

Package ‘popbio’

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Title Construction and Analysis of Matrix Population Models

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Suggests quadprog

Description

Construct and analyze projection matrix models from a demography study of marked individuals classified by age or stage. The package covers methods described in Matrix Population Models by Caswell (2001) and Quantitative Conservation Biology by Morris and Doak (2002).

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Description

Popbio is a package for the construction and analysis of matrix population models. First, the package consists of the R translation of Matlab code found in Caswell (2001) or Morris and Doak (2002). A list of converted functions within each book can be accessed using `help(Caswell)` and `help(Morris)` within R, or by following the links to [02.Caswell](#) and [03.Morris](#) from the help content pages.

Second, the popbio package includes functions to estimate vital rates and construct projection matrices from raw census data typically collected in plant demography studies. In these studies, vital rates can often be estimated directly from annual censuses of tagged individuals using transition frequency tables. To estimate vital rates in animal demography using capture-recapture methods, try the Rcapture or mra package instead.

Finally, the package includes plotting methods and sample datasets consisting of either published projection matrices or annual census data from demography studies. Three sample demonstrations illustrate some of the package capabilities (`Caswell`, `fillmore` and `stage.classify`). A description of the package in the Journal of Statistical Software is available at <http://www.jstatsoft.org/v22/i11>.

Author(s)

Chris Stubben

References

To cite the popbio package in publications, type `citation('popbio')`. For details on matrix population models, see

Caswell, H. 2001. Matrix population models: Construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

Description

Chapter 2. Age-classified matrix models

[pop.projection](#) section 2.2. Projection of population growth rates.

Chapter 4. Stage-classified matrix models

`lambda` section 4.4. Returns the dominant eigenvalue
`stable.stage` section 4.5. Returns the stable stage distribution (right eigenvector)
`reproductive.value` section 4.6. Returns the reproductive value (left eigenvector)
`damping.ratio` section 4.7. Returns the damping ratio
`eigen.analysis` section 4.8. Computes eigenvalues and vectors, including the dominant eigenvalue, stable stage distribution, reproductive value, damping ratio, sensitivities, and elasticities. Since version 2.0, these are now included as separate functions as well

Chapter 5. Events in the Life Cycle

`fundamental.matrix` section 5.3.1. Calculate age-specific survival from a stage classified matrix using the fundamental matrix N
`net.reproductive.rate` section 5.3.4. Calculate the net reproductive rate of a stage classified matrix using the dominant eigenvalue of the matrix R.
`generation.time` section 5.3.5. Calculate the generation time of a stage-classified matrix

Age-specific survivorship and fertility curves in Fig 5.1 and 5.2 are now included in `demo(Caswell)`.

Chapter 6. Parameter estimation

`projection.matrix` section 6.1.1. Estimate vital rates and construct a projection matrix using transition frequency tables
`QPmat` section 6.2.2. Construct a projection matrix from a time series of individuals per stage using Wood's quadratic programming method. Requires `quadprog` library.

Chapter 9. Sensitivity analysis

`sensitivity` section 9.1. Calculate sensitivities
`elasticity` section 9.2. Calculate elasticities
`secder` section 9.7. Second derivatives of eigenvalues

Chapter 10. Life Table Response Experiments

`LTRE` section 10.1 and 10.2. Fixed designs in LTREs. See `demo(Caswell)` for variance decomposition in random design (Fig 10.10).

Chapter 12. Statistical inference

`boot.transitions` section 12.1.4. Resample observed census transitions in a stage-fate data frame
`resample` section 12.1.5.2. Resample transitions in a projection matrix from a multinomial distribution (and fertilities from a log normal)

Chapter 14. Environmental stochasticity

`stoch.growth.rate` section 14.3. Calculate the log stochastic growth rate by simulation and Tuljapukar's approximation
`stoch.sens` section 14.4.1. Sensitivity and elasticity of stochastic growth rate from numerical simulations

[stoch.projection](#) section 14.5.3. Project stochastic growth from a sequence of matrices in a uniform and nonuniform environment

Chapter 15. Demographic stochasticity

[multiresultm](#) section 15.1.3. Incorporate demographic stochasticity into population projections. The example uses the [whale](#) dataset to create a plot like figure 15.3.

Author(s)

Chris Stubben

03.Morris

Converted Matlab functions from Morris and Doak (2002)

Description

Chapter 3

[grizzly](#) Table 3.1. Grizzly bear population counts. The example includes code to calculate mean, variance and confidence intervals using regression and other procedures

[extCDF](#) Box 3.3. Count-based extinction time cumulative distribution function

[countCDFxt](#) Box 3.4. Count-based extinction probabilities with bootstrap confidence intervals

Chapter 7

[stoch.projection](#) Box 7.3. Project stochastic growth from a sequence of matrices

[stoch.growth.rate](#) Box 7.4. Calculate the log stochastic growth rate by Tuljapukar's approximation and by simulation

[stoch.quasi.ext](#) Box 7.5. Estimate quasi-extinction threshold

Chapter 8

[Kendall](#) Box 8.2. Kendall's method to correct for sampling variation

[betaval](#) Box 8.3. Generate beta-distributed random numbers

[lnorms](#) Box 8.4. Generate random lognormal values

[stretchbetaval](#) Box 8.5. Generate stretched beta-distributed random numbers

[vitalsim](#) Box 8.10. Calculate stochastic growth rate and extinction time CDF using vital rates

[multiresultm](#) Box 8.11. Incorporate demographic stochasticity into population projections

Chapter 9

[vitalsens](#) Box 9.1. Vital rate sensitivity and elasticity

aq.census

Annual census data for Aquilegia chrysantha

Description

Demography census data from *Aquilegia chrysantha* in Fillmore Canyon, Organ Mountains, New Mexico, 1996-2003.

Usage

aq.census

Format

A data frame with 2853 rows on the following 8 variables:

plot Plot number

year Year of census

plant Plant id number

status Plant status recorded in field: dead, dormant, recruit0 (with cotyledons only), recruit1, flowering or vegetative.

rose Total number of rosettes

leaf Total number of leaves

infl Total number of inflorescences or flowering stalks

fruits Total number of mature fruits

Details

This sample data set includes census data from 10 of the 15 total demography plots established in 1995.

Source

Data set owners: Brook Milligan, Chris Stubben, Allan Strand

See Also

[aq.trans](#) for annual transitions with stage and fate in same row

Examples

```
head2(aq.census)
sv <- table(aq.census$status, aq.census$year)
sv
stage.vector.plot(sv[-1, ], prop = FALSE)
```

aq.matrix *Create a projection matrix for Aquilegia*

Description

Creates a projection matrix for *Aquilegia* from annual transition data, assuming new seeds and seed bank seeds have an equal chance for successful germination and equal survival rates.

Usage

```
aq.matrix(trans, recruits, summary = TRUE, seed.survival = 0.126,
          seed.bank.size = 10000, seeds.per.fruit = 120, ...)
```

Arguments

trans	A data frame with transitions listing ordered stages and fates and counts of mature fruits
recruits	The number of observed recruits in year $t + 1$.
summary	Output projection matrix and summaries. Otherwise output transition table with added individual fertilities.
seed.survival	Estimated seed survival rate for both new seeds and seed bank. Default is 12.6 percent survival.
seed.bank.size	Estimated size of the seed bank. Seed bank and new seeds contribute to a common germinant pool with equal chance for germination. Default is 10,000 seeds in seed bank.
seeds.per.fruit	The number of seeds produced per mature fruit. Default is 120 seeds.
...	additional arguments passed to projection.matrix

Details

Adds individual fertilities to annual transitions using a prebreeding census.

Value

If summary is TRUE, a list with

recruits	total number of recruits
seed.survival	seed survival rate
seed.bank	total number of seeds in seed bank
seeds.from.plants	total number of new seeds just released from fruits
recruitment.rate	recruitment rate calculated as $\text{recruits}/(\text{seed.bank.size} + \text{seeds.from.plants})$
A	projection matrix

lambda population growth rate
 n initial population vector
 n1 final population vector

If summary is FALSE, a data frame with individual fertilities added to the transition data frame only.

Author(s)

Chris Stubben

See Also

[projection.matrix](#)

Examples

```
x <- subset(aq.trans, year==1996)
## number of recruits in 1997
rec <- nrow(subset(aq.trans, year==1997 & stage == "recruit"))
aq.matrix(x, recruits=rec)
aq.matrix(x, recruits=rec, seed.survival=.7, seed.bank=3000)
```

aq.trans

Annual transition data for Aquilegia chrysantha

Description

Transition data listing stages and fates from *Aquilegia chrysantha* in Fillmore Canyon, Organ Mountains, New Mexico, 1996-2003.

Usage

aq.trans

Format

A data frame with 1637 rows on the following 9 variables:

plot Plot number
 year Starting year of census
 plant Plant id number
 stage Initial stage class with ordered factor levels seed < recruit < small < large < flower.
 leaf Total number of leaves
 rose Total number of rosettes
 fruits Total number of mature fruits
 fate Final stage class or fate with levels seed < recruit < small < large < flower < dead
 rose2 Final number of rosettes

Details

The five stage classes include seeds in the seed bank, new recruits or seedlings, small vegetative plants with 1 rosette, large vegetative plants with 2 or more rosettes, and flowering plants. Stage classes were assigned to census plants using a combination of status and size data recorded in the field. See `demo(stage.classify)` for more details.

Source

Data set owners: Brook Milligan, Chris Stubben, Allan Strand

See Also

[aq.census](#)

Examples

```
head2(aq.trans)
sv <- table(aq.trans$stage, aq.trans$year)
addmargins(sv)
stage.vector.plot(sv[-1, ], prop = FALSE, main = "Aquilegia stage vectors")
## plot proportions with barplot
## use xpd to draw legend outside plot boundaries
op <- par(mar = c(5, 4, 4, 1), xpd = TRUE)
x <- barplot(prop.table(sv[-1, ], 2),
  las = 1, col = rainbow(4), ylim = c(0, 1),
  xaxt = "n", space = .5, xlab = "Year", ylab = "Proportion in stage class"
)
yrs <- substr(colnames(sv), 3, 4)
axis(1, x, yrs)
legend(2.7, 1.25, rev(rownames(sv)[-1]), fill = rev(rainbow(4)), bty = "n", ncol = 2)
par(op)
```

betaval

Generate beta-distributed random numbers

Description

Calculates a random number from a beta distribution and uses the R function `pbeta(x,vv,ww)`.

Usage

```
betaval(mn, sdev, fx = runif(1))
```

Arguments

mn	mean rate between 0 and 1
sdev	standard deviation
fx	cumulative distribution function, default is a random number between 0 and 1

Details

This function is used by [vitalsim](#)

Value

a random beta value

Author(s)

Original MATLAB code by Morris and Doak (2002: 277- 278), adapted to R by Patrick Nantel, 20 June 2005

Source

converted Matlab code from Box 8.3 in Morris and Doak (2002)

References

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

See Also

Beta Distribution [rbeta](#)

Examples

```
betaval(.5, sd=.05)
betaval(.5, sd=.05)
## histogram with mean=0.5 and sd=0.05
x <- sapply(1:100, function(x) betaval(0.5, 0.05))
hist(x, seq(0,1,.025), col="green", ylim=c(0,25), xlab="Value",
main="Beta distribution with mean=0.5 and sd=0.05")
# generates a graph similar to Figure 8.2 A in Morris & Doak (2002:264)
# a much simpler version of BetaDemo in Box 8.3
x <- matrix(numeric(3*1000), nrow=3)
sd <-c(.05, .25, .45)
for (i in 1:3){
  for (j in 1:1000){
    x[i,j]<-betaval(.5,sd[i])
  }
}
plot(0,0,xlim=c(0,1), ylim=c(0,0.4), type='n', ylab='Frequency',
xlab='Value', main="Examples of beta distributions")
for (i in 1:3){
  h <- hist(x[i,], plot=FALSE, breaks=seq(0,1,.02) )
  lines(h$mids, h$counts/1000, type='l', col=1+i, lwd=2, lty=i)
}
legend(0.5,0.4, c("(0.50, 0.05)", "(0.50, 0.25)", "(0.50, 0.45)"),
lty=1:3, lwd=2, col=2:4, title="mean and sd")
```

boot.transitions	<i>Bootstrap observed census transitions</i>
------------------	--

Description

Calculate bootstrap distributions of population growth rates (λ), stage vectors, and projection matrix elements by randomly sampling with replacement from a stage-fate data frame of observed transitions

Usage

```
boot.transitions(transitions, iterations, by.stage.counts = FALSE, ...)
```

Arguments

transitions	a stage-fate data frame with stage or age class in the current census, fate in the subsequent census, and one or more fertility columns
iterations	Number of bootstrap iterations
by.stage.counts	Resample transitions with equal probability (default) or by subsets of initial stage counts
...	additional options passed to projection.matrix

Value

A list with 3 items

lambda	A vector containing bootstrap values for λ
matrix	A matrix containing bootstrap transition matrices with one projection matrix per row.
vector	A matrix containing bootstrap stage vectors with one stage vector per row.

Author(s)

Chris Stubben

References

see Morris and Doak 2005 in <http://esapubs.org/Archive/mono/M075/004/appendix-A.htm> for resampling by stage class counts

See Also

[projection.matrix](#)

Examples

```

## create stage-fate dataframe using merge and subset
trans01 <- subset(
  merge(test.census, test.census, by="plant", sort=FALSE),
  year.x==2001 & year.y==2002)
## format column and row names
trans01 <- trans01[,c(1:4,6)]
colnames(trans01)[2:5] <- c("year", "stage", "fruits", "fate")
rownames(trans01) <- 1:nrow(trans01)
# order stage columns corresponding to matrix
trans01$stage <- ordered(trans01$stage,
  levels = c("seedling", "vegetative", "reproductive"))
## add individual fertilities using prebreeding census with no seed bank
## based on the proportional reproductive outputs of flowering plants
## and the total number of seedlings at the end of the projection interval
seedlings <- nrow(subset(test.census, year==2002 & stage=="seedling"))
trans01$seedling <- trans01$fruits/sum(trans01$fruits) * seedlings
trans01
## Step by step instructions for bootstrapping dataframe
n <- nrow(trans01)
n
set.seed(77)
x <- sample(n, replace=TRUE)
x
bt <- trans01[x,]
bt
projection.matrix(bt)
## or respample by stage class counts
lapply(split(trans01, trans01$stage, drop=TRUE),
  function(x) x[sample(nrow(x), replace=TRUE),])
## using boot.transitions
boot.transitions(trans01, 5)
boot.transitions(trans01, 5, by.stage=TRUE)
## Aquilegia example
x <- subset(aq.trans, year==1996)
# calculate lamda, seed survival and recruitment rate using aq.matrix
rec <- nrow(subset(aq.trans, year==1997 & stage == "recruit"))
aq.96 <- aq.matrix(x, rec)
# add individual fertilities to data frame only
aq.96.trans <- aq.matrix(x, rec, summary=FALSE)
# pass estimated transitions in aq.96 to projection matrix
aq.96.boot <- boot.transitions(aq.96.trans, 200,
  add=c(1,1, aq.96$seed.survival, 2,1, aq.96$recruitment.rate) )
# calculate percentile intervals using quantile()
ci <- quantile(aq.96.boot$lambda, c(0.025,0.975) )
aq.96$lambda
ci
# plot histogram
hist(aq.96.boot$lambda, col="green", xlab="Lambda",
  main=paste('Bootstrap estimates of population\ngrowth rate from 1996-1997'))
abline(v=ci, lty=3)

```

calathea

*Projection matrices for a tropical understory herb***Description**

Projection matrices for a tropical understory herb (*Calathea ovandensis*) for plots 1-4 in years 1982-1985 and the pooled matrix. Matrices were constructed using a post-breeding census with 8 size classes: seed, seedling, juvenile, pre-reproductive, and 4 reproductive classes divided by leaf area.

Usage

```
calathea
```

Format

A list of 17 matrices ordered by plot then year, with the pooled matrix last.

Source

Table 7 in Horvitz and Schemske (1995). The pooled matrix is from Table 8.

References

Horvitz, C.C. and D.W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: Projection matrix analysis. *Ecological Monographs* 65:155-192.

Examples

```
calathea
## Single matrix
calathea[[11]]
image2(calathea[[11]], text.cex = .8)
title(paste("Calathea", names(calathea[11])), line = 3)
## MEAN matrix (exclude pooled matrix)
mean(calathea[-17])
## all plot 1
calathea[1:4]
## all 1982 matrices
calathea[ grep("1982", names(calathea)) ]
# OR
# calathea[seq(1,16,4)]
# split(calathea, 1:4)[[1]]
## Growth rates -see Figure 7
x <- sapply(calathea[-17], lambda)
x <- matrix(x, nrow = 4, byrow = TRUE, dimnames = list(paste("plot", 1:4), 1982:1985))
x
matplot2(x, type = "b", ylab = "Growth rate", main = "Calathea growth rates")
```

countCDFxt	<i>Count-based extinction probabilities and bootstrap confidence intervals</i>
------------	--

Description

This function takes parameters derived from population counts and calculates the probability of extinction with bootstrap confidence intervals for a density-independent model, using a diffusion approximation.

Usage

```
countCDFxt(mu, sig2, nt, Nc, Ne, tq = nt, tmax = 50, Nboot = 500,
plot = TRUE)
```

Arguments

mu	estimated value of mean mu
sig2	estimated value of sample variance
nt	number of transitions in the data set
Nc	current population size
Ne	quasi-extinction threshold
tq	length of the census (in years), default is number of transitions
tmax	latest time to calculate extinction probability, default 50
Nboot	number of bootstrap samples for calculating confidence intervals for extinction probabilities, default 500)
plot	draw extinction time CDF plot with log-scale on y-axis

Details

converted Matlab code from Box 3.4 in Morris and Doak (2002)

Value

The function plots the cumulative probabilities of quasi-extinction through time with 95% confidence intervals. It also returns a data frame with the extinction time CDF for the best parameter estimates (Gbest), and the lower and upper bootstrap confidence limits for extinction probabilities (Glo, Gup).

Author(s)

Adapted to R by Patrick Nantel, 4 May 2005, from program 'extprob' of Morris & Doak (2002: 79-86)

References

- Dennis et al. 1991, Ecological Monographs 61: 115-143
- Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

See Also

[extCDF](#)

Examples

```
## plot like Figure 3.8 in Morris and Doak (2002).  
logN <- log(grizzly$N[-1]/grizzly$N[-39])  
countCDFxt(mu=mean(logN), sig2=var(logN), nt=38, tq=38, Nc=99, Ne=20)
```

damping.ratio

Damping ratio

Description

Calculate the damping ratio of a projection matrix

Usage

```
damping.ratio(A)
```

Arguments

A A projection matrix

Details

see section 4.7 in Caswell (2001)

Value

Damping ratio

Note

The damping ratio is calculated by dividing the dominant eigenvalue by the eigenvalue with the second largest magnitude.

Author(s)

Chris Stubben

References

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

See Also

[lambda](#)

Examples

```
## whale converges slowly to stable stage distribution
matplot2(pop.projection(whale, c(1,1,1,1), 60)$stage.vectors,
prop=TRUE, legend=NA,
main=paste("whale damping ratio = ", round(damping.ratio(whale),3) ) )
# Calathea - compare to Table 12 in Horvitz and Schemske (1995)
x <- sapply(calathea[-17], damping.ratio)
x <- matrix(x, nrow=4, byrow=TRUE, dimnames= list(paste("plot", 1:4), 1982:1985))
x
matplot2(x, type='b', ylab="Damping ratio", main="Calathea")
```

eigen.analysis

Eigenvalue and eigenvector analysis of a projection matrix

Description

Calculate population growth rate and other demographic parameters from a projection matrix model using matrix algebra

Usage

```
eigen.analysis(A, zero = FALSE)
```

Arguments

A	A projection matrix
zero	Set sensitivities for unobserved transitions to zero, default is FALSE

Details

The calculation of eigenvalues and eigenvectors partly follows Matlab code in section 4.8.1 (p. 107) in Caswell (2001). Since popbio version 2.0, each part returned by eigen.analysis is now included as a separate function.

Value

A list with 6 items

lambda1	dominant eigenvalue with largest real part
stable.stage	proportional stable stage distribution
sensitivities	matrix of eigenvalue sensitivities
elasticities	matrix of eigenvalue elasticities
repro.value	reproductive value scaled so $v[1]=1$
damping.ratio	damping ratio

Note

If matrix A is singular, then eigen.analysis will return elasticities, sensitivities, and reproductive values with NAs.

Author(s)

Original code by James Holland Jones, Stanford University, August 2005

References

Caswell, H. 2001. Matrix population models: construction, analysis and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

See Also

[eigen](#) and [pop.projection](#)

Examples

```
## Imprimitive matrix
A <- matrix(c(0,0,2,.3,0,0,0,.6,0), nrow=3,byrow=TRUE)
A
ev <- eigen(A)
ev$values
Mod(ev$values)
lmax <- which.max(Re(ev$values))
lmax
Re(ev$values)[lmax]
## damping ratio is NA
eigen.analysis(A)
## cycles every 3 years
stage.vector.plot(pop.projection(A, c(1,1,1), 10)$stage.vectors)
### Teasel
a <- eigen.analysis(teasel)
a
barplot(a$stable.stage, col="green", ylim=c(0,1),
        ylab="Stable stage proportion", xlab="Stage class", main="Teasel")
box()
```

```

op <- par(mfrow=c(2,2))
image2(teasel, cex=.8, mar=c(0.5,3,4,1) )
title("Teasel projection matrix", line=3)
image2(a$elasticities, cex=.8, mar=c(0.5,3,4,1) )
title("Elasticity matrix", line=3)
## default is sensitivity for non-zero elements in matrix
image2(a$sensitivities, cex=.8, mar=c(0.5,3,4,1) )
title("Sensitivity matrix 1", line=3)
## use zero=FALSE to get sensitivities of all elements
image2(eigen.analysis(teasel, zero=FALSE)$sensitivities, cex=.8, mar=c(0.5,3,4,1) )
title("Sensitivity matrix 2", line=3)
par(op)

```

elasticity

Elasticity analysis of a projection matrix

Description

Calculate the elasticities of eigenvalues to changes in the projection matrix elements

Usage

```
elasticity(A)
```

Arguments

A A projection matrix

Details

see section 9.2 in Caswell (2001)

Value

An elasticity matrix

Author(s)

Chris Stubben

References

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

See Also

[sensitivity](#)

Examples

```

elas <- elasticity(teasel)
image2(elas, mar=c(1,3.5,5,1) )
  title("Teasel elasticity matrix", line=2.5)
# Summed elasticities for teasel.
# fertility in last column, stasis P on diagonal, and growth in bottom-left triangle
c(F=sum(elas[,6]), P=sum(diag(elas)), G=sum(elas[row(elas)>col(elas)]))

elas <- elasticity(tortoise[["med.high"]])
image2(elas, mar=c(1,3.5,5,1), log=FALSE)
  title("Tortoise elasticity matrix", line=2.5)
# Summed elasticities for tortoise (see example 9.4)
# fertility in top row, stasis on diagonal, and growth on subdiagonal
c(F=sum(elas[1,]), P=sum(diag(elas)), G=sum(elas[row(elas)==col(elas)+1]))

```

extCDF

Count-based extinction time cumulative distribution function

Description

Returns the extinction time cumulative distribution function using parameters derived from population counts.

Usage

```
extCDF(mu, sig2, Nc, Ne, tmax = 50)
```

Arguments

mu	estimated value of mean mu
sig2	estimated value of sample variance
Nc	current population size
Ne	quasi-extinction threshold
tmax	latest time to calculate extinction probability, default 50

Details

converted Matlab code from Box 3.3 and equation 3.5 in Morris and Doak 2002

Value

A vector with the cumulative probabilities of quasi-extinction from $t=0$ to $t=tmax$.

Author(s)

Chris Stubben

References

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

See Also

[countCDFxt](#) for bootstrap confidence intervals

Examples

```
logN <- log(grizzly$N[-1]/grizzly$N[-39])
mu <- mean(logN)
sig2 <- var(logN)
## grizzly cdf (log scale)
ex <- extCDF(mu, sig2, Nc=99, Ne=20)
plot(ex, log='y', type='l', pch=16, col="blue", yaxt='n',
      xlab="Years", ylab="Quasi-extinction probability",
      main="Yellowstone Grizzly bears")
pwrs <- seq(-15,-5,5)
axis(2, at = 10^pwrs, labels=parse(text=paste("10^", pwrs, sep = "")), las=1)
##plot like fig 3.10 (p 90)
n <- seq(20, 100, 2)
exts <- numeric(length(n))
for (i in 1:length(n) ){
  ex <- extCDF(mu, sig2, Nc=n[i], Ne=20)
  exts[i] <- ex[50]
}
plot(n, exts, type='l', las=1,
      xlab="Current population size",
      ylab="Probability of quasi-extinction by year 50")
```

fundamental.matrix

Fundamental matrix and age-specific survival

Description

Age-specific survival calculations from stage-classified matrices. Includes the mean, variance and coefficient of variation (cv) of the time spent in each stage class and the mean and variance of the time to death

Usage

```
fundamental.matrix(A, ...)
```

Arguments

A projection matrix
 ... additional items are passed to [splitA](#) and are used to split A into T and F matrices

Details

see section 5.3.1 in Caswell (2001).

Value

A list with 5 items

N	fundamental matrix or mean of the time spent in each stage class
var	variance of the time spent in each stage class
cv	coefficient of variation (sd/mean)
meaneta	mean of time to death
vareta	variance of time to death

Author(s)

Chris Stubben

References

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

See Also

see [generation.time](#) and [net.reproductive.rate](#) for other age-specific traits

Examples

```
fundamental.matrix(whale)
```

generation.time	<i>Generation time</i>
-----------------	------------------------

Description

Calculates the generation time of a stage-classified matrix

Usage

```
generation.time(A, ...)
```

Arguments

A	projection matrix
...	additional items are passed to splitA and are used to split A into T and F matrices

Details

see section 5.3.5 in Caswell (2001).

Value

Generation time. If the transition matrix is singular, then NA is returned.

Author(s)

Chris Stubben

References

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

See Also

see [fundamental.matrix](#) and [net.reproductive.rate](#) for other age-specific traits

Examples

```
generation.time(whale)
## fertilities in last column
generation.time(teasel, r=1:6, c=6)
## Plot 3 from Calathea
sapply(calathea[9:12], generation.time)
```

grizzly

Population sizes of grizzly bears in Yellowstone from 1959-1997

Description

Estimated number of adult female grizzly bears in the Greater Yellowstone population from 1959-1997.

Usage

```
grizzly
```

Format

A data frame with 39 rows on the following 2 variables.

year Year of census

N Estimated number of female grizzlies

Source

Table 3.1 in Morris and Doak 2002. Original data from Eberhardt et al. 1986 and Haroldson 1999.

References

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

Examples

```

grizzly
## plot like Fig 3.6 (p. 66)
plot(grizzly$year, grizzly$N,
     type = "o", pch = 16, las = 1, xlab = "Year",
     ylab = "Adult females", main = "Yellowstone grizzly bears"
)
## calculate log(Nt+1/Nt)
nt <- length(grizzly$N) ## number transitions
logN <- log(grizzly$N[-1] / grizzly$N[-nt])
## Mean and var
c(mean = mean(logN), var = var(logN))
## or using linear regression
## transformation for unequal variances (p. 68)
x <- sqrt(grizzly$year[-1] - grizzly$year[-length(grizzly$year)])
y <- logN / x
mod <- lm(y ~ 0 + x)
summary(mod)
## plot like Fig 3.7
plot(x, y,
     xlim = c(0, 1.2), ylim = c(-.3, .3), pch = 16, las = 1,
     xlab = expression(paste("Sqrt time between censuses ", (t[t + 1] - t[i])^{
       1 / 2
     })),
     ylab = expression(log(N[t + 1] / N[t]) / (t[t + 1] - t[i])^{
       1 / 2
     })),
     main = expression(paste("Estimating ", mu, " and ", sigma^2, " using regression")))
)
abline(mod)
## MEAN (slope)
mu <- coef(mod)
## VAR (mean square in analysis of variance table)
sig2 <- anova(mod)[["Mean Sq"]][2]
c(mean = mu, var = sig2)
## Confidence interval for mean (page 72)
confint(mod, 1)
## Confidence interval for sigma 2 (equation 3.13)
df1 <- length(logN) - 1
df1 * sig2 / qchisq(c(.975, .025), df = df1)
## test for outliers using dffits (p.74)
dffits(mod)[dffits(mod) > 2 * sqrt(1 / 38) ]
## plot like fig 3.11

```

```
plot(grizzly$N[-nt], logN,
     pch = 16, xlim = c(20, 100), ylim = c(-.3, .3), las = 1,
     xlab = "Number of females in year T",
     ylab = expression(log(N[t + 1] / N[t])),
     main = "Grizzly log population growth rates"
)
cor(grizzly$N[-nt], logN)
abline(lm(logN ~ grizzly$N[-nt]), lty = 3)
```

head2

Return the first and last part of a matrix or dataframe

Description

Returns the first and last rows using output from both [head](#) and [tail](#) and separates the two parts with dots. Useful for viewing ordered datasets such as longitudinal census data.

Usage

```
head2(x, head = 3, tail = 1, dotrows = 1)
```

Arguments

x	A matrix or dataframe
head	The number of first rows
tail	The number of last rows
dotrows	The number of rows of dots

Value

A smaller object with first and last rows only

Author(s)

Chris Stubben

Examples

```
head2(aq.trans)
```

`hudcorrs`*Correlation matrices for Hudsonia vital rates*

Description

Within year and between year correlation matrices from *Hudsonia montana* vital rates. Correlations were calculated from first 13 growth and survival rates only, since fertility rates vary little.

Usage`hudcorrs`**Format**

A list with 2 correlation matrices, `corrin` (within year correlation) and `corrout` (between year correlation).

Source

The correlation matrices in Morris and Doak 2002 include some correlations > 1 . A corrected set of correlations was sent by the D. Doak on 8/4/2007.

References

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

See Also

[vitalsim](#)

Examples`hudcorrs`

`hudmxdef`*Matrix definition program for Hudsonia vital rates*

Description

Creates a projection matrix from *Hudsonia* vital rates (survival, growth, and reproduction). Growth rates are defined as a set of binomial choices as in Table 8.4 B in Morris and Doak (2002).

Usage`hudmxdef(vrs)`

Arguments

vrs Vital rate means in [hudvrs](#)

Value

A projection matrix

Author(s)

Chris Stubben

References

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

See Also

[vitalsim](#)

Examples

```
hudmxdef(hudvrs$mean)
```

hudsonia

Projection matrices for mountain golden heather

Description

Projection matrices for the mountain golden heather (*Hudsonia montana*) for years 1985 through 1988 with 6 size classes: seeds, seedlings, and 4 size classes divided by plant area.

Usage

```
hudsonia
```

Format

A list of 4 matrices from 1985-1988

Source

Table 6.7 in Morris and Doak 2002. The original data is from Frost 1990.

References

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

Examples

```
hudsonia
sapply(hudsonia, lambda)
## mean matrix
x <- mean(hudsonia)
image2(x, mar = c(1, 4, 5.5, 1))
title("Hudsonia mean matrix", line = 2.5)
lambda(x)
# variance
var2(hudsonia)
```

hudvrs

Best Kendall estimates of Hudsonia vital rate means and variances

Description

Best Kendall estimates of vital rate means (9 growth, 4 survival, and 11 fertility rates) for *Hudsonia montana*.

Usage

```
hudvrs
```

Format

A data frame with 24 rows and 2 columns:

mean vital rate means

var vital rate variances

Source

Data listed in Box 8.10 for the [vitalsim](#) function. See also Table 8.5 in Morris and Doak (2002).

References

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

Examples

```
hudvrs
hudmxdef(hudvrs$mean)
```

 image2

Display a matrix image

Description

Creates a grid of colored rectangles to display a projection, elasticity, sensitivity or other matrix.

Usage

```
image2(x, col = c("white", rev(heat.colors(23))), breaks, log = TRUE,
       border = NA, box.offset = 0.1, round = 3, cex, text.cex = 1,
       text.col = "black", mar = c(1, 3, 3, 1), labels = 2:3,
       label.offset = 0.1, label.cex = 1, srt = 90)
```

Arguments

x	A numeric matrix with row and column names
col	A vector of colors for boxes
breaks	A numeric vector of break points or number of intervals into which x is to be cut . Default is the length of col
log	Cut values in x using a log scale, default TRUE
border	The border color for boxes, default is no borders
box.offset	Percent reduction in box size (a number between 0 and 1), default is 10% reduction
round	Number of decimal places to display values of x in each box
cex	Magnification size of text and labels, if specified this will replace values in both text.cex and label.cex
text.cex	Magnification size of text in cells only
text.col	Color of text in cells, use NA to skip text labels
mar	Margins on four sides of plot
labels	A vector giving sides of the plot (1=bottom, 2=left, 3=top, 4=right) for row and column labels
label.offset	Amount of space between label and boxes
label.cex	Magnification size of labels
srt	String rotation for labels on top and bottom of matrix

Value

A image plot of the matrix

Note

The minimum value in x is usually assigned to the first color category and the rest of the values are then cut into equally spaced intervals. This was added to show transitions with very low probabilities in a new color category, eg, $2e-06$ would usually be grouped with 0 using [image](#). Note if all elements > 0 , then the first color will not be used.

Author(s)

Chris Stubben

See Also

[image](#)

Examples

```
A <- calathea[[11]]
op <- par(mfrow=c(2,2))
image2(A, text.cex=.8)
## with gray border and labels on bottom right
image2( A, text.cex=.8, border="gray70", labels=c(1,4), mar=c(3,1,1,3))
## no text or box offset
image2( A, box.offset=0, text.col=NA)
# set zeros to NA to print everything but zero
A[A == 0] <- NA
image2( A, box.offset=0 , text.cex=.8)
## if comparing two or more matrices, get the log10 range
## of values (not including zero) and pass to breaks
x <- unlist(calathea[-17])
x <- log10(range(x[x!=0]))
par(mfrow=c(4,4))
for(i in 1:16){
  A <- calathea[[i]]
  A[A == 0] <- NA
  image2(A, cex=.7, box.offset=0, breaks=seq(x[1], x[2], len=24))
  title(names(calathea[i]), line=3)
}
par(op)
```

Kendall

Find the best Kendall's estimates of mean and environmental variance for beta-binomial vital rates

Description

Finds the best estimates of mean and environmental variance for beta-binomial vital rates, using a brute force search for the best adjusted estimates from a very large number of combinations of different possible mean and variance values.

Usage

```
Kendall(rates, grades = 1000, maxvar = 0.2, minvar = 1e-05,
        maxmean = 1, minmean = 0.01)
```

Arguments

rates	amatrix or dataframe with four columns: Rate identifier, Year, Total number of starting individuals, Number growing (or surviving).
grades	numberof different levels of means and variances to try, default is 1000
maxvar	maximumvariance to search over, default is 0.20. The maximum possible is 0.25 and searching a narrower range will improve the accuracy of the answer.
minvar	minimumvariance to search, default is 0.00001
maxmean	maximumlimit on the mean values to search, default 1
minmean	minimumlimit on the mean values to search, default 0.01

Details

converted Matlab code from Box 8.2 in Morris and Doak (2002)

Value

A list with estimates and confidence intervals

est	a matrix with 5 columns: (1) estimated mean, (2) Kendall's MLE mean, (3) estimated variance, (4) Kendall's MLE variance, (5) Kendall's unbiased MLE variance.
ci	a matrix with 95% confidence limits for the Kendall's mean and unbiased variance estimates with 4 columns: (1) low and (3) high mean limits, (3) low and (4) high variance limits.

Note

may deliver warning messages of: 'no finite arguments to min; returning Inf', indicating use of very low values for variance, but this is not a malfunction.

Author(s)

Adapted to R from Morris & Doak (2002: 267-270) by Patrick Nantel.

References

- Kendall, B. E. 1998. Estimating the magnitude of environmental stochasticity in survivorship data. *Ecological Applications* 8(1): 184-193.
- Morris, W. F., and D. F. Doak. 2002. *Quantitative conservation biology: Theory and practice of population viability analysis*. Sinauer, Sunderland, Massachusetts, USA.

See Also[varEst](#)**Examples**

```
## desert tortoise input from Box 8.2 - compare results to Table 8.3
tor <- data.frame(rate=rep(c("g4","g5","g6"), each=3),
  year=rep(1:3,3),      ## representing 70s, early 80s, late 80s
  start=c(17,15,7,22,19,4,32,31,10),
  grow=c(8,1,0,5,5,0,2,1,0)
)
## use fewer grades for faster loop
tor.est<-Kendall(tor, grades=200)
tor.est
wp.est <- Kendall(woodpecker, grades=200)
wp.est
```

lambda	<i>Population growth rate</i>
--------	-------------------------------

Description

Calculates the population growth rate of a projection matrix

Usage

```
lambda(A)
```

Arguments

A A projection matrix

Details

see section 4.4 in Caswell (2001)

Value

The dominant eigenvalue

Note

The built-in [eigen](#) function returns eigenvalues in decreasing order of magnitude or modulus. The dominant eigenvalue of imprimitive matrices with d eigenvalues of equal modulus is the one with the largest real part (`which.max(Re(eigen(A)$values))`).

Author(s)

Chris Stubben

References

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

See Also

[eigen](#) and [pop.projection](#)

Examples

```
A <- matrix(c(0,0,2,.3,0,0,0,.6,0), nrow=3,byrow=TRUE)
lambda(A)
Re(eigen(A)$values)
sapply(hudsonia, lambda)
```

Inorms

Generate random lognormal values for fertility rates

Description

Converts standard normal random values to lognormals with defined means and variances

Usage

```
lnorms(n, mean = 2, var = 1)
```

Arguments

n	number of observations
mean	mean value of the fertility rate, default 2
var	variance of the vital rate (not standard deviation), default 1

Details

converted Matlab code from Box 8.4 in Morris and Doak (2002)

Value

A vector of random lognormal values

Note

This function could probably be replaced with built-in functions for the Log Normal Distribution [rlnorm](#)

Author(s)

Original Matlab code by Morris and Doak (2002: 281). Adapted to R by Patrick Nantel, 20 June 2005.

References

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

See Also

[stretchbetaval](#)

Examples

```
lnorms(1)
# Generate lognormal random fertilities
# for a population of 1000 mature individuals with mean fertility of
# 3 and inter-individual variance in fertility of 1.5.
rndfert <- lnorms(1000, 3,1.5)
summary(rndfert)
hist(rndfert,40, main="Lognormal random fertilities",
xlab="Fertility rate", col="blue")
```

logi.hist.plot

Plot logistic regression

Description

Plot combined graphs for logistic regressions

Usage

```
logi.hist.plot(independ, depend, logi.mod = 1, type = "dit",
  boxp = TRUE, rug = FALSE, ylabel = "Probability",
  ylabel2 = "Frequency", xlabel = "", mainlabel = "", las.h = 1,
  counts = FALSE, ...)
```

Arguments

independ	explanatory variable
depend	dependent variable, typically a logical vector
logi.mod	type of fitting, 1 = logistic; 2 = "gaussian" logistic
type	type of representation, "dit" = dit plot; "hist" = histogram
boxp	TRUE = with box plots, FALSE = without

rug	TRUE = with rug plots, FALSE = without
ylabel	y-axis label
ylabel2	2nd y-axis label
xlabel	x-axis label
mainlabel	overall title for plot
las.h	orientation of axes labels (0 = vertical, 1 = horizontal)
counts	add counts above histogram bars
...	additional options passed to logi.hist

Value

A logistic regression plot

Author(s)

M. de la Cruz Rot

References

de la Cruz Rot, M. 2005. Improving the Presentation of Results of Logistic Regression with R. ESA Bulletin 86:41-48. <http://esapubs.org/bulletin/backissues/086-1/bulletinjan2005.htm>

Examples

```
aq.trans$survived <- aq.trans$fate!="dead"
a <- subset(aq.trans, leaf<50 & stage!="recruit", c(leaf,survived))
logi.hist.plot(a$leaf, a$survived,
  type="hist", boxp=FALSE, counts=TRUE, int=10,
  ylabel="Survival probability", ylabel2="Number of plants",
  xlab="Number of leaves")
b <- glm(survived ~ leaf, binomial, data=a)
summary(b)
```

LTRE

Life Table Response Experiment

Description

Evaluate sensitivities in a fixed Life Table Response Experiment (LTRE)

Usage

LTRE(trts, ref)

Arguments

trts	A treatment matrix or a list of two or more treatment matrices
ref	A reference matrix

Details

Sensitivities are evaluated midway between the treatment and reference matrices as described in section 10.1.1 in Caswell (2001).

Value

A matrix of contributions (equation 10.4 in Caswell) or a list of matrices with one matrix of contributions per treatment

Note

The examples of a fixed LTRE are from Horvitz, C. C., D. W. Schemske, and H. Caswell. 1997. The relative importance of life-history stages to population growth: prospective and retrospective analyses. Pages 247-271 in S. Tuljapurkar and H. Caswell, editors. Structured population models in marine, terrestrial and freshwater systems. Chapman and Hall, New York. A.L. Angert. 2006. Demography of central and marginal populations of monkeyflowers (*Mimulus cardinalis* and *M. lewisii*). *Ecology* 87:2014-2025.

Author(s)

Chris Stubben

See Also

Check the demo(Caswell) for variance decomposition in a random design using killer whale.

Examples

```
##### Calathea ovandensis
calathea_pool <- calathea[['pooled']]
## Create plots like FIGURE 7 in Horvitz et al 1997
plots <- split(calathea[-17], rep(1:4,each=4))
## use Mean matrix since pooled not available by plot
plots <- lapply(plots, mean)
Cm <- LTRE(plots, calathea_pool)
pe <- sapply(Cm, sum)
barplot(pe, xlab="Plot", ylab="Plot effect" , ylim=c(-.25, .25),
col="blue", las=1)
abline(h=0)
box()
title(expression(italic("Calathea ovandensis")))

##YEARS -- split recycles vector
yrs <- split(calathea[-17], 1:4)
yrs <- lapply(yrs, mean)
```

```

names(yrs) <- 1982:1985
Cm <- LTRE(yrs, calathea_pool)
ye <- sapply(Cm, sum)
barplot(ye, xlab="Year", ylab="Year effect" , ylim=c(-.25, .25), col="blue", las=1)
abline(h=0)
box()
title(expression(italic("Calathea ovandensis")))
## INTERACTION
Cm <- LTRE(calathea[-17], calathea_pool)
ie <- sapply(Cm, sum)
## minus plot, year effects
ie<- ie - rep(pe, each=4) - rep(ye, 4)
names(ie) <- NULL
names(ie)[seq(1,16,4)] <- 1:4
barplot(ie, xlab="Plot (years 82-83 to 85-86)", ylab="Interaction effect" ,
  ylim=c(-.25, .25), col="blue", las=1)
abline(h=0)
box()
title(expression(italic("Calathea ovandensis")))

##### Mimulus
## Pooled M. cardinalis reference matrix kindly provided by Amy Angert 1/2/2008.
m_card_pool <- matrix( c(
1.99e-01, 8.02e+02, 5.82e+03, 3.05e+04,
2.66e-05, 7.76e-02, 2.31e-02, 1.13e-03,
7.94e-06, 8.07e-02, 3.22e-01, 2.16e-01,
2.91e-07, 1.58e-02, 1.15e-01, 6.01e-01), byrow=TRUE, nrow=4)
## Population effects using pooled population matrices
card <- subset(monkeyflower, species=="cardinalis" & year=="pooled")
## split rows into list of 4 matrices
Atrt <- lapply(split(as.matrix(card[,4:19]), 1:4), matrix, nrow=4, byrow=TRUE)
names(Atrt) <- card$site
Cm <- LTRE(Atrt, m_card_pool)
x <- sapply(Cm, sum)
x
names(x) <- c("BU", "RP", "WA", "CA")
## Plot like Figure 2A in Angert (2006)
op <- par(mar=c(5,5,4,1))
barplot(x, xlab="Population", ylab="", xlim=c(0,6.5), ylim=c(-.4, .4),
  las=1, space=.5, col="blue")
abline(h=0)
mtext(expression(paste(sum(a[ij]), " contributions")), 2, 3.5)
title(expression(paste(italic("M. cardinalis"), " Population effects")))
box()
## and Plot like Figure 3A
x <- matrix(unlist(Cm), nrow=4, byrow=TRUE)
colnames(x) <- paste("a", rep(1:4, each=4), 1:4, sep="")
bp <- barplot(x[1:2,], beside=TRUE, ylim=c(-.2, .2), las=1,
  xlab="Transition", ylab="", xaxt='n')
mtext(expression(paste("Contribution of ", a[ij], "to variation in ", lambda)), 2, 3.5)
## rotate labels
text(bp[1,]-0.5, -.22, labels=colnames(x), srt=45, xpd=TRUE)
title(expression(paste(italic("M. cardinalis"), " Range center")))

```

```
box()
par(op)
```

matplot2

Plot a matrix

Description

Plot the rows of a matrix. Useful for displaying a matrix of stage vectors, survival rates and sensitivities.

Usage

```
matplot2(x, proportions = FALSE, legend = "topright", xlab = NULL,
  ylab = NULL, type = "l", las = 1, pch = c(15:18, 1:3), lwd = 1,
  lty = 1:nrow(x), col = rainbow(nrow(x)), lcex = 1, lbty = "o",
  lcol = 1, ltitle = NULL, lsort = TRUE, ...)
```

Arguments

x	a matrix
proportions	If TRUE, then plot proportional changes
legend	a legend keyword or vector of x,y coordinates, defaults to top-right corner
xlab	a label for the x axis
ylab	a label for the y axis
type	plot type, default line
las	style of axis labels, default horizontal
pch	point types
lwd	line width
lty	line type
col	color
lcex	legend size expansion
lbty	legend box type
lcol	number of columns in legend
ltitle	legend title
lsort	sort legend by decreasing order of mean number in row
...	additional options are passed to plot function

Value

A matrix plot

Note

Only a few basic legend options are available. For more control, set legend=NA and run separately

Author(s)

Chris Stubben

See Also

[matplot](#) and [stage.vector.plot](#)

Examples

```
# survival rates
x <- calathea[9:12]
x <- sapply(x, function(x) colSums(splitA(x, r=1:2)$T))
matplot2(t(x), legend="bottomright", ylab="Survival",
  main="Calathea survival curves")
# Growth rates - do not sort legend
x <- sapply(calathea[-17], lambda)
x <- matrix(x, nrow=4, byrow=TRUE, dimnames= list(paste("plot", 1:4), 1982:1985))
matplot2(x, type='b', lsort=FALSE, ylab="Growth rate", main="Calathea growth rates")
# Convergence to stable stage (excluding seeds)
x <- pop.projection(calathea[[7]], rep(1,8), 10)
matplot2(x$stage.vectors[-1,], prop=TRUE,
  main="Calathea stage vectors", lcex=.7)
```

matrix2

Square matrices

Description

Create a square matrix from a given set of values

Usage

```
matrix2(x, stages, byrow = TRUE)
```

Arguments

x	a vector of matrix elements
stages	a vector of row names (also assigned to columns)
byrow	fill matrix by rows , default TRUE

Value

a square matrix

Author(s)

Chris Stubben

See Also

[matrix](#)

Examples

```
# Centaurea corymbosa from Freville 2004
ceco <- c(0,0,5.905,0.368,0.639, 0.025, 0.001, 0.152, 0.051)
stages <- c("seedling", "vegetative", "flowering")
# shortcut for
matrix(ceco, nrow=3, byrow=TRUE, dimnames=list(stages,stages))
matrix2(ceco, stages)
```

mean.list

Mean matrix

Description

Calculates mean matrix from a list of matrices

Usage

```
## S3 method for class 'list'
mean(x, ...)
```

Arguments

x A list of two or more matrices
... Additional arguments passed to [rowMeans](#)

Details

Returns the mean matrix from a list of matrices using a combination of [unlist](#) and [rowMeans](#). See example for details.

Value

The mean matrix

Note

S3 method for the [mean](#) of a list of matrices

Author(s)

Chris Stubben

See Also[var2](#)**Examples**

```
mean(hudsonia)
# or
x <- matrix(unlist(hudsonia), ncol=length(hudsonia) )
matrix2(rowMeans(x), colnames(hudsonia[[1]]))
```

 monkeyflower

Projection matrices for monkeyflower

Description

Pooled and annual projection matrices of central and marginal populations of monkeyflowers (*Mimulus cardinalis* and *M. lewisii*)

Usage

```
monkeyflower
```

Format

A data frame with 32 matrices, arranged with one matrix per row

species M. cardinalis or M. lewisii

site Study site

year Start year of projection interval or pooled for all three years

a11 matrix element a11; seed to seed transition or seed bank survival

a12 matrix element a12; small nr to seed - fertility

a13 matrix element a13; large nr to seed - fertility

a14 matrix element a14; reprod to seed - fertility

a21 matrix element a21; seed to small nr - growth

a22 matrix element a22; small nr to small nr -stasis

a23 matrix element a23; large nr to small nr - regress

a24 matrix element a24; reprod to small nr - regress

a31 matrix element a31; seed to large nr - growth

a32 matrix element a32; small nr to large nr - growth

a33 matrix element a33; large nr to large nr - stasis
 a34 matrix element a34; reprod to large nr - regress
 a41 matrix element a41; seed to reprod - growth
 a42 matrix element a42; small nr to reprod - growth
 a43 matrix element a43; large nr to reprod - growth
 a44 matrix element a44; reprod to reprod - stasis

Details

Matrix constructed using a post-breeding census with four stage classes: Seeds, small non-reproductive, large non-reproductive, and reproductive.

Source

<http://www.esapubs.org/archive/ecol/E087/126/appendix-E.htm>

References

Amy Lauren Angert. 2006. Demography of central and marginal populations of monkeyflowers (*Mimulus cardinalis* and *M. lewisii*). *Ecology* 87:2014-2025.

Examples

```
monkeyflower
## convert M. cardinalis rows to list of 16 matrices
A <- subset(monkeyflower, species == "cardinalis")
# use as.matrix to convert data.frame to numeric matrix
A <- split(as.matrix(A[, 4:19]), paste(A$site, A$year))
stages <- c("seed", "sm.nr", "lg.nr", "repro")
## convert to list of 16 matrices
A <- lapply(A, matrix, nrow = 4, byrow = TRUE, dimnames = list(stages, stages))
A[8]
image2(A[[8]], round = 8, mar = c(1, 3, 4.5, 1))
title(paste("M. cardinalis - ", names(A[8])), line = 2.5)
## plot like figure 1A
x <- matrix(sapply(A, lambda), ncol = 4)
colnames(x) <- c("BU", "CA", "RP", "WA")
rownames(x) <- c(2000:2002, "pooled")
x <- x[, c(1, 3, 4, 2)]
colrs <- gray(0:3 / 3)[c(1, 3, 2, 4)]
barplot(x, beside = TRUE, las = 1, col = colrs, ylim = c(0, 2),
  ylab = "Population growth rate", main = "Mimulus cardinalis")
box()
abline(h = 1, lwd = .5)
legend(1, 1.95, rownames(x), fill = colrs, bty = "n")
```

`multiresultm`*Incorporate demographic stochasticity into population projections*

Description

Generates multinomial random numbers for state transitions and lognormal or binomial (for clutch size=1) random numbers for fertilities and returns a vector of the number of individuals per stage class at $t+1$.

Usage

```
multiresultm(n, T, F, varF = NULL)
```

Arguments

<code>n</code>	the vector of numbers of individuals per class at t
<code>T</code>	a transition T matrix
<code>F</code>	a fertility F matrix
<code>varF</code>	a matrix of inter-individual variance in fertilities, default is <code>NULL</code> for simulating population where clutch size = 1, so that fertilities give the probabilities of birth

Details

Adapted from Matlab code in Box 8.11 in Morris and Doak (2002) and section 15.1.3 in Caswell (2001)

Value

a vector of the number of individuals per class at $t+1$.

Author(s)

Patrick Nantel

References

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

Examples

```

x <- splitA(whale)
whaleT <- x$T
whaleF <- x$F
multiresultm(c(1,9,9,9),whaleT, whaleF)
multiresultm(c(1,9,9,9),whaleT, whaleF)
## create graph similar to Fig 15.3 a
reps <- 10 # number of trajectories
tmax <- 200 # length of the trajectories
totalpop <- matrix(0,tmax,reps) # initializes totalpop matrix to store trajectories
nzero <- c(1,1,1,1) # starting population size
for (j in 1:reps) {
  n <- nzero
  for (i in 1:tmax) {
    n <- multiresultm(n,whaleT,whaleF)
    totalpop[i,j] <- sum(n)
  }
}
matplot(totalpop, type = 'l', log="y",
        xlab = 'Time (years)', ylab = 'Total population')

```

nematode

Population densities for the sugarbeet cyst nematode

Description

A time-series of population vectors for the sugarbeet cyst nematode *Heterodera schachtii*. Individuals were classified into three stages (J2, J3+J4, and adult) and densities (per 60 cc of soil) were averaged over four replicates, measured every two days, for 10 days. .

Usage

```
nematode
```

Format

A matrix listing densities from 3 stage classes over 6 time periods

Source

Example 6.3 in Caswell (2001).

References

Caswell, H. 2001. Matrix population models. Construction, Analysis and interpretation. 2nd ed. Sinauer, Sunderland, Massachusetts.

See Also[QPmat](#)**Examples**

```
nematode
stage.vector.plot(nematode,
  prop = FALSE, log = "y", ylim = c(.3, 200),
  xlab = "Time", ylab = "Nematode density"
)
```

net.reproductive.rate *Net reproductive rate*

Description

Calculates the net reproductive rate of a stage classified matrix using the dominant eigenvalue of the matrix R

Usage

```
net.reproductive.rate(A, ...)
```

Arguments

A	projection matrix
...	additional items are passed to splitA and are used to split A into T and F matrices

Value

Net reproductive rate. If the transition matrix is singular, then NA is returned.

Author(s)

Chris Stubben

References

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

See Also

see [fundamental.matrix](#) and [generation.time](#) for other age-specific traits

Examples

```
net.reproductive.rate(whale)
## fertilities in last column
net.reproductive.rate(teasel, r=1:6, c=6)
## Plot 3 from Calathea - values are not the same as p. 105 in Caswell.
sapply(calathea[9:12], net.reproductive.rate)
```

pfister.plot

Create log-log plots of variance vs. sensitivity and CV vs. elasticity

Description

Create log-log plots of both variance vs. sensitivity and CV vs. elasticity in matrix elements. Plots are based on Figure 2 in Pfister(1998)

Usage

```
pfister.plot(A)
```

Arguments

A A list of two or more projection matrices

Details

Calculates mean, variance and coefficient of variation (CV) of matrix elements from a list of two or more projection matrices. The sensitivity and elasticity matrices are then calculated from the mean matrix using [eigen.analysis](#)

Value

Creates two log-log plots similar to Figure 2 in Pfister(1998) and outputs a data.frame with 5 columns listing mean, variance, CV, sensitivity and elasticity for matrix elements with a mean and variance > 0

Author(s)

Chris Stubben

References

Pfister, CA. 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. PNAS 95:213-218.

Examples

```
## 4 Hudsonia matrices
pfister.plot(hudsonia)
## 3 Mimulus cardinalis matrices at Carlon
mim <- subset(monkeyflower, species == "cardinalis" &
  site == "Carlon" & year != "pooled", select = c(4:19))
## convert data frame to list of matrices using split
mim1 <-split(mim, 2000:2002)
mim2 <-lapply(mim1, matrix, nrow=4, byrow=TRUE)
vr1 <- pfister.plot(mim2)
vr1
## PLOT using labels
plot(vr1$cv, vr1$elas, xlab="CV", ylab="Elasticity", log="xy", type='n')
# Split matrix elements into transitions representing F (fertility),
# S (survival), G (growth), and R (retrogression).
# Fertility on top row, survival on diagonal, growth is above diagonal
# and retrogression below diagonal.
rownames(vr1)
y2 <- expression(S[11],G[21],G[31],G[41],
  F[12],S[22],G[32],G[42],
  F[13],R[23],S[33],G[43],
  F[14],R[34],S[44])
text(vr1$cv, vr1$elas, y2)
### add trend line
abline(lm(log10(vr1$elas)~log10(vr1$cv)), col="red")
## include Spearman's rank correlation
a <- cor.test(vr1$cv, vr1$elas, method="spearman")
a
text(10, .0015, substitute(rho == x, list(x=round(a$estimate,2))), col="blue")
```

pop.projection

Calculate population growth rates by projection

Description

Calculates the population growth rate and stable stage distribution by repeated projections of the equation $n(t+1) = An(t)$

Usage

```
pop.projection(A, n, iterations = 20)
```

Arguments

A	A projection matrix
n	An initial age or stage vector
iterations	Number of iterations

Details

Eventually, structured populations will converge to a stable stage distribution where each new stage vector is changing by the same proportion (λ).

Value

A list with 5 items

<code>lambda</code>	Estimate of λ using change between the last two population counts
<code>stable.stage</code>	Estimate of stable stage distribution using proportions in last stage vector
<code>stage.vector</code>	A matrix with the number of projected individuals in each stage class
<code>pop.sizes</code>	Total number of projected individuals
<code>pop.changes</code>	Proportional change in population size

Author(s)

Chris Stubben

References

see section 2.2 in Caswell 2001

See Also

[stage.vector.plot](#) to plot stage vectors

Examples

```
## mean matrix from Freville et al 2004
stages <- c("seedling", "vegetative", "flowering")
A <- matrix(c(
  0,      0,      5.905,
  0.368, 0.639,  0.025,
  0.001, 0.152,  0.051
), nrow=3, byrow=TRUE,
  dimnames=list(stages,stages))
n <- c(5,5,5)
p <- pop.projection(A,n, 15)
p
damping.ratio(A)
stage.vector.plot(p$stage.vectors, col=2:4)
A <- whale
#n <- c(4,38,36,22)
n <- c(5,5,5,5)
p <- pop.projection(A,n, 15)
p
stage.vector.plot(p$stage.vectors, col=2:4, ylim=c(0, 0.6))
## convergence is slow with damping ratio close to 1
damping.ratio(A)
pop.projection(A, n, 100)$pop.changes
```

projection.matrix *Construct projection matrix models using transition frequency tables*

Description

Construct an age or stage-structure projection model from a transition table listing stage in time t , fate in time $t+1$, and one or more individual fertility columns.

Usage

```
projection.matrix(transitions, stage = NULL, fate = NULL,
  fertility = NULL, sort = NULL, add = NULL, TF = FALSE)
```

Arguments

transitions	a stage-fate data frame with stage or age class in the current census, fate in the subsequent census, and one or more fertility columns
stage	a column name or position of the stage column in the stage-fate data frame. Defaults to "stage".
fate	name of the fate column in the stage-fate data frame. Defaults to "fate"
fertility	one or more names of fertility columns in the stage-fate data frame. By default, any column names matching stage class names are assumed to contain individual fertilities
sort	a vector listing stage classes that correspond to the rows and columns of the desired projection matrix. Currently, names in this vector must match a level in the stage column. Also, this option should only be used if stages are not ordered , since the default is to sort by levels in the stage column.
add	a vector listing row, column and value, used to add <i>estimated</i> transtions to the transition matrix (e.g., a transition from seed bank to seedling). May be repeated.
TF	output separate transition (T) and fertility (F) matrices. Default is FALSE and outputs a single projection matrix A

Details

The state transition rates are estimated using transition frequency tables (see section 6.1.1, Caswell 2001), so this technique will most likely apply to demographic studies of plants or other sessile organisms where individuals are tagged and then consistently relocated in annual censuses. The fertility rates are calculated by averaging individuals fertilities by stage class; therefore, some care should be taken to correctly estimate individual fertilities based on the timing of the census.

Value

The default output is a single projection matrix A. If the TF flag is true, then a list with 2 items where $A=T+F$

Note

Individual fertilities should be the total number of offspring at the end of the census interval. Therefore, fertilities should include offspring survival in a prebreeding censuses (and more than one offspring class may be present). In a postbreeding census, new offspring were born just before the census, so the fertility rate is just the number of offspring in this case.

Author(s)

Chris Stubben

Examples

```
trans01 <- subset(merge(test.census, test.census, by = "plant", sort =FALSE),
                  year.x==2001 & year.y==2002 )
## Add individual fertilities using "anonymous reproduction" based on the
## proportional reproductive outputs of flowering plants and the total number
## of seedlings at the end of the projection interval
trans01$seedferts <- trans01$fruits.x/sum(trans01$fruits.x) * 5
trans01
stages <- c("seedling", "vegetative", "reproductive")
## three ways to specify columns
projection.matrix(trans01, stage.x, stage.y, seedferts, stages)
projection.matrix(trans01, 3, 6, 8, c(3,4,2))
projection.matrix(trans01, "stage.x", "stage.y", "seedferts", stages)
## BEST to use column default (fertility column (seedling) now matches stage class name)
names(trans01)[c(3, 6, 8)] <- c("stage", "fate", "seedling")
# AND order stages in dataframe
trans01$stage <- ordered(trans01$stage, stages)
projection.matrix(trans01)
projection.matrix(trans01, TF=TRUE)
## Example using Aquilegia data
sf <- subset(aq.trans, year==1998 & plot==909, c(year, plant, stage, fruits, fate))
## rows and columns of final matrix
levels(sf$stage)
## seedlings next year
seedlings <- nrow(subset(aq.trans, plot==909 & year==1999 & stage=="recruit"))
## ADD individual fertility estimates for recruits and seeds assuming seed bank and
## new seeds contribute to a common germinant pool with equal chance of recruitment
seed.survival <- .4
seed.bank.size <- 1000
seeds.per.fruit <- 50
seeds.from.plants <- sum(sf$fruits)*seeds.per.fruit
recruitment.rate <- seedlings/(seed.bank.size + seeds.from.plants)
## add two fertility columns
sf$recruit <- sf$fruits/sum(sf$fruits) * seeds.from.plants * recruitment.rate
sf$seed <- sf$fruits * seeds.per.fruit * seed.survival
## add seed bank survival and seed bank recruitment rate to transition matrix
A <- projection.matrix(sf, add=c(1,1, seed.survival, 2,1, recruitment.rate ))
A
max(Re(eigen(A)$values))
```

 QPmat

Build a projection matrix from a time series of individuals (or densities) per stage

Description

Builds one projection matrix from a time series of number (or densities) of individuals per stage (size classes or life stages) using Wood's quadratic programming method. The matrix model also requires a constraint matrix C, vector b, and vector listing nonzero elements of desired projection matrix.

Usage

```
QPmat(nout, C, b, nonzero)
```

Arguments

nout	A time series of population vectors
C	constraint matrix
b	b vector
nonzero	indices of the non-zero elements of the transition matrix (counting by column)

Details

converted Matlab code from Example 6.3 in Caswell (2001)

Value

A projection matrix.

Note

This function requires solve.QP in the quadprog package.

Author(s)

Adapted to R by Patrick Nantel

Examples

```
## Not run:
## list nonzero elements
nonzero <- c(1, 2, 5, 6, 7, 9)
## create C matrix
C <- rbind(diag(-1,6), c(1,1,0,0,0,0), c(0,0,1,1,0,0), c(0,0,0,0,0,1))
## calculate b (transpose is not necessary - either way works)
b <- apply(C, 1, max)
QPmat(nematode, C,b,nonzero)
```

```
## End(Not run)
```

reproductive.value *Reproductive value*

Description

Calculates the reproductive values of a projection matrix

Usage

```
reproductive.value(A)
```

Arguments

A A projection matrix

Details

see section 4.5 in Caswell (2001)

Value

A vector containing the scaled reproductive values so $v[1]=1$

Author(s)

Chris Stubben

References

Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*, Second edition. Sinauer, Sunderland, Massachusetts, USA.

Examples

```
v <- reproductive.value(teasel)
v
dotchart(log10(v), pch=16, xlab="Reproductive value (log10)")
```

`resample`*Resample a projection matrix*

Description

Resample a projection matrix using a multinomial distribution for transitions and a log normal distribution for fertilities

Usage

```
resample(A, n, fvar = 1.5, ...)
```

Arguments

<code>A</code>	a projection matrix
<code>n</code>	either a stage vector with the number of transitions to sample in each column or a single value that is applied to all columns
<code>fvar</code>	either a vector of different fertility variances or a single variance of fertility (default 1.5) that is applied to all rates
<code>...</code>	additional items are passed to <code>splitA</code> and are used to split <code>A</code> into T and F matrices

Details

The projection matrix `A` is first split into separate transition and fertility matrices. Dead fates are added to the transition matrix and the columns are then sampled from a `Multinomial` distribution based on the size in each corresponding stage class in `n`. The fertility rates are sampled from a Log Normal distribution using the `lnorms` function. The variance can be a single value which is applied to all rates, or vector of different values to apply to each rate. In this case, the values are recycled to match the number of non-zero fertilities.

Value

A resampled projection matrix

Note

see section 12.1.5.2 on parametric bootsrap in Caswell (2001)

Author(s)

Chris Stubben

See Also

[boot.transitions](#)

Examples

```

A <- hudsonia[[1]]
lambda(A)
## NOTE fertilities are in first two rows, so use r=1:2 for splitting this matrix
## resample transitions 100 times each
resample(A, 100, r=1:2)
## set higher fvar in stage 4 and 6
## because there are two fertilities per stage (8 total), need to repeat values
resample(A,1000, fvar=c(1.5, 1.5, 3, 3), r=1:2)
## OR resample based on number of plants surveyed
# data from table 6.4 and box 7.3)
n <- c(4264,3, 30, 16, 24,5)
## create a list with 1000 resampled matrices
x <- lapply(1:1000, function(x) resample(A,n, r=1:2))
mean(x)
## use var2 to check variances, especially if using different fvar values
var2(x)
## growth rates
y <- sapply(x, lambda)
quantile( y, c(0.025, .975) )
hist(y, br=30, col="palegreen", xlab="Lambda", main="1985 Hudsonia growth rates")
abline(v=quantile(y, c(0.025, .975)), lty=3)
## double the sample size (and quadruple seedlings) and you may be able to detect a decline
n <- n * 2
n[2] <- n[2] * 2
x <- lapply(1:1000, function(x) resample(A, n * 2, r=1:2))
quantile( sapply(x, lambda), c(0.025, .975) )

```

secder

Second derivatives of the dominant eigenvalue

Description

Calculates the second derivatives of the dominant eigenvalue of the demographic projection matrix for all non-zero transitions with respect to one specified transition

Usage

```
secder(A, k, l)
```

Arguments

A	projection matrix
k	row index for the specified transition
l	column index for the specified transition

Details

Function copied from demogR package after it was removed from CRAN. See section 9.7 in Caswell 2001.

Value

A square matrix of the same rank as A where each element $s_{i,j}$ is the second derivative of the dominant eigenvalue of A.

Note

The eigenvalue second derivatives are essential for calculating both perturbation analyses of the eigenvalue elasticities and stochastic sensitivities.

Author(s)

James Holland Jones

References

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

Caswell, H. 1996. Second derivatives of population growth rate: Calculation and applications. Ecology 77 (3):870-879.

See Also

[eigen.analysis](#)

Examples

```
## eigenvalue second derivatives of the US projection matrix from 1967
## with respect to infant survival
x1 <- c(0, 0.0010478, 0.0820086, 0.2884376, 0.3777064,
        0.2647110, 0.1405144, 0.0585568, 0.0134388, 0.0003327)
x2 <- diag(c(0.9972036, 0.9983625, 0.9978063, 0.9967535,
            0.9961039, 0.9948677, 0.9923658, 0.9885968, 0.9828676))
usa <- rbind(x1, cbind(x2,0))
sd21 <- secder(usa,2,1)
sd21
```

sensitivity

Sensitivity analysis of a projection matrix

Description

Calculate the sensitivities of eigenvalues to changes in the projection matrix elements

Usage

```
sensitivity(A, zero = FALSE)
```

Arguments

A	A projection matrix
zero	Set sensitivities for unobserved transitions to zero, default is FALSE

Details

see section 9.1 in Caswell (2001)

Value

A sensitivity matrix

Author(s)

Chris Stubben

References

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

See Also

[elasticity](#)

Examples

```
sens <- sensitivity(teasel)
## IMAGE plot with smaller boxes
image2(sens, mar=c(1,3.5,5,1), box.offset=.1)
  title("Sensitivity matrix using image2", line=2.5)
## MATPLOTT
matplot2(sens, log='y', type='b', yaxt='n', ltitle="Fate",
  ylab=expression(paste("Sensitivity of ",lambda)),
  main="Sensitivity matrix using matplot2")
pwrs <- -4:1
axis(2, 10^pwrs, parse(text=paste("10^", pwrs, sep = ""))), las=1)
```

`splitA`*Split a projection matrix into separate T and F matrices*

Description

Splits a projection matrix into transition and fertility matrices where $A = T + F$

Usage

```
splitA(A, r = 1, c = -1)
```

Arguments

A	a projection matrix
r	rows containing fertilities (default is first row) OR a logical matrix where TRUE is the location of a fertility value OR a complete fertility matrix
c	columns containing fertilities, default is all columns except first

Details

see section 5.1 in Caswell (2001)

Value

A list with T and F matrices

Note

By default, the fertility matrix will include elements in the first row (except first element). In some cases, it is not possible to split a projection matrix using only row and column indexes. Therefore, a logical matrix (where TRUE is the location of a fertility value) or the complete fertility matrix is also accepted.

Author(s)

Chris Stubben

References

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

See Also

functions like [generation.time](#) and [net.reproductive.rate](#) use `splitA` to split the matrix

Examples

```
splitA(whale)
# teasel -fertilitiles in last column
splitA(teasel, r=1:6, c=6)
# hudsonia - fertilities in first two columns
A <- hudsonia[[1]]
splitA(A, r=1:2)
## example using a logical matrix (if fertilities were in the upper diagonal)
splitA(A, row(A)<col(A))
# survival curves
x <- sapply(hudsonia, function(x) colSums(splitA(x, r=1:2)$T))
matplot2(t(x), legend="bottomright", ylab="Survival",
  main="Hudsonia survival curves")
```

stable.stage

Stable stage distribution

Description

Calculates the stable stage distribution of a projection matrix

Usage

```
stable.stage(A)
```

Arguments

A A projection matrix

Details

see section 4.5 in Caswell (2001)

Value

A vector containing the stable stage distribution

Author(s)

Chris Stubben

References

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

Examples

```
w <- stable.stage(teasel)
w
barplot(w, col="green", ylim=c(0,1), las=1, main="Teasel",
        ylab="Stable stage proportion", xlab="Stage class")
box()
```

stage.vector.plot *Plot stage vector projections*

Description

Plots short-term dynamics and convergence to stage stage distribution using stage vector projections

Usage

```
stage.vector.plot(stage.vectors, proportions = TRUE,
                 legend.coords = "topright", ylim = NULL, xlab = "Years",
                 ylab = NULL, col = rainbow(8), ...)
```

Arguments

stage.vectors	a matrix listing stage class vectors in columns
proportions	plot proportional changes or total numbers, defaults to proportions
legend.coords	a legend keyword or vector of x,y coordinates, defaults to top-right corner
ylim	the y limits of the plot, defaults to min and max values in stage.vectors
xlab	a label for the x axis
ylab	a label for the y axis
col	vector of line colors, defaults to rainbow(8)
...	additional options are passed to plot function

Details

see section 2.2 in Caswell 2001

Value

A plot of stage or age class projections

Author(s)

Chris Stubben

See Also

see [pop.projection](#)

Examples

```

## matrix from Example 2.1 in Caswell
A <- matrix2(c(
  0, 0.3, 0,
  1, 0, 0.5,
  5, 0, 0
), 1:3)
n <- c(1,0,0)
p <- pop.projection(A,n,60)
## Plots in Figure 2.3
stage.vector.plot(p$stage.vector[,1:15], col='black', las=1, prop=FALSE)
stage.vector.plot(p$stage.vector[,1:40], col=2:4, las=1)
## log-scale with custom y-axis
stage.vector.plot(p$stage.vector, col=2:4, prop=FALSE,
ylim=c(.01, 10), log='y', legend="bottomright", yaxt='n')
pwrs <- -2:1
# major ticks
axis(2, at = 10^pwrs, labels=parse(text=paste("10^", pwrs, sep = "")),
las=1, tcl= -.6)
# minor ticks
axis(2, at = 1:9 * rep(10^pwrs[-1] / 10, each = 9),
tcl = -0.3, labels = FALSE)

```

stoch.growth.rate *Log stochastic growth rate*

Description

Calculates the log stochastic growth rate by Tuljapukar's approximation and by simulation

Usage

```

stoch.growth.rate(matrices, prob = NULL, maxt = 50000,
  verbose = TRUE)

```

Arguments

matrices	a list with two or more projection matrices, or a matrix with one projection matrix per column, with elements filled by columns
prob	a vector of probability weights used by sample for selecting the projection matrices, defaults to equal probabilities
maxt	number of time intervals, default 50000
verbose	Print comment at start of time 1, 10000, 20000, etc.

Details

converted Matlab code from Box 7.4 in Morris and Doak (2002)

Value

A list with 3 items

approx	log stochastic growth rate by Tuljapukar's approximation
sim	log stochastic growth rate by simulation
sim.CI	confidence interval for simulation

Author(s)

Chris Stubben

References

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

See Also

[stoch.projection](#) to output population sizes from simulation

Examples

```
sgr <- stoch.growth.rate(hudsonia)
sgr
exp(sgr$approx)
```

stoch.projection

Project stochastic growth from a sequence of matrices

Description

Projects stochastic growth using whole matrix selection techniques in an independently and identically distributed (iid) environment from a set of two or more projection matrices

Usage

```
stoch.projection(matrices, n0, tmax = 50, nreps = 5000, prob = NULL,
  nmax = NULL, sumweight = rep(1, length(n0)), verbose = FALSE)
```

Arguments

matrices	a list with two or more projection matrices
n0	initial population vector
tmax	number of time steps or projection intervals to predict future population size
nreps	number of iterations
prob	a vector of probability weights used by sample for selecting the projection matrices, defaults to equal probabilities
nmax	a maximum number of individuals beyond which population projections cannot exceed. Default is no density dependence
sumweight	A vector of ones and zeros used to omit stage classes when checking density threshold. Default is to sum across all stage classes
verbose	Print comments at start of iteration 1, 100, 200, 300, etc.

Details

converted Matlab code from Box 7.3 in Morris and Doak (2002) with nmax option added to introduce simple density dependence

Value

A matrix listing final population sizes by stage class with one iteration per row.

Author(s)

Chris Stubben

References

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

Examples

```
n <- c(4264, 3,30,16,25,5)
names(n) <- c("seed", "seedlings", "tiny", "small", "medium" , "large")
## use equal and unequal probabilities for matrix selection
x.eq <- stoch.projection(hudsonia, n, nreps=1000)
x.uneq <- stoch.projection(hudsonia, n, nreps=1000, prob=c(.2,.2,.2,.4))
hist(apply(x.eq, 1, sum), xlim=c(0,5000), ylim=c(0,200), col="green",
breaks=seq(0,5000, 100), xlab="Final population size at t=50", main='')
par(new=TRUE)
## use transparency for overlapping distributions - may not work on all systems
hist(apply(x.uneq, 1, sum), xlim=c(0,5000), ylim=c(0,200), col=rgb(0, 0, 1, 0.2),
xaxt='n', yaxt='n', ylab='', xlab='', breaks=seq(0,10000, 100), main='')
legend(2500,200, c("equal", "unequal"),fill=c("green", rgb(0, 0, 1, 0.2)))
title(paste("Projection of stochastic growth for Hudsonia
using equal and unequal probabilities"), cex.main=1)
## initial pop size
```

```
sum(n)
abline(v=sum(n), lty=3)
```

stoch.quasi.ext

Quasi-extinction threshold

Description

Estimate the quasi-extinction probability by simulation for a structured population in an an independently and identically distributed stochastic environment

Usage

```
stoch.quasi.ext(matrices, n0, Nx, tmax = 50, maxruns = 10,
  nreps = 5000, prob = NULL, sumweight = NULL, verbose = TRUE)
```

Arguments

matrices	a list with two or more projection matrices, or a matrix with one projection matrix per column, with elements filled by columns
n0	initial population vector
Nx	quasi-extinction threshold
tmax	number of time steps or projection intervals
maxruns	number of times to simulate cumulative distribution function
nreps	number of iterations
prob	a vector of probability weights used by sample for selecting the projection matrices
sumweight	A vector of ones and zeros used to omit stage classes when checking quasi-extinction threshold. Default is to sum across all stage classes
verbose	Print comment at start of run 1,2,3,etc.

Details

converted Matlab code from Box 7.5 in Morris and Doak (2002)

Value

A matrix with quasi-extinction probabilities for each run by columns

Author(s)

Chris Stubben

References

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

See Also

[stoch.projection](#)

Examples

```
n <- c(4264, 3,30,16,25,5)
names(n) <- c("seed", "seedlings", "tiny", "small", "medium" , "large")
## exclude seeds using sumweight. Using 100 nreps for speed
x <- stoch.quasi.ext(hudsonia, n, Nx=10, nreps=100, sumweight=c(0,1,1,1,1,1))
matplot(x, xlab="Years", ylab="Quasi-extinction probability",
        type='l', lty=1, col=rainbow(10), las=1,
        main="Time to reach a quasi-extinction threshold
of 10 above-ground individuals")
```

stoch.sens

Stochastic growth rate sensitivity

Description

Calculates the sensitivity of the stochastic growth rate to perturbations in the mean demographic projection matrix

Usage

```
stoch.sens(A, tlimit = 100)
```

Arguments

A	a list of matrices
tlimit	time limit, default 100

Details

Function copied from demogR package after it was removed from CRAN. See section 14.4.1 in Caswell 2001.

Value

A list with two elements:

sensitivities	sensitivities of the stochastic growth rate
elasticities	elasticities of the stochastic growth rate

Author(s)

James Holland Jones

References

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, Second edition. Sinauer, Sunderland, Massachusetts, USA.

Haridas, C. V., and S. Tuljapurkar. 2005. Elasticities in variable environments: Properties and implications. American Naturalist 166 (4):481-495.

Tuljapurkar, S. 1990. Population dynamics in variable environments. Vol. 85, Lecture notes in biomathematics. Berlin: Springer-Verlag.

Tuljapurkar, S., and C. V. Haridas. 2006. Temporal autocorrelation and stochastic population growth. Ecology Letters 9 (3):324-334.

See Also

[eigen.analysis](#)

Examples

```
stoch.sens(hudsonia)
```

stretchbetaval

Stretched beta-distributed random numbers

Description

Generate a stretched beta number with mean, standard deviation, minimum and maximum values and CDF value for bounded fertility estimates

Usage

```
stretchbetaval(mn, std, minb, maxb, fx)
```

Arguments

mn	mean of a fertility rate
std	standard deviation
minb	minimum value
maxb	maximum value
fx	Cumulative Distribution Function value

Details

converted Matlab code from Box 8.5 in Morris and Doak (2002)

Value

Returns a stretched beta number with mean `mn`, standard deviation `std`, minimum and maximum values (`minb`, `maxb`) and CDF value `fx`.

Author(s)

Adapted to R by Patrick Nantel, 11 July 2005.

References

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

See Also

[betaval](#)

Examples

```
stretchbetaval(3, 1.2, 1, 20, runif(1))
# Generates stretchbeta random
# fertilities for a population of 1000 mature individuals (Ni) with mean
# fertility (f) of 3.0 and inter-individual variance in fertility (varF) of 1.5.
Ni <- 1000
f <- 2.5
varF <- 1
fmin <- 1
fmax <- 5
rndfert<-numeric(Ni)
for(i in 1:Ni) rndfert[i] <- stretchbetaval(f, sqrt(varF), fmin, fmax, runif(1))
hist(rndfert,20, main="Stretched beta-distributed random fertilities",
     xlab="Fertility rate", , col="blue")
```

teasel

Projection matrix for teasel

Description

Projection matrix with six stage classes for the plant teasel

Usage

```
teasel
```

Format

A 6 x 6 matrix

Source

Example 5.2 in Caswell 2001.

References

Caswell, H. 2001. Matrix population models. Construction, Analysis and interpretation. 2nd ed. Sinauer, Sunderland, Massachusetts.

Examples

```
teasel
image2(teasel, mar = c(1, 3.5, 5, 1), box.offset = .1)
title("Teasel projection matrix", line = 2.5)
# fertilities for a monocarpic plant in a prebreeding census in last column
splitA(teasel, r = 1:6, c = 6)
lambda(teasel)
```

test.census

Census data for hypothetical plant

Description

Three years of census data for a hypothetical plant with three stage classes

Usage

```
test.census
```

Format

A data frame with 41 census rows and 4 columns:

plant Plant id number

year Year of census

stage Stage class: seedling, vegetative, or reproductive

fruits Total number of fruits

Examples

```
test.census
stages <- c("seedling", "vegetative", "reproductive")
## Cross-tabulate stage vectors and order rows by stage
sv <- table(test.census$stage, test.census$year)[stages, ]
sv
stage.vector.plot(sv)
## set xaxt='n' to avoid fractions of a year (2002.5)
stage.vector.plot(sv, prop = FALSE, xaxt = "n", las = 1)
axis(1, 2001:2003, c(2001, 2002, 2003))
```

```

## Convert census data to state-fate transition table using reshape
reshape(test.census, direction = "wide", idvar = "plant", timevar = "year")
## Convert census data to state-fate transition table using merge
trans <- subset(
  merge(test.census, test.census, by = "plant", sort = FALSE),
  year.x == year.y - 1
)
trans
## Format column and row names
trans <- trans[, c(1:4, 6)]
colnames(trans)[2:5] <- c("year", "stage", "fruits", "fate")
rownames(trans) <- 1:nrow(trans)
## Order stage and fate columns
trans$stage <- ordered(trans$stage, levels = stages)
trans$fate <- ordered(trans$fate, levels = c(stages, "dead"))
## Select transitions for 2001-2002 and count offspring (seedlings)
trans01 <- subset(trans, year == 2001)
seedlings <- nrow(subset(test.census, year == 2002 & stage == "seedling"))
## Add individual fertilities using "anonymous reproduction" based on the
## proportional reproductive outputs of flowering plants and the total number
## of seedlings at the end of the projection interval
trans01$seedling <- trans01$fruits / sum(trans01$fruits) * seedlings
trans01
## Create transition frequency table and build T matrix
tf <- table(trans01$fate, trans01$stage)
tf
## remove "dead" fate from matrix
## T.mat<-prop.table(tf,2)[-4,]
T.mat <- prop.table(tf, 2)[stages, ]
T.mat
## Summarize stage-specific fertility rates and build F matrix
fert <- tapply(trans01$seedling, trans01$stage, mean)
fert
F.mat <- T.mat * fert
F.mat[1, ] <- fert
F.mat
## The final projection matrix is just
T.mat + F.mat
## OR use projection matrix function -
projection.matrix(trans01)

```

Description

Projection matrices for the desert tortoise *Gopherus agassizii* with 4 different fertility estimates (low, medium low, medium high, and high)

Usage

tortoise

Format

A list of 4 matrices

Source

Table 5 in Doak et al (1994). Used by Caswell (2001) in chapter 9 on sensitivity analysis.

References

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, Massachusetts, USA.

Examples

```
tortoise
A <- tortoise[["med.high"]]
# log color scale not needed
image2(A, mar = c(1, 3.5, 5, 1), log = FALSE, box.off = .1)
title("Tortoise projection matrix", line = 3)
splitA(A)
lambda(A)
sapply(tortoise, lambda)
```

var2

Variance matrix

Description

Calculates the variances from a list of matrices

Usage

var2(x)

Arguments

x A list of two or more matrices

Value

A matrix containing variances

Author(s)

Chris Stubben

Examples

```
var2(hudsonia)
```

```
varEst
```

Estimate the variance of beta-binomial vital rates

Description

Finds the best estimates of mean and environmental variance for beta-binomial vital rates using the approximation method of Akcakaya (2002)

Usage

```
varEst(rates, weighted = 1)
```

Arguments

rates	a matrix or dataframe with four columns: Rate identifier, Year, Total number of starting individuals, Number surviving (or growing)
weighted	either 1 for weighted average demographic variance, or 0 for unweighted average, default is 1

Value

A matrix with 3 columns: (1) total observed variance, (2) estimate of variance due to demographic stochasticity, and (3) estimate of variance due to environmental stochasticity.

Author(s)

Patrick Nantel, 20 June 2005. Last modified May 1st 2007.

References

Akcakaya, H. R. 2002. Estimating the variance of survival rates and fecundities. *Animal Conservation* 5: 333-336.

Kendall, B. E. 1998. Estimating the magnitude of environmental stochasticity in survivorship data. *Ecological Applications* 8(1): 184-193.

See Also

[Kendall](#)

Examples

```
varEst(woodpecker)
```

vitalsens

Vital rate sensitivities and elasticities

Description

Calculates deterministic sensitivities and elasticities of lambda to lower-level vital rates using partial derivatives

Usage

```
vitalsens(elements, vitalrates)
```

Arguments

elements	An object of mode <code>expression</code> with all matrix elements represented by zeros or symbolic vital rates
vitalrates	A list of vital rates with <code>names</code> matching expressions in elements above

Details

Vital rate sensitivities and elasticities are discussed in example 9.3 and 9.6 in Caswell (2001). Also see Chapter 9 and Box 9.1 for Matlab code in Morris and Doak (2002).

Value

A dataframe with vital rate estimates, sensitivities, and elasticities

Note

The element expressions should return the actual matrix element estimates after evaluating the variables using `eval` below.

```
A<-sapply(elements,eval,vitalrates,NULL)
```

In addition, these expressions should be arranged by rows so the following returns the projection matrix.

```
matrix(A,nrow=sqrt(length(elements)),byrow=TRUE)
```

Author(s)

Chris Stubben. Based on code posted by Simon Blomberg to R-help mailing list

References

Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*, Second edition. Sinauer, Sunderland, Massachusetts, USA.

Morris, W. F., and D. F. Doak. 2002. *Quantitative conservation biology: Theory and practice of population viability analysis*. Sinauer, Sunderland, Massachusetts, USA.

Examples

```

## emperor goose in Morris and Doak 2002.
goose.vr <- list( Ss0=0.1357, Ss1=0.8926, Sf2=0.6388, Sf3= 0.8943)
goose.el <- expression(
  0, 0, Sf2*Ss1,Sf3*Ss1,
  Ss0,0, 0, 0,
  0, Ss1,0, 0,
  0, 0, Ss1, Ss1)
## first plot effects of changing vital rates -- Figure 9.1
n <- length(goose.vr)
vr <- seq(0,1,.1)
vrсен <- matrix(numeric(n*length(vr)), ncol=n, dimnames=list(vr, names(goose.vr)))
for (h in 1:n) {
  goose.vr2 <- list( Ss0=0.1357, Ss1=0.8926, Sf2=0.6388, Sf3= 0.8943)
  for (i in 1:length(vr))
  {
    goose.vr2[[h]] <- vr[i]
    A <- matrix(sapply(goose.el, eval,goose.vr2 , NULL), nrow=sqrt(length(goose.el)), byrow=TRUE)
    vrсен[i,h] <- max(Re(eigen(A)$values))
  }
}
matplot(rownames(vrсен), vrсен, type='l', lwd=2, las=1,
  ylab="Goose population growth", xlab="Value of vital rate",
  main="Effects of changing goose vital rates")
vrн <- expression(s[0], s[""]>=1], f[2], f[""]>=3])
legend(.8, .4, vrн, lty=1:4, lwd=2, col=1:4, cex=1.2)
## then calculate sensitivities -- Table 9.1
x <- vitalsens(goose.el, goose.vr)
x
sum(x$elasticity)
barplot(t(x[,2:3]), beside=TRUE, legend=TRUE, las=1, xlab="Vital rate",
  main="Goose vital rate sensitivity and elasticity")
abline(h=0)
## Table 7 endangered lesser kestrel in Hiraldo et al 1996
kest.vr <- list(b = 0.9321, co = 0.3847, ca = 0.925, so = 0.3409, sa = 0.7107)
kest.el <- expression( co*b*so, ca*b*so, sa, sa)
x <- vitalsens(kest.el, kest.vr)
x
sum(x$elasticity)
barplot(t(x[,2:3]), beside=TRUE, las=1, xlab="Vital rate",
  main="Kestrel vital rate sensitivity and elasticity")
legend(1,1, rownames(t(x[,2:3])), fill=grey.colors(2))
abline(h=0)

```

Description

Calculates the extinction time CDF and stochastic growth rate by sampling vital rates from a beta, stretched beta, or lognormal distribution and includes within-year, auto- and cross-correlations

Usage

```
vitalsim(vrmeans, vrvars, corrin, corrou, makemx, n0, yrspan, Ne = 500,
        tmax = 50, runs = 500, vrtypes = NULL, vrmins = NULL,
        vrmaks = NULL, sumweight = NULL)
```

Arguments

vrmeans	means of vital rates
vrvars	variance of vital rates
corrin	within year correlation
corrou	between year correlations
makemx	a function that creates a square projection matrix from a vector of vrmeans
n0	initial population vector
yrspan	the number of years of correlations to build into the M12 matrix
Ne	quasi-extinction threshold
tmax	latest time to calculate extinction probability, default 50
runs	the number of trajectories, default is 500. 1000 is recommended
vrtypes	identifies the distribution for each rate in vrmeans where 1 =beta, 2 = stretched beta, 3 = lognormal, default is all ones
vrmins	minimum value for each vital rate; use zeros for rates that are not stretched betas, default is all zeros
vrmaks	maximum value for each vital rate; use zeros for rates that are not stretched betas, default is all zeros
sumweight	a vector of weights, with 0 to omit a class and 1 to include it when computing the summed density to compare to the quasi-extinction threshold, default is to include all classes

Details

Vital rates used must be either fertility values or binomial probabilities, i.e., probabilities for events with only two possible outcomes (such as survival). Means and variances of the vital rates should preferably be corrected to remove sampling errors and demographic stochasticity. Note that this version of the function does not simulate demographic stochasticity and is density-independent.

Value

Plots a histogram of log stochastic growth rates and the cumulative probability of quasi-extinction and returns a list with 4 items:

detLambda the deterministic population growth rate computed from the mean matrix

stochlambda the mean stochastic growth rate with 95% confidence intervals.
 logLambdas a vector of all log stochastic growth rates in first plot
 CDFExt a vector of cumulative probabilities of quasi-extinction in second plot

Note

The correlation matrices for *Hudsonia* in Morris and Doak 2002 include some correlations > 1 . A corrected set of correlations was sent by D. Doak on 8/4/2007. Therefore the results from the simulation below are different than the book.

Author(s)

Original MATLAB code from Box 8.10 in Morris and Doak (2002). Adapted to R by Patrick Nantel, 12 July 2005

See Also

[hudmxdef](#), [hudvrs](#) and [hudcorrs](#)

Examples

```
## set vrtypes
hudvrtypes <- c(rep(1,13), rep(3,5), rep(1,6))
## run Full model- using 100 runs here for speed
full <- vitalsim(hudvrs$mean, hudvrs$var, hudcorrs$corrin,
  hudcorrs$corrout, hudmxdef, vrtypes=hudvrtypes,
  n0=c(4264,3,30,16,25,5), yrspan=20 , runs=100)
## deterministic and stochastic lambda
full[1:2]
## log stochastic lambda
log(full$stochLambda)
sd(full$logLambdas)
## SKIP the next two simulations- however, sample output is included for plotting
##NO between year correlations so corrout = diag(0,13) - all zeros
# no.between <- vitalsim(hudvrs$mean, hudvrs$var, hudcorrs$corrin,
# diag(0,13), hudmxdef, vrtypes=hudvrtypes,
# n0=c(4264,3,30,16,25,5), yrspan=20 )
no.between <- list(CDFExt=c(rep(0,40),0.01,0.04,0.12,0.15,
0.20,0.31,0.49,0.58,0.72,0.78))
##NO correlations so corrout = diag(0,13) AND corrin=diag(13) - ones on diagonal
# no.corr<-vitalsim(hudvrs$mean, hudvrs$var, diag(13),
# diag(0,13), hudmxdef, vrtypes=hudvrtypes,
# n0=c(4264,3,30,16,25,5), yrspan=20 )
no.corr <- list(CDFExt=c(rep(0,39),0.03,0.03,0.06,0.12,0.20,
0.30,0.42,0.52,0.65,0.76,0.83))
## Figure 8.3 with corrected correlation matrices for full model
matplot(cbind(a=full$CDFExt, no.between$CDFExt, no.corr$CDFExt), type='l',
  ylim=c(0,1), lty=1:3, col=2:4, lwd=2, las=1,
  xlab="Years into the future", ylab="Cumulative probability of quasi-extinction")
legend(2,1, c("Full model", "No between-year correlations", "No correlations"),
  lty=1:3, col=2:4, lwd=2)
```

whale	<i>Projection matrix for killer whale</i>
-------	---

Description

Projection matrix for killer whales with 4 size classes: yearling, juvenile, mature and post-reproductive

Usage

whale

Format

A 4 x 4 matrix

Source

Example 5.1 in Caswell (2001)

References

Caswell, H. 2001. Matrix population models. Construction, Analysis and interpretation. 2nd ed. Sinauer, Sunderland, Massachusetts.

Examples

```
whale
splitA(whale)
lambda(whale)
sensitivity(whale)
# plot sensitivity
matplot2(sensitivity(whale),
  type = "b", legend = "topleft", ltitle = "Fate",
  main = "Killer Whale sensitivity"
)
```

woodpecker	<i>Survivorship data for adult and juvenile Acorn Woodpeckers</i>
------------	---

Description

Number of juvenile and adult Acorn Woodpeckers and survival in the Water Canyon, New Mexico population, reconstructed from Stacey and Taper (1992).

Usage

woodpecker

Format

A data frame with 18 rows and 4 columns

rate Adult or juvenile stage

year Year

start Total number of starting individuals

surv Number surviving to spring

Source

Stacey, P.B., and M. Taper. 1992. Environmental variation and the persistence of small populations. *Ecological Applications* 2: 18-29.

References

Akcakaya, H. R. 2002. Estimating the variance of survival rates and fecundities. *Animal Conservation* 5: 333-336. Kendall, B. E. 1998. Estimating the magnitude of environmental stochasticity in survivorship data. *Ecological Applications* 8(1): 184-193.

See Also

[Kendall](#) and [varEst](#)

Examples

```
woodpecker
x <- subset(woodpecker, rate == "adult")
plot(x$year, x$start,
     type = "o", pch = 16,
     ylab = "Number of adults", xlab = "Year",
     main = "Acorn Woodpeckers in Water Canyon"
)
## stage-specific survival rate
x <- aggregate(
  list(Nstart = woodpecker$start, Nsurv = woodpecker$surv),
  list(stage = woodpecker$rate), sum
)
x$survival <- x[, 3] / x[, 2]
x
```

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