumulative density of the duration of speciation

Author(s)

Rampal S. Etienne

See Also

```
pbd_durspec_density
pbd_durspec_mean
pbd_durspec_mode
pbd_durspec_quantile
pbd_durspec_moment
pbd_durspec_var
```

Examples

```
pbd\_durspec\_cumdensity(pars = c(0.5, 0.3, 0.1), 3)
```

pbd_durspec_density

Probability density for duration of speciation under protracted birthdeath model of diversification

Description

pbd_durspec_density computes the probability density of the duration of speciation under the protracted speciation model for a given set of parameters

```
pbd_durspec_density(
    pars,
    tau
)
```

pbd_durspec_mean 9

Arguments

pars Vector of parameters:

pars[1] corresponds to b (= la_3 in Etienne & Rosindell R2012) = speciation

initiation rate

 $\verb|pars[2]| corresponds to la_1 (= la_2 in Etienne \& Rosindell 2012) = speciation$

completion rate

pars[3] corresponds to mu_2 (= mu_i in ER2012) = extinction rate of incipient

species

tau The duration of speciation for which the density must be computed

Value

The probability density

Author(s)

Rampal S. Etienne

See Also

```
pbd_durspec_cumdensity
pbd_durspec_mean
pbd_durspec_mode
pbd_durspec_quantile
pbd_durspec_moment
pbd_durspec_var
```

Examples

```
pbd_durspec_density(pars = c(0.5, 0.3, 0.1), tau = 1)
```

pbd_durspec_mean

Mean duration of speciation under protracted birth-death model of diversification

Description

pbd_durspec_mean computes the mean duration of speciation under the protracted speciation model for a given set of parameters

```
pbd_durspec_mean(
    pars
)
```

pbd_durspec_mode

Arguments

pars

Vector of parameters:

pars[1] corresponds to b (= la_3 in Etienne & Rosindell R2012) = speciation initiation rate

pars[2] corresponds to la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate

pars[3] corresponds to mu_2 (= mu_i in ER2012) = extinction rate of incipient

species

Value

The expected duration of speciation

Author(s)

Rampal S. Etienne

See Also

```
pbd_durspec_density
pbd_durspec_cumdensity
pbd_durspec_mode
pbd_durspec_quantile
pbd_durspec_moment
pbd_durspec_var
```

Examples

```
pbd_durspec_mean(pars = c(0.5, 0.3, 0.1))
```

pbd_durspec_mode

mode of the duration of speciation under protracted birth-death model of diversification

Description

pbd_durspec_mode computes the mode of the duration of speciation under the protracted speciation model for a given set of parameters

```
pbd_durspec_mode(
    pars
)
```

pbd_durspec_moment 11

Arguments

pars Vector of parameters:

pars[1] corresponds to b (= la_3 in Etienne & Rosindell R2012) = speciation initiation rate

 $\verb|pars[2]| corresponds to la_1 (= la_2 in Etienne \& Rosindell 2012) = speciation$

completion rate

pars[3] corresponds to mu_2 (= mu_i in ER2012) = extinction rate of incipient

species

Value

The expected duration of speciation

Author(s)

Rampal S. Etienne

See Also

```
pbd_durspec_density
pbd_durspec_cumdensity
pbd_durspec_mean
pbd_durspec_quantile
pbd_durspec_moment
pbd_durspec_var
```

Examples

```
pbd_durspec_mode(pars = c(0.5, 0.3, 0.1))
```

pbd_durspec_moment

Moments of duration of speciation under protracted birth-death model of diversification

Description

pbd_durspec_moment computes the moments of the duration of speciation under the protracted speciation model for a given set of parameters

```
pbd_durspec_moment(
    pars,
    order
)
```

Arguments

pars Vector of parameters:

pars[1] corresponds to b (= la_3 in Etienne & Rosindell R2012) = speciation initiation rate
pars[2] corresponds to la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate
pars[3] corresponds to mu_2 (= mu_i in ER2012) = extinction rate of incipient species

order order of the moment to compute (1 is first moment, giving the mean)

Value

The moment of the duration of speciation

Author(s)

Rampal S. Etienne

See Also

```
pbd_durspec_density
pbd_durspec_cumdensity
pbd_durspec_mean
pbd_durspec_mode
pbd_durspec_quantile
pbd_durspec_var
```

Examples

```
pbd_durspec_moment(pars = c(0.5, 0.3, 0.1), 2)
```

pbd_durspec_quantile Quantiles of duration of speciation under protracted birth-death model of diversification

Description

pbd_durspec_quantile computes a quantile of the duration of speciation under the protracted speciation model for a given set of parameters

```
pbd_durspec_quantile(
    pars,
    p
)
```

pbd_durspec_var 13

Arguments

pars [1] corresponds to b (= la_3 in Etienne & Rosindell R2012) = speciation initiation rate

pars[2] corresponds to la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate

pars[3] corresponds to mu_2 (= mu_i in ER2012) = extinction rate of incipient species

p Quantile (e.g. p = 0.5 gives the median)

Qualitie (e.g. p = 0.3 gives the median

Value

The quantil of the duration of speciation

Author(s)

Rampal S. Etienne

See Also

```
pbd_durspec_density
pbd_durspec_cumdensity
pbd_durspec_mean
pbd_durspec_mode
pbd_durspec_moment
pbd_durspec_var
```

Examples

```
pbd_durspec_quantile(pars = c(0.5, 0.3, 0.1), 0.5)
```

pbd_durspec_var

Variance in duration of speciation under protracted birth-death model of diversification

Description

pbd_durspec_var computes the variance in the duration of speciation under the protracted speciation model for a given set of parameters

```
pbd_durspec_var(
    pars
)
```

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Arguments

pars

Vector of parameters:

```
pars[1] corresponds to b (= la_3 in Etienne & Rosindell R2012) = speciation initiation rate pars[2] corresponds to la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate pars[3] corresponds to mu_2 (= mu_i in ER2012) = extinction rate of incipient species
```

Value

The variance in the duration of speciation

Author(s)

Rampal S. Etienne

See Also

```
pbd_durspec_density
pbd_durspec_cumdensity
pbd_durspec_mean
pbd_durspec_mode
pbd_durspec_quantile
pbd_durspec_moment
```

Examples

```
pbd_durspec_var(pars = c(0.5, 0.3, 0.1))
```

pbd_loglik

Loglikelihood for protracted birth-death model of diversification

Description

pbd_loglik computes the loglikelihood of the parameters of the protracted speciation model given a set of branching times and number of missing species

```
pbd_loglik(
    pars1,
    pars1f = c(function(t,pars) {pars[1]},function(t,pars) {pars[2]},
function(t,pars) {pars[3]}, function(t,pars) {pars[4]}),
    pars2 = c(1,1,2,1,"lsoda",0,0),
```

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```
brts,
missnumspec = 0
)
```

Arguments

pars1

Vector of parameters:

pars1[1] corresponds to b (= la_1 in Etienne & Rosindell R2012) = speciation initiation rate

pars1[2] corresponds to mu_1 (= mu_g in Etienne & Rosindell 2012) = extinction rate of good species

pars1[3] corresponds to la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate

pars1[4] corresponds to mu_2 (= mu_i in ER2012) = extinction rate of incipient species

When rates depend on time this time dependence should be specified in pars1f and pars1 then becomes the parameters used in pars1f

pars1f

Vector of functions how the rates depend on time, default functions are constant functions of the parameters in pars1:

pars1f[1] corresponds to time-dependence of b (= la_1 in Etienne & Rosindell R2012) = speciation initiation rate

pars1f[2] corresponds to time-dependence of mu_1 (= mu_g in Etienne & Rosindell 2012) = extinction rate of good species

pars1f[3] corresponds to tiem-dependence of la_1 (= la_2 in Etienne & Rosin-dell 2012) = speciation completion rate

pars1f[4] corresponds to time-dependence of mu_2 (= mu_i in ER2012) = extinction rate of incipient species

pars2

Vector of model settings:

pars2[1] set the conditioning on non-extinction of the clade (1) or not (0)

pars2[2] sets whether the likelihood is for the branching times (0) or the phylogeny (1)

pars2[3] sets whether the first element of the branching times is the stem (1) or the crown (2) age

pars2[4] sets whether the parameters and likelihood should be shown on screen (1) or not (0)

pars2[5] sets which method should be used in the ode-solver. Default is 'lsoda'. See package deSolve for details.

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pars2[6]Sets the lower bound of the number of species on which conditioning should be done when cond = 2. Set this to 0 when conditioning should be done on precisely the number of species (default)

pars2[7]Sets the upper bound of the number of species on which conditioning should be done when cond = 2. Set this to 0 when conditioning should be done on precisely the number of species (default)

brts A set of branching times of a phylogeny, all positive

missnumspec The number of species that are in the clade but missing in the phylogeny

Value

The loglikelihood

Author(s)

Rampal S. Etienne

See Also

```
pbd_ML
```

Examples

```
pbd_loglik(pars1 = c(0.2,0.1,1,0.1), pars2 = c(1,1,2,0,"lsoda"),brts = 1:10)
```

pbd_LR

Bootstrap likelihood ratio test of protracted birth-death model of diversification

Description

This function computes the maximum likelihood and the associated estimates of the parameters of a protracted birth-death model of diversification for a given set of phylogenetic branching times. It then performs a bootstrap likelihood ratio test of the protracted birth-death (PBD) model against the constant-rates (CR) birth-death model. Finally, it computes the power of this test.

```
pbd_LR(
  brts,
  initparsoptPBD,
  initparsoptCR,
  missnumspec,
```

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```
outputfilename = NULL,
seed = 42,
endmc = 1000,
alpha = 0.05,
plotit = TRUE,
parsfunc = c(function(t,pars) {pars[1]},
function(t,pars) {pars[2]},
function(t,pars) {pars[3]},
function(t,pars) {pars[4]}),
cond = 1,
btorph = 1,
soc = 2,
methode = 'lsoda',
n_low = 0,
n_{up} = 0,
tol = c(1E-6, 1E-6, 1E-6),
maxiter = 2000,
optimmethod = 'subplex',
verbose = FALSE
```

Arguments

brts A set of branching times of a phylogeny, all positive

initparsoptPBD The initial values of the parameters that must be optimized for the protracted

birth-death (PBD) model: b, mu and lambda

initparsoptCR The initial values of the parameters that must be optimized for the constant-rates

(CR) model: b and mu

missnumspec The number of species that are in the clade but missing in the phylogeny

outputfilename The name (and location) of the file where the output will be saved. Default is no

save

seed The seed for the pseudo random number generator for simulating the bootstrap

data

endmc The number of bootstraps

alpha The significance level of the test

plotit Boolean to plot results or not

parsfunc Specifies functions how the rates depend on time, default functions are constant

functions

cond Conditioning:

cond == 0: conditioning on stem or crown age

cond == 1 : conditioning on stem or crown age and non-extinction of the phy-

logeny

cond == 2: conditioning on stem or crown age and on the total number of extant

taxa (including missing species)

cond == 3: conditioning on the total number of extant taxa (including missing

species)

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Note: cond == 3 assumes a uniform prior on stem age, as is the standard in constant-rate birth-death models, see e.g. D. Aldous & L. Popovic 2004. Adv. Appl. Prob. 37: 1094-1115 and T. Stadler 2009. J. Theor. Biol. 261: 58-66. Sets whether the likelihood is for the branching times (0) or the phylogeny (1) Sets whether stem or crown age should be used (1 or 2)

The numerical method used to solve the master equation, such as 'lsoda' or 'ode45'.

Sets the lower bound of the number of species on which conditioning should be done when cond = 2. Set this to 0 when conditioning should be done when cond = 2. Set this to 0 when conditioning should be done when cond = 2. Set this to 0 when conditioning should be done when cond = 2. Set this to 0 when conditioning should be done on precisely the number of species (default)

tol Sets the tolerances in the optimization. Consists of:

reltolx = relative tolerance of parameter values in optimization reltolf = relative tolerance of function value in optimization abstolx = absolute tolerance of parameter values in optimization

maxiter Sets the maximum number of iterations in the optimization

optimmethod Method used in optimization of the likelihood. Current default is 'subplex'.

Alternative is 'simplex'.

verbose if TRUE, explanatory text will be shown

Details

btorph soc

methode

n_low

n_up

The output is a list with 3 elements:

Value

brtsCR a list of sets of branching times generated under the constant-rates model using

the ML parameters under the CR model

brtsDD a list of sets of branching times generated under the protracted birth-death model

using the ML parameters under the PBD model

out a dataframe with the parameter estimates and maximum likelihoods for pro-

tracted birth-death and constant-rates models \$model - the model used to gener-

ate the data. 0 = unknown (for real data), 1 = CR, 2 = PBD

\$mc - the simulation number for each model
 \$b_CR - speciation rate estimated under CR
 \$mu_CR - extinction rate estimated under CR
 \$LL_CR - maximum likelihood estimated under CR

\$conv_CR - convergence code for likelihood optimization; conv = 0 means convergence

reigence

\$b_PBD1 - speciation-initation rate estimated under PBD for first set of initial

values

\$mu_PB1 - extinction rate estimated under DD for first set of initial values

 $\$ rate estimated under PBD for first set of

initial values

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\$LL_PBD1 - maximum likelihood estimated under DD for first set of initial values

\$conv_PBD1 - convergence code for likelihood optimization for first set of initial values; conv = 0 means convergence

\$b_PBD2 - speciation-initation rate estimated under PBD for second set of initial values

\$mu_PB2 - extinction rate estimated under DD for second set of initial values \$lambda_PB2 - speciation-completion rate estimated under PBD for second set of initial values

\$LL_PBD2 - maximum likelihood estimated under DD for second set of initial values

\$conv_PBD2 - convergence code for likelihood optimization for second set of initial values; conv = 0 means convergence
\$LR - likelihood ratio between DD and CR

pvalue p-value of the test

LRalpha Likelihood ratio at the signifiance level alpha power of the test for significance level alpha

Author(s)

Rampal S. Etienne

References

- Etienne, R.S. et al. 2016. Meth. Ecol. Evol. 7: 1092-1099, doi: 10.1111/2041-210X.12565

See Also

```
pbd_loglik, pbd_ML
```

pbd_ML

Maximization of loglikelihood under protracted birth-death model of diversification

Description

Likelihood maximization for protracted birth-death model of diversification

```
pbd_ML(
    brts,
    initparsopt = c(0.2,0.1,1),
    idparsopt = 1:length(initparsopt),
    idparsfix = NULL,
    parsfix = NULL,
```

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```
exteq = 1,
  parsfunc = c(function(t,pars) {pars[1]},function(t,pars) {pars[2]},
function(t,pars) {pars[3]}, function(t,pars) {pars[4]}),
  missnumspec = 0,
  cond = 1,
  btorph = 1,
  soc = 2,
  methode = "lsoda",
  n_low = 0,
  n_up = 0,
  tol = c(1E-6, 1E-6, 1E-6),
  maxiter = 1000 * round((1.25)^length(idparsopt)),
  optimmethod = 'subplex',
  verbose = TRUE
)
```

Arguments

brts A set of branching times of a phylogeny, all positive

initparsopt The initial values of the parameters that must be optimized

idparsopt The ids of the parameters that must be optimized, e.g. 1:4 for all parameters.

The ids are defined as follows:

id == 1 corresponds to b (speciation-initiation rate)

id == 2 corresponds to mu_1 (extinction rate of good species) id == 3 corresponds to la_1 (speciation-completion rate)

id == 4 corresponds to mu 2 (extinction rate of incipient species)

idparsfix The ids of the parameters that should not be optimized, e.g. c(2,4) if mu_1 and

mu_2 should not be optimized, but only b and la_1. In that case idparsopt must

be c(1,3).

parsfix The values of the parameters that should not be optimized

exteq Sets whether incipient species have the same (1) or different (0) extinction rate

as good species. If exteq = 0, then idparsfix and idparsopt should together have

all parameters 1:4

parsfunc Specifies functions how the rates depend on time, default functions are constant

functions

missnumspec The number of species that are in the clade but missing in the phylogeny

cond Conditioning:

cond == 0: conditioning on stem or crown age

cond == 1 : conditioning on stem or crown age and non-extinction of the phy-

logeny

cond == 2 : conditioning on stem or crown age and number of extant taxa

btorph Sets whether the likelihood is for the branching times (0) or the phylogeny (1)

soc Sets whether the first element of the branching times is the stem (1) or the crown

(2) age

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methode	Sets which method should be used in the ode-solver. Default is 'Isoda'. See package deSolve for details.
n_low	Sets the lower bound of the number of species on which conditioning should be done when $cond = 2$. Set this to 0 when conditioning should be done on precisely the number of species (default)
n_up	Sets the upper bound of the number of species on which conditioning should be done when $cond = 2$. Set this to 0 when conditioning should be done on precisely the number of species (default)
tol	Sets the tolerances in the optimization. Consists of: reltolx = relative tolerance of parameter values in optimization reltolf = relative tolerance of function value in optimization abstolx = absolute tolerance of parameter values in optimization
maxiter	Sets the maximum number of iterations in the optimization
optimmethod	Method used in optimization of the likelihood. Current default is 'subplex'. Alternative is 'simplex' (default of previous versions)
verbose	if TRUE, explanatory text will be shown

Value

A data frame with the following components:

b	gives the maximum likelihood estimate of b
mu_1	gives the maximum likelihood estimate of mu_1
la_1	gives the maximum likelihood estimate of la_1
mu_2	gives the maximum likelihood estimate of mu_2
loglik	gives the maximum loglikelihood
df	gives the number of estimated parameters, i.e. degrees of feedom
conv	gives a message on convergence of optimization; conv = 0 means convergence

Author(s)

Rampal S. Etienne

See Also

```
pbd_loglik
```

Examples

```
pbd_ML(1:10,initparsopt = c(4.640321,4.366528,0.030521), exteq = 1)
```

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pbd_sim

Function to simulate the protracted speciation process

Description

Simulating the protracted speciation process using the Doob-Gillespie algorithm. This function differs from pbd_sim_cpp that 1) it does not require that the speciation-initiation rate is the same for good and incipient species, and 2) that it simulates the exact protracted speciation process, and not the approximation made by the coalescent point process. This function provides also the conversion to the approximation as output.

Usage

```
pbd_sim(
  pars,
  age,
  soc = 2,
  plotit = FALSE,
  limitsize = Inf
)
```

Arguments

pars	Vector of parameters:
------	-----------------------

pars[1] corresponds to b_1, the speciation-initiation rate of good species

pars[2] corresponds to la_1, the speciation-completion rate

pars[3] corresponds to b_2, the speciation-initiation rate of incipient species

pars[4] corresponds to mu_1, the extinction rate of good species pars[5] corresponds to mu_2, the extinction rate of incipient species

age Sets the age for the simulation

soc Sets whether this age is the stem (1) or crown (2) age

Sets whether the various trees produced by the function should be plotted or not

limitsize Sets a maximum to the number of incipient + good species that are created

during the simulation; if exceeded, the simulation is aborted and removed.

Value

out A list with the following elements:

tree is the tree of extant species in phylo format stree_random is a tree with one random sample per species in phylo format stree_oldest is a tree with the oldest sample per species in phylo format stree_youngest is a tree with the youngest sample per species in phylo format L is a matrix of all events in the simulation where pbd_sim_cpp 23

- the first column is the incipient-level label of a species
- the second column is the incipient-level label of the parent of the species
- the third column is the time at which a species is born as incipient species
- the fourth column is the time of speciation-completion of the species

If the fourth element equals -1, then the species is still incipient. - the fifth column is the time of extinction of the species

If the fifth element equals -1, then the species is still extant. - The sixth column is the species-level label of the species

sL_random is a matrix like L but for stree_random

sL_oldest is a matrix like L but for stree_oldest

sL_youngest is a matrix like L but for stree_youngest

igtree.extinct is the tree in simmap format with incipient and good flags and including extinct species

igtree.extant is the tree in simmap format with incipient and good flags without extinct species

recontree is the reconstructed tree in phylo format, reconstructed using the approximation in Lambert et al. 2014

reconL is the matrix corresponding to recontree

L0 is a matrix where the crown age is at 0; for internal use only

Author(s)

Rampal S. Etienne

See Also

```
pbd_sim_cpp
```

Examples

```
pbd_sim(c(0.2,1,0.2,0.1,0.1),15)
```

pbd_sim_cpp

Function to simulate the approximate protracted speciation process

Description

Simulating the protracted speciation process according to the approximate model of Lambert et al. 2014. This function differs from pbd_sim that 1) it requires that the speciation-initiation rate is the same for good and incipient species, and 2) that it does not simulate the exact protracted speciation process, but an approximation made by the coalescent point process.

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Usage

```
pbd_sim_cpp(
 pars,
 parsf = c(function(t,pars) {pars[1]},function(t,pars) {pars[2]},
function(t,pars) {pars[3]},function(t,pars) {pars[4]}),
  age,
  soc = 2,
 plotltt = 1,
 methode = "lsoda"
```

Arguments

pars

Vector of parameters:

pars[1] corresponds to b (= la_1 in Etienne & Rosindell R2012) = speciation initiation rate

pars[2] corresponds to mu_1 (= mu_g in Etienne & Rosindell 2012) = extinction rate of good species

pars[3] corresponds to la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate

pars[4] corresponds to mu_2 (= mu_i in ER2012) = extinction rate of incipient species

When rates depend on time this time dependence should be specified in pars1f and pars1 then becomes the parameters used in pars1f

parsf

Vector of functions how the rates depend on time, default functions are constant functions of the parameters in pars1:

parsf[1] corresponds to time-dependence of b (= la_1 in Etienne & Rosindell R2012) = speciation initiation rate

parsf[2] corresponds to time-dependence of mu_1 (= mu_g in Etienne & Rosindell 2012) = extinction rate of good species

parsf[3] corresponds to tiem-dependence of la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate

parsf[4] corresponds to time-dependence of mu_2 (= mu_i in ER2012) = extinction rate of incipient species

Sets the crown age for the simulation age

Determines whether the simulation should start at stem (1) or crown (2) age

plotltt Sets whether the lineage-through-time plot should be plotted (1) or not (0)

Sets which method should be used in the ode-solver. Default is 'Isoda'. See

soc

methode

package deSolve for details.

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Value

A set of branching times

Author(s)

Rampal S. Etienne

See Also

```
pbd_sim
```

Examples

```
pbd_sim_cpp(pars = c(0.2,1,0.2,0.1), age = 15)
```

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