

Package ‘PBD’

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Type Package

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Suggests knitr, rmarkdown, testthat

Description Conducts maximum likelihood analysis and simulation of the
protracted birth-death model of diversification. See
Etienne, R.S. & J. Rosindell 2012 <[doi:10.1093/sysbio/syr091](https://doi.org/10.1093/sysbio/syr091)>;
Lambert, A., H. Morlon & R.S. Etienne 2014, <[doi:10.1007/s00285-014-0767-x](https://doi.org/10.1007/s00285-014-0767-x)>;
Etienne, R.S., H. Morlon & A. Lambert 2014, <[doi:10.1111/evo.12433](https://doi.org/10.1111/evo.12433)>.

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URL <https://github.com/rsetienne/PBD>

BugReports <https://github.com/rsetienne/PBD/issues>

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pbd_bootstrap	<i>Bootstrap analysis under protracted birth-death model of diversification</i>
---------------	---

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.

Usage

```
pbd_bootstrap(
  brts,
  initparsopt = c(0.2, 0.1, 1),
  idparsopt = 1:length(initparsopt),
  idparsfix = NULL,
  parsfix = NULL,
  exteq = (length(initparsopt) < 4),
```

```

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-04, 1e-04, 1e-06),
maxiter = 1000 * round((1.25)^length(idparsopt)),
endmc = 100,
seed = 42,
optimmethod = "subplex",
num_cycles = 1,
verbose = FALSE
)

```

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

<code>missnumspec</code>	The number of species that are in the clade but missing in the phylogeny
<code>cond</code>	Conditioning: <code>cond == 0</code> : conditioning on stem or crown age <code>cond == 1</code> : conditioning on stem or crown age and non-extinction of the phylogeny
<code>btorph</code>	Sets whether the likelihood is for the branching times (0) or the phylogeny (1)
<code>soc</code>	Sets whether the first element of the branching times is the stem (1) or the crown (2) age
<code>plotlitt</code>	Sets whether the lineage-through-time plot should be plotted (1) or not (0)
<code>methode</code>	Sets which method should be used in the ode-solver. Default is 'lsoda'. See package <code>deSolve</code> for details.
<code>n_low</code>	Sets the lower bound of the number of species on which conditioning should be done when <code>cond = 2</code> . Set this to 0 when conditioning should be done on precisely the number of species (default)
<code>n_up</code>	Sets the upper bound of the number of species on which conditioning should be done when <code>cond = 2</code> . Set this to 0 when conditioning should be done on precisely the number of species (default)
<code>tol</code>	Sets the tolerances in the optimization. Consists of: <code>reltolx</code> = relative tolerance of parameter values in optimization <code>reltolf</code> = relative tolerance of function value in optimization <code>abstolx</code> = absolute tolerance of parameter values in optimization
<code>maxiter</code>	Sets the maximum number of iterations in the optimization
<code>endmc</code>	Sets the number of simulations for the bootstrap
<code>seed</code>	Sets the seed for the simulations of the bootstrap
<code>optimmethod</code>	Method used in optimization of the likelihood. Current default is 'subplex'. Alternative is 'simplex' (default of previous versions)
<code>num_cycles</code>	Number of cycles of the optimization (default is 1).
<code>verbose</code>	if TRUE, explanatory text will be shown

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:

<code>ntips</code>	gives the number of tips
<code>b</code>	gives the maximum likelihood estimate of <code>b</code>
<code>mu_1</code>	gives the maximum likelihood estimate of <code>mu_1</code>
<code>la_1</code>	gives the maximum likelihood estimate of <code>la_1</code>
<code>mu_2</code>	gives the maximum likelihood estimate of <code>mu_2</code>
<code>loglik</code>	gives the maximum loglikelihood

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

Author(s)

Rampal S. Etienne

See Also

[pbd_ML](#)

pbd_brts_density	<i>Node depth probability density for protracted birth-death model of diversification</i>
------------------	---

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 μ_1 (= μ_g in Etienne & Rosindell 2012) = extinction rate of good species
`pars1[3]` corresponds to λ_1 (= λ_2 in Etienne & Rosindell 2012) = speciation completion rate
`pars1[4]` corresponds to μ_2 (= μ_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`

<code>pars1f</code>	Vector of functions how the rates depend on time, default functions are constant functions of the parameters in <code>pars1</code>: <code>pars1f[1]</code> corresponds to time-dependence of b (= λ_1 in Etienne & Rosindell 2012) = speciation initiation rate <code>pars1f[2]</code> corresponds to time-dependence of μ_1 (= μ_g in Etienne & Rosindell 2012) = extinction rate of good species <code>pars1f[3]</code> corresponds to time-dependence of λ_1 (= λ_2 in Etienne & Rosindell 2012) = speciation completion rate <code>pars1f[4]</code> corresponds to time-dependence of μ_2 (= μ_i in ER2012) = extinction rate of incipient species
<code>methode</code>	sets which method should be used in the ode-solver. Default is 'lsoda'. See package <code>deSolve</code> for details.
<code>brts</code>	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 birth-death 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

Usage

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

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 μ_2 (= μ_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	<i>Probability density for duration of speciation under protracted birth-death model of diversification</i>
---------------------	---

Description

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

Usage

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

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 μ_2 (= μ_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	<i>Mean duration of speciation under protracted birth-death model of diversification</i>
------------------	--

Description

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

Usage

```
pbd_durspec_mean(pars)
```

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_mean_impl *Actual calculation of the mean duration of speciation (equations 19 and 20 of reference article) assuming all inputs are correct*

Description

Actual calculation of the mean duration of speciation (equations 19 and 20 of reference article) assuming all inputs are correct

Usage

pbd_durspec_mean_impl(la2, la3, mu2)

Arguments

la2	lambda_2, the speciation completion rate, in probability per time unit
la3	lambda_3, speciation initiation rate of incipient species, in probability per time unit
mu2	mu_2 extinction rate of the incipient species, in probability per time unit

Author(s)

Rampal S. Etienne

References

Etienne, Rampal S., and James Rosindell. "Prolonging the past counteracts the pull of the present: protracted speciation can explain observed slowdowns in diversification." *Systematic Biology* 61.2 (2012): 204-213.

See Also

pbd_mean_durspec

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

Usage

pbd_durspec_mode(pars)

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 μ_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))
```

<code>pbd_durspec_moment</code>	<i>Moments of duration of speciation under protracted birth-death model of diversification</i>
---------------------------------	--

Description

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

Usage

```
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 μ_2 (= μ_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

Usage

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

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
p	Quantile (e.g. p = 0.5 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	<i>Variance in duration of speciation under protracted birth-death model of diversification</i>
-----------------	---

Description

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

Usage

```
pbd_durspec_var(pars)
```

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 μ_2 (= μ_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

Usage

```
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),
  brts,
  misnumspec = 0
)

```

Arguments

pars1	Vector of parameters: pars1[1] corresponds to b (= la_1 in Etienne & Rosindell R2012) = speciation initiation rate pars1[2] corresponds to μ_1 (= μ_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 μ_2 (= μ_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 μ_1 (= μ_g in Etienne & Rosindell 2012) = extinction rate of good species pars1f[3] corresponds to time-dependence of la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate pars1f[4] corresponds to time-dependence of μ_2 (= μ_i in ER2012) = extinction rate of incipient species
pars2	Vector of model settings: pars2[1] sets 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.

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	<i>Bootstrap likelihood ratio test of protracted birth-death model of diversification</i>
--------	---

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.

Usage

```

pbd_LR(
  brts,
  initparsoptPBD,
  initparsoptCR,
  missnumspec,
  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-06, 1e-06, 1e-06),
  maxiter = 2000,
  optimmethod = "subplex",
  num_cycles = num_cycles,
  verbose = FALSE
)

```

Arguments

<code>brts</code>	A set of branching times of a phylogeny, all positive
<code>initparsoptPBD</code>	The initial values of the parameters that must be optimized for the protracted birth-death (PBD) model: <code>b</code> , <code>mu</code> and <code>lambda</code>
<code>initparsoptCR</code>	The initial values of the parameters that must be optimized for the constant-rates (CR) model: <code>b</code> and <code>mu</code>
<code>missnumspec</code>	The number of species that are in the clade but missing in the phylogeny
<code>outputfilename</code>	The name (and location) of the file where the output will be saved. Default is no save.
<code>seed</code>	The seed for the pseudo random number generator for simulating the bootstrap data
<code>endmc</code>	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 phylogeny 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) 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.
btorph	Sets whether the likelihood is for the branching times (0) or the phylogeny (1)
soc	Sets whether stem or crown age should be used (1 or 2)
methode	The numerical method used to solve the master equation, such as 'lsoda' or 'ode45'.
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'.
num_cycles	Number of cycles of the optimization (default is 1).
verbose	if TRUE, explanatory text will be shown

Details

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 protracted birth-death and constant-rates models \$model - the model used to generate 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 \$b_PBD1 - speciation-initiation rate estimated under PBD for first set of initial values \$mu_PB1 - extinction rate estimated under DD for first set of initial values \$lambda_PB1 - speciation-completion rate estimated under PBD for first set of initial values \$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-initiation 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 significance level alpha
poweroftest	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

[pbid_loglik](#), [pbid_ML](#)

pbd_mean_durspec	<i>Calculate the mean duration of speciation (equations 19 and 20 of reference article), non-vectorized</i>
------------------	---

Description

Calculate the mean duration of speciation (equations 19 and 20 of reference article), non-vectorized

Usage

```
pbd_mean_durspec(eri, scr, siri)
```

Arguments

eri	one single extinction rate of the incipient species, or mu_2 in article, in probability per time unit
scr	one single speciation completion rate, or lambda_2 in article, in probability per time unit
siri	one single speciation initiation rate of incipient species, or lambda_3 in article, in probability per time unit

Value

the means duration of speciation, in time units

Author(s)

Richel J.C. Bilderbeek

References

Etienne, Rampal S., and James Rosindell. "Prolonging the past counteracts the pull of the present: protracted speciation can explain observed slowdowns in diversification." *Systematic Biology* 61.2 (2012): 204-213.

Examples

```
eri <- 0.1 # extinction rate of incipient species
scr <- 0.2 # speciation completion rate
siri <- 0.3 # speciation initiation rate of incipient species
mean_durspec <- pbd_mean_durspec(eri, scr, siri)
expected_mean_durspec <- 2.829762
testthat::expect_equal(mean_durspec, expected_mean_durspec,
  tolerance = 0.000001)
```

pbd_mean_durspecs	<i>Calculate the mean durations of speciation (equations 19 and 20 of reference article)</i>
-------------------	--

Description

Calculate the mean durations of speciation (equations 19 and 20 of reference article)

Usage

```
pbd_mean_durspecs(eris, scrs, siris)
```

Arguments

eris	one or more extinction rates of the incipient species, or mu_2 in article, in probability per time unit. These values will be recycled if needed
scrs	one or more speciation completion rates, or lambda_2 in article, in probability per time unit. These values will be recycled if needed
siris	one or more speciation initiation rates of incipient species, or lambda_3 in article, in probability per time unit. These values will be recycled if needed

Value

the means durations of speciation, in time units. Puts an NA at each invalid combination of inputs

Author(s)

Richel J.C. Bilderbeek

References

Etienne, Rampal S., and James Rosindell. "Prolonging the past counteracts the pull of the present: protracted speciation can explain observed slowdowns in diversification." *Systematic Biology* 61.2 (2012): 204-213.

See Also

pbd_mean_durspec

Examples

```
eris <- c(0.1, 0.2) # extinction rates of incipient species
scrs <- c(0.2, 0.3) # speciation completion rates
siris <- c(0.3, 0.4) # speciation initiation rates of incipient species
mean_durspecs <- pbd_mean_durspecs(eris, scrs, siris)
expected_mean_durspecs <- c(2.829762, 1.865386)
testthat::expect_equal(mean_durspecs, expected_mean_durspecs,
  tolerance = 0.000001)
```

pbd_ML	<i>Maximization of loglikelihood under protracted birth-death model of diversification</i>
--------	--

Description

Likelihood maximization for protracted birth-death model of diversification

Usage

```
pbd_ML(
  brts,
  initparsopt = c(0.2, 0.1, 1),
  idparsopt = 1:length(initparsopt),
  idparsfix = NULL,
  parsfix = NULL,
  exteq = 1,
  parsfunc = c(function(t, pars) {
    pars[1]
  }, function(t, pars) {
    pars[2]
  },
  function(t, pars) {
    pars[3]
  }, function(t, pars) {
    pars[4]
  }),
  misnumspec = 0,
  cond = 1,
  btorph = 1,
  soc = 2,
  methode = "lsoda",
  n_low = 0,
  n_up = 0,
  tol = c(1e-06, 1e-06, 1e-06),
  maxiter = 1000 * round((1.25)^length(idparsopt)),
  optimmethod = "subplex",
  num_cycles = 1,
  verbose = TRUE
)
```

Arguments

<code>brts</code>	A set of branching times of a phylogeny, all positive
<code>initparsopt</code>	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 phylogeny 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
methode	Sets which method should be used in the ode-solver. Default is 'lsoda'. 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)
num_cycles	Number of cycles of the optimization (default is 1).
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 freedom
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)
```

pbd_numspec_mean	<i>Mean number of species under protracted birth-death model of diversification</i>
------------------	---

Description

pbd_numspec_mean computes the mean number of species under the protracted speciation model for a given set of parameters

Usage

```
pbd_numspec_mean(
  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,
    methode = "lsoda"
  )

```

Arguments

<code>pars</code>	Vector of parameters: <code>pars[1]</code> corresponds to b (= $la_1 = la_3$ in Etienne & Rosindell R2012) = speciation initiation rate <code>pars[2]</code> corresponds to μ_1 (= μ_g in ER2012) = extinction rate of good species <code>pars[3]</code> corresponds to la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate <code>pars[4]</code> corresponds to μ_2 (= μ_i in ER2012) = extinction rate of incipient species
<code>parsf</code>	Vector of functions how the rates depend on time, default functions are constant functions of the parameters in <code>pars1</code>: <code>parsf[1]</code> corresponds to time-dependence of b (= la_1 in Etienne & Rosindell R2012) = speciation initiation rate <code>parsf[2]</code> corresponds to time-dependence of μ_1 (= μ_g in Etienne & Rosindell 2012) = extinction rate of good species <code>parsf[3]</code> corresponds to time-dependence of la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate <code>parsf[4]</code> corresponds to time-dependence of μ_2 (= μ_i in ER2012) = extinction rate of incipient species
<code>age</code>	the stem or crown age (see <code>soc</code>)
<code>soc</code>	specify whether it is the stem or the crown age
<code>methode</code>	Sets which method should be used in the ode-solver. Default is 'lsoda'. See package <code>deSolve</code> for details.

Details

The number of representative species at time $t = T$ when starting with one lineage at time $t = 0$ is geometrically distributed with parameter equal to $g(T)$ where $g(T)$ follows from the set of ODEs in Etienne et al. 2014.

Value

The expected number of representative species

Author(s)

Rampal S. Etienne

See Also

[pbd_numspec_quantile](#)
[pbd_numspec_median](#)

Examples

```
pbd_numspec_mean(pars = c(0.3,0.1,0.5,0.1), age = 10, soc = 2)
```

pbd_numspec_median	<i>Median number of species under protracted birth-death model of diversification</i>
--------------------	---

Description

pbd_numspec_median computes the median number of species under the protracted speciation model for a given set of parameters

Usage

```
pbd_numspec_median(
  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,
  methode = "lsoda"
)
```

Arguments

pars Vector of parameters:

pars[1] corresponds to b (= $\lambda_{a1} = \lambda_{a3}$ in Etienne & Rosindell R2012) = speciation initiation rate
 pars[2] corresponds to μ_{a1} (= μ_{a_g} in ER2012) = extinction rate of good

	species pars[3] corresponds to λ_1 (= λ_2 in Etienne & Rosindell 2012) = speciation completion rate pars[4] corresponds to μ_2 (= μ_i in ER2012) = extinction rate of incipient species
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 (= λ_1 in Etienne & Rosindell R2012) = speciation initiation rate parsf[2] corresponds to time-dependence of μ_1 (= μ_g in Etienne & Rosindell 2012) = extinction rate of good species parsf[3] corresponds to time-dependence of λ_1 (= λ_2 in Etienne & Rosindell 2012) = speciation completion rate parsf[4] corresponds to time-dependence of μ_2 (= μ_i in ER2012) = extinction rate of incipient species
age	the stem or crown age (see soc)
soc	specify whether it is the stem or the crown age
methode	Sets which method should be used in the ode-solver. Default is 'lsoda'. See package deSolve for details.

Value

The mean number of representative species

Author(s)

Rampal S. Etienne

See Also

[pbd_numspec_quantile](#)
[pbd_numspec_mean](#)

Examples

```
pbd_numspec_median(pars = c(0.3,0.1,0.5,0.1), age = 10, soc = 2)
```

pbd_numspec_quantile *Number of species for a given quantile under protracted birth-death model of diversification*

Description

pbd_numspec_quantile computes the number of species for a given quantile under the protracted speciation model for a given set of parameters

Usage

```
pbd_numspec_quantile(
  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,
  methode = "lsoda",
  quantile
)
```

Arguments

pars	Vector of parameters: pars[1] corresponds to b (= $la_1 = la_3$ in Etienne & Rosindell R2012) = speciation initiation rate pars[2] corresponds to μ_1 (= μ_g in ER2012) = extinction rate of good species pars[3] corresponds to la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate pars[4] corresponds to μ_2 (= μ_i in ER2012) = extinction rate of incipient species
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 μ_1 (= μ_g in Etienne & Rosindell 2012) = extinction rate of good species
 parsf[3] corresponds to time-dependence of λ_1 (= λ_2 in Etienne & Rosindell 2012) = speciation completion rate
 parsf[4] corresponds to time-dependence of μ_2 (= μ_i in ER2012) = extinction rate of incipient species

age	the stem or crown age (see soc)
soc	specify whether it is the stem or the crown age
methode	Sets which method should be used in the ode-solver. Default is 'lsoda'. See package deSolve for details.
quantile	the quantile

Value

The number of species at a given quantile

Author(s)

Rampal S. Etienne

See Also

[pbd_numspec_mean](#)
[pbd_numspec_median](#)

Examples

```
pbd_numspec_quantile(pars = c(0.3,0.1,0.5,0.1), age = 10, soc = 2, quantile = 0.95)
```

pbd_numspec_vec	<i>Mean number of good and incipient species under protracted birth-death model of diversification</i>
-----------------	--

Description

pbd_numspec_vec computes the mean number of good and incipient species under the protracted speciation model for a given set of parameters

Usage

```
pbd_numspec_vec(pars, age, initvec = c(1, 0))
```

Arguments

pars	Vector of parameters: pars[1] corresponds to b_G (= la_1 in Etienne & Rosindell R2012) = speciation initiation rate of good species pars[2] corresponds to b_I (= la_3 in Etienne & Rosindell R2012) = speciation initiation rate of incipient species pars[3] corresponds to mu_G = extinction rate of good species pars[4] corresponds to mu_I = extinction rate of incipient species pars[5] corresponds to la (= la_2 in Etienne & Rosindell 2012) = speciation completion rate
age	the stem age
initvec	initial vector of good and incipient species. Default is 1 good species.

Details

The result follows from a simple 2D system of differential equations for G and I.

Value

The expected number of good and incipient species

Author(s)

Rampal S. Etienne

See Also

[pbd_numspec_mean](#)
[pbd_numspec_quantile](#)
[pbd_numspec_median](#)

Examples

```
pbd_numspec_vec(pars = c(0.3,0.3,0.1,0.1,0.2), age = 10)
```

pbd_numspec_vec2	<i>Mean number of good species with n incipient species and of n orphaned incipient species under protracted birth-death model of diversification</i>
------------------	---

Description

pbd_numspec_vec2 computes the mean number of good species with n incipient daughter species and the number of cases with n orphaned incipient siblings under the protracted speciation model for a given set of parameters

Usage

```
pbd_numspec_vec2(
  pars = c(0.3, 0.3, 0.1, 0.1, 100),
  age = 10,
  initvec = c(1, rep(0, 20)),
  abstolint = 1e-10,
  reltolint = 1e-10,
  methode = "odeint::runge_kutta_cash_karp54"
)
```

Arguments

pars	Vector of parameters: pars[1] corresponds to b_G (= la_1 in Etienne & Rosindell R2012) = speciation initiation rate of good species pars[2] corresponds to b_I (= la_3 in Etienne & Rosindell R2012) = speciation initiation rate of incipient species pars[3] corresponds to mu_G = extinction rate of good species pars[4] corresponds to mu_I = extinction rate of incipient species pars[5] corresponds to la (= la_2 in Etienne & Rosindell 2012) = speciation completion rate
age	the stem age
initvec	initial vector. Default is 1 good species with 0 incipient species.
abstolint	absolute tolerance in integration
reltolint	relative tolerance in integration
methode	integration method, one of the odeint solvers

Value

The expected number of good species with n incipient species and the number of cases with n orphaned incipient siblings

Author(s)

Rampal S. Etienne

See Also

[pbd_numspec_mean](#)
[pbd_numspec_quantile](#)
[pbd_numspec_median](#)
[pbd_numspec_vec](#)

Examples

```
pbd_numspec_vec2(pars = c(0.3,0.3,0.1,0.1,0.2), age = 10)
```

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,
  add_shortest_and_longest = FALSE
)
```

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
plotit	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.
add_shortest_and_longest	Gives the output of the new samplemethods 'shortest' and 'longest'.

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
 - 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_checked

Checked and safer version of PBD::pbd_sim

Description

Checked and safer version of PBD::pbd_sim

Usage

```
pbd_sim_checked(
  erg,
  eri,
  scr,
  sirg,
  siri,
  stem_age = NULL,
  crown_age = NULL,
  max_n_taxa = Inf,
  add_shortest_and_longest = FALSE
)
```

Arguments

erg	extinction rate of a good species
eri	extinction rate of an incipient species
scr	speciation completion rate
sirg	speciation initiation rate of a good species
siri	speciation initiation rate of an incipient species
stem_age	stem age. Set either the stem age or the crown age.
crown_age	crown age. Set either the stem age or the crown age.
max_n_taxa	maximum number of taxa. If this value is exceeded, the simulation is aborted and removed.
add_shortest_and_longest	Gives the output of the new samplemethods 'shortest' and 'longest'.

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.

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,
  ntips = NULL,
  soc = 2,
  plotlft = 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 μ_1 (= μ_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 μ_2 (= μ_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 μ_1 (= μ_g in Etienne & Rosindell 2012) = extinction rate of good species parsf[3] corresponds to time-dependence of la_1 (= la_2 in Etienne & Rosindell 2012) = speciation completion rate parsf[4] corresponds to time-dependence of μ_2 (= μ_i in ER2012) = extinction rate of incipient species
age	Sets the crown age for the simulation
ntips	Set the number of tips. If NULL (default) the number of tips will be sampled
soc	Determines whether the simulation should start at stem (1) or crown (2) age
plotlft	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 'lsoda'. See package deSolve for details.

Value

A set of branching times

Author(s)

Rampal S. Etienne

See Also

[pbdd_sim](#)

Examples

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

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