Package 'popbio'

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01.Introduction

Introduction to the popbio Package

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.

02.Caswell

Converted Matlab functions from Caswell (2001)

Description

Chapter 2. Age-classified matrix models

pop. projection section 2.2. Projection of population growth rates.

Chapter 4. Stage-classified matrix models

4 02.Caswell

```
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 transiton 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 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 fertilites 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. Senstivity and elasticity of stochastic growth rate from numerical simultations

03.Morris 5

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 matricesstoch.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

1norms 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

6 aq.census

aq.census

Annual census data for Aquilegia in the southwestern US

Description

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

Usage

```
data(aq.census)
```

Format

A data frame with 2853 observations 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 infloresences 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. Please contact the data set owners to access the complete census data from 1995-2006.

Source

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

See Also

aq. trans for annual transitions with stage and fate in same row

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

aq.matrix 7

aq.matrix Create a pro	ejection 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

A data frame with transitions listing ordered stages and fates and counts of mature fruits.						
The number of observed recruits in year t + 1.						
Output projection matrix and summaries. Otherwise output transition table with added individual fertilities.						
Estimated seed survival rate for both new seeds and seed bank. Default is 12.6 percent survival.						
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 fertilites 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 recruits/(seed.bank.size + seeds.from.plants)

A projection matrix
```

8 aq.trans

lambda population growth raten initial population vectorn1 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

```
data(aq.trans)

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)</pre>
```

aq.trans

Annual transition data for Aquilegia in the southwestern US

Description

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

Usage

```
data(aq.trans)
```

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Format

plot Plot number year Staring 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

A data frame with 1637 observations on the following 9 variables.

See Also

aq.census

```
data(aq.trans)
head(aq.trans,3)
sv<-table(aq.trans$stage, aq.trans$year)</pre>
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,</pre>
xlab="Year", ylab="Proportion in stage class",
col=rainbow(4), ylim=c(0,1), xaxt='n', space=.5)
yrs<-substr(colnames(sv),3,4)</pre>
axis(1,x, yrs)
legend(2.7,1.25, rev(rownames(sv)[-1]), fill=rev(rainbow(4)), bty='n', ncol=2)
par(op)
```

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betaval

Generate beta-distributed random numbers

Description

This function 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

Returns 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

boot.transitions 11

Examples

```
betaval(.5, sd=.05)
betaval(.5, sd=.05)
## histogram with mean=0.5 and sd=0.05
x \leftarrow 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)</pre>
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

Bootstrap observed census transitions

Description

Calculate bootstrap distributions of population growth rates (lambda), 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, ...)
```

12 boot, transitions

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 lambda

matrix A matrix containing bootstrap transtion 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
```

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```
## 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"))</pre>
trans01$seedling<-trans01$fruits/sum(trans01$fruits) * seedlings</pre>
trans01
## Step by step instructions for bootstrapping dataframe
n<-nrow(trans01)
set.seed(77)
x <- sample(n, replace=TRUE)</pre>
bt<-trans01[x,]
bt
projection.matrix(bt)
## or respample by stage class counts
 lapply(split(trans01, trans01$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
data(aq.trans)
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"))</pre>
aq.96<- aq.matrix(x, rec)</pre>
# add individual fertilities to data frame only
aq.96.trans<-aq.matrix(x, rec, summary=FALSE)</pre>
# pass estimated transitions in aq.96 to projection matrix
aq.96.boot<-boot.transitions(aq.96.trans, 200,</pre>
            add=c(1,1, aq.96$seed.survival, 2,1, aq.96$recruitment.rate) )
# calculate percentile intervals using quantile()
ci<- quantile(aq.96.boot$lambda, c(0.025,0.975) )</pre>
aq.96$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

14 calathea

Description

Projection matrices for a tropical understory herb (*Calathea ovandensis*) for plots 1-4 and years 1982-1985 and the pooled matrix

Usage

```
data(calathea)
```

Format

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

Details

A projection matrix constructed using a post-breeding census with 8 size classes: seed, seedling, juvenile, pre-reproductive, and 4 reproductive classes divided by leaf area.

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.

```
data(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)) ]
# calathea[seq(1,16,4)]
# split(calathea, 1:4)[[1]]
## Growth rates -see Figure 7
x<-sapply(calathea[-17], lambda)</pre>
x<-matrix(x, nrow=4, byrow=TRUE, dimnames= list(paste("plot", 1:4), 1982:1985))
matplot2(x, type='b', ylab='Growth rate', main='Calathea growth rates')
```

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countCDFxt	Count-based extinction probabilities and bootstrap confidence intervals
	vais

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

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 probabilites (Glo, Gup).

Author(s)

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

Source

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

16 damping.ratio

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).
data(grizzly)
logN<-log(grizzly$N[-1]/grizzly$N[-39])
countCDFxt(mu=mean(logN), sig2=var(logN), nt=38, tq=38, Nc=99, Ne=20)</pre>
```

damping.ratio

Damping ratio

Description

Calculates the damping ratio of a projection matrix

Usage

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

Arguments

Α

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

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References

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

See Also

1ambda

Examples

```
## whale converges slowly to stable stage distribution
data(whale)
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)
data(calathea)
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")</pre>
```

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=TRUE)
```

Arguments

A A projection matrix

zero Set sensitivities for unobserved transitions to zero

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 inleuded as a separate function.

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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.

This function is also included in demogR package.

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
```

```
## 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
data(teasel)</pre>
```

elasticity 19

```
a<-eigen.analysis(teasel)
barplot(a$stable.stage, col="green", ylim=c(0,1),
       ylab="Stable stage proportion", xlab="Stage class", main="Teasel")
box()
op<-par(mfrow=c(2,2))</pre>
image2(teasel, cex=.8, mar=c(0.5,3,4,1))
title("Teasel projection matrix", line=3)
image2(a\$elasticities, cex=.8, mar=c(0.5,3,4,1))
title("Elasticity matrix", line=3)
## default is sensitivity for non-zero elements in matrix
image2(a\$sensitivities, cex=.8, mar=c(0.5,3,4,1))
title("Sensitivity matrix 1", line=3)
## use zero=FALSE to get sensitivities of all elements
image2(eigen.analysis(teasel, zero=FALSE)$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

Α

A projection matrix

Details

```
see section 9.2 in Caswell (2001).
```

Value

An elasticity matrix

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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

```
data(teasel)
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)]))

data(tortoise)
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]))</pre>
```

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)
```

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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

Value

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

Author(s)

Chris Stubben

Source

converted Matlab code from Box 3.3 and equation 3.5 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.

See Also

countCDFxt for bootstrap confidence intervals

```
data(grizzly)
logN<-log(grizzly$N[-1]/grizzly$N[-39])</pre>
mu<-mean(logN)</pre>
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 = "")),
##plot like fig 3.10 (p 90)
n<-seq(20, 100, 2)
exts<-numeric(length(n))</pre>
for (i in 1:length(n) )
   ex<-extCDF(mu, sig2, Nc=n[i], Ne=20)
   exts[i] < -ex[50]
}
```

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```
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 ma-

trices

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)

mean eta 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.

generation.time 23

See Also

```
see generation.time and net.reproductive.rate for other age-specific traits
```

Examples

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

generation.time

Generation time

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.

Note

Previous versions required separate T and F matrices as input

Author(s)

Chris Stubben

References

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

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See Also

see fundamental.matrix and net.reproductive.rate for other age-specific traits

Examples

```
data(whale)
generation.time(whale)
## fertilities in last column
data(teasel)
generation.time(teasel, r=1:6, c=6)
## Plot 3 from Calathea
data(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

```
data(grizzly)
```

Format

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

```
year Year of census
```

N Estimated number of female grizzlies

Details

The grizzly bear data set is used in count based PVAs in chapter 3 in Morris and Doak 2002.

Source

Table 3.1 in Morris and Doak 2002. Original data from Eberhardt et al. 1986 and Haroldson 1999. Additional details on the Interagency Grizzly Bear Study Team is available at http://nrmsc.usgs.gov/research/igbst-home.htm.

References

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

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Examples

```
data(grizzly)
attach(grizzly)
## plot like Fig 3.6 (p. 66)
plot(year, N, type='o', pch=16, las=1, xlab="Year",
ylab="Adult females", main="Yellowstone grizzly bears")
## calcualte log(Nt+1/Nt)
nt<-length(N) ## number transitions</pre>
logN < -log(N[-1]/N[-nt])
## Mean and var
c(mean=mean(logN), var=var(logN))
## or using linear regression
## transformation for unequal variances (p. 68)
x<-sqrt(year[-1]-year[-length(year)])</pre>
y<-logN/x
mod < -lm(y \sim 0 + x)
## plot like Fig 3.7
plot(x,y, xlim=c(0,1.2), ylim=c(-.3,.3), pch=16, las=1,
xlab=expression((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)</pre>
## VAR (mean square in analysis of variance table)
sig2<-anova(mod)[["Mean Sq"]][2]</pre>
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(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(N[-nt], logN)
abline(lm(logN \sim N[-nt]), lty=3)
detach(grizzly)
```

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.

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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 like x with first and last rows only

Author(s)

Chris Stubben

Examples

```
data(aq.trans)
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

```
data(hudcorrs)
```

Format

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

Author(s)

Original dataset from Morris and Doak (2002)

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.

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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

data(hudcorrs)
hudcorrs\$corrin

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

Source

Original MATLAB 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

vitalsim

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

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hudsonia

Projection matrices for mountain golden heather

Description

Projection matrices for the mountain golden heather (*Hudsonia montana*) for the years 1985 through 1988

Usage

```
data(hudsonia)
```

Format

A list of 4 matrices from 1985-1988

Details

A projection matrix with 6 size classes: seeds, seedlings, and 4 size classes divided by plant area.

Source

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

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

```
data(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)</pre>
```

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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

```
data(hudvrs)
```

Format

A data frame with 24 observations on the following 2 variables.

```
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

```
data(hudvrs)
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)
```

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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% reduc-

tion

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

Details

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.

Value

A image plot of the matrix in x

Author(s)

Chris Stubben

See Also

image

Kendall 31

Examples

```
data(calathea)
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
ΑΓΑ==01<-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

This function 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=0.00001, maxmean=1, minmean=0.01)
```

Arguments

rates

a matrix or dataframe with four columns: Rate identifier, Year, Total number of starting individuals, Number growing (or surviving).

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grades number of different levels of means and variances to try, default is 1000

maxvar maximum variance to search over, default is 0.20. The maximum ever possible

is 0.25 and searching a narrower range will improve the accuracy of the answer.

minvar minimum variance to search, default is 0.00001.

maximum limit on the mean values to search, default 1 minmean minimum limit on the mean values to search, default 0.01

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 vari-

ance estimates with 4 columns: (1) low and (3) high mean limits, (3) low and

(4) high variance limits.

Note

Note that it 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.

Source

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

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

```
## 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))</pre>
```

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```
## use fewer grades for faster loop
tor.est<-Kendall(tor, grades=200)
tor.est

data(woodpecker)
wp.est <- Kendall(woodpecker, grades=200)
wp.est</pre>
```

lambda

Population growth rate

Description

Calculates the population growth rate of a projection matrix

Usage

lambda(A)

Arguments

Α

A projection matrix

Details

```
see section 4.4 in Caswell (2001)
```

Value

The dominant eigenvalue

Note

The built-in eigen function returns eigenvalues in descreasing 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
```

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Examples

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

data(hudsonia)
sapply(hudsonia, lambda)</pre>
```

1norms

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 value of the fertility rate

var variance of the vital rate (not standard deviation)

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.

Source

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

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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")</pre>
```

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

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ylabel2 2nd y-axis label xlabel x-axix 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

Note

Added options for axis labels

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

```
data(aq.trans)
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)</pre>
```

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LTRE

Life Table Response Experiment

Description

Function to 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.

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

Author(s)

Chris Stubben

References

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

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```
###### Calathea ovandensis
data(calathea)
calathea_pool<-calathea[['pooled']]</pre>
## Create plots like FIGURE 7 in Horvitz et al 1997
##PLOTS
plots<- split(calathea[-17], rep(1:4,each=4))</pre>
## use Mean matrix since pooled not available by plot
plots<- lapply(plots, mean)</pre>
Cm<-LTRE(plots, calathea_pool)</pre>
pe<-sapply(Cm, sum)</pre>
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)</pre>
yrs <- lapply(yrs, mean)</pre>
names(yrs)<-1982:1985
Cm<-LTRE(yrs, calathea_pool)</pre>
ye<-sapply(Cm, sum)</pre>
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)</pre>
## 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(</pre>
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
```

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```
data(monkeyflower)
card<-subset(monkeyflower, species=="cardinalis" & year=="pooled")</pre>
## 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</pre>
Cm<-LTRE(Atrt, m_card_pool)</pre>
x<-sapply(Cm, sum)
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")))
## and Plot like Figure 3A
x<-matrix(unlist(Cm), nrow=4, byrow=TRUE)</pre>
colnames(x)<-paste("a", rep(1:4, each=4), 1:4, sep="")</pre>
bp<-barplot(x[1:2,], beside=TRUE, ylim=c(-.2,.2), las=1,</pre>
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")))
par(op)
```

matplot2

Plot a matrix

Description

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

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, ...)
```

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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

1sort sort legend by decreasing order of mean number in row

... additional options are passed to plot function

Details

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

Value

A matrix plot

Author(s)

Chris Stubben

See Also

```
matplot and stage.vector.plot
```

```
data(calathea)
# 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")</pre>
```

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```
# 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)</pre>
```

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

```
#Centaurea corymbosa from Freville 2004 ceco<-c(\emptyset,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)
```

42 mean.list

mean.list

Calculate mean matrix

Description

Calculates mean matrix from a list of matrices

Usage

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

Arguments

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

```
data(hudsonia)
mean(hudsonia)
## or
x <- matrix(unlist(hudsonia), ncol=length(hudsonia) )
matrix(rowMeans(x), 6, 6)</pre>
```

monkeyflower 43

monkeyflower

Projection matrices for monkeyflower

Description

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

Usage

```
data(monkeyflower)
```

Format

```
A data frame with 32 projection 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

all matrix element all; 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.

44 multiresultm

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

```
data(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")</pre>
## 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")</pre>
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

This function 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)
```

multiresultm 45

Arguments

n the vector of numbers of individuals per class at t

T a transition T matrix

F a fertility F matrix

varF a matrix of inter-individual variance in fertilities, default is NULL for simulating

population where clutch size = 1, so that fertilities give the probabilities of birth.

Value

The function returns a vector of the number of individuals per class at t+1.

Author(s)

Adapted to R by Patrick Nantel.

Source

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

References

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

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

```
data(whale)
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 \leftarrow 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)</pre>
      totalpop[i,j] <- sum(n)</pre>
   }
```

46 nematode

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

```
data(nematode)
```

Format

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

Source

Used in 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

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

net.reproductive.rate 47

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

Details

```
see section 5.3.4 in Caswell (2001).
```

Value

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

Note

Previous versions required separate T and F matrices as input

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

pfister.plot

Examples

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

Α

A list of two or more annual 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.

pop.projection 49

Examples

```
## 4 Hudsonia matrices
data(hudsonia)
pfister.plot(hudsonia)
## 3 Mimulus cardinalis matrices at Carlon
data(monkeyflower)
mim <- subset(monkeyflower, species == "cardinalis" &</pre>
    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)</pre>
vr1 <- pfister.plot(mim2)</pre>
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],</pre>
                 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")</pre>
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)
```

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Arguments

A A projection matrix

n An initial age or stage vector

iterations Number of iterations

Details

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

Value

A list with 5 items

lambda Estimate of lambda using change between the last two population counts stable.stage Estimate of stable stage distribution using proportions in last stage vector stage.vector A matrix with the number of projected individuals in each stage class pop.sizes Total number of projected individuals

pop. changes 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
```

```
## 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)</pre>
```

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```
####

data(whale)
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</pre>
```

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

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> transitions 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

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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

T Transition matrix
F Fertility matrix

Note

Individual fertilities should be the total number of offspring at the end of the census interval. Therefore, fertilites 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

```
data(test.census)
trans01 <- subset(merge(test.census, test.census, by = "plant",</pre>
                                                                    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")</pre>
## 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")</pre>
# AND order stages in dataframe
trans01$stage<-ordered(trans01$stage, stages)</pre>
```

QPmat 53

```
projection.matrix(trans01)
projection.matrix(trans01, TF=TRUE)
## Example using Aquilegia data
data(aq.trans)
sf<- subset(aq.trans, year==1998 & plot==909, c(year, plant, stage, fruits, fate))
## rows and columns of final matrix
levels(sf$stage)
## seedlings next year
seedlings<-nrow(subset(aq.trans, plot==909 & year==1999 & stage=="recruit"))</pre>
## ADD individual fertility estimates for recruits and seeds assuming seed bank and
## new seeds contribute to a common germinant pool with equal chance of recruitment
seed.survival<-.4
seed.bank.size<-1000
seeds.per.fruit<-50
seeds.from.plants<-sum(sf$fruits)*seeds.per.fruit</pre>
recruitment.rate<-seedlings/(seed.bank.size + seeds.from.plants)</pre>
## add two fertility columns
sf$recruit<- sf$fruits/sum(sf$fruits) * seeds.from.plants * recruitment.rate
sf$seed<-sf$fruits * seeds.per.fruit * seed.survival
## add seed bank survival and seed bank recruitment rate to transition matrix
A<-projection.matrix(sf, add=c(1,1, seed.survival, 2,1, recruitment.rate ))
max(Re(eigen(A)$values))
```

QPmat

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

Description

This function 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

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C C constraint matrix

b b vector

nonzero indices of the non-zero elements of the transition matrix (counting by column)

Value

A projection matrix.

Note

This function required solve.QP in the 'quadprog' package , which should be installed and loaded on the user's system.

Author(s)

Original Matlab code in Caswell (2001: 148). Adapted to R by Patrick Nantel

Source

converted Matlab code from Example 6.3 in Caswell (2001)

References

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

Examples

```
## Not run:
data(nematode)
## 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(0,0,0,0,1))
## calculate b (transpose is not necessary - either way works)
b <- apply(C, 1, max)
QPmat(nematode, C,b,nonzero)
## End(Not run)</pre>
```

reproductive.value

Stable stage distribution

Description

Calculates the reproductive values of a projection matrix

resample 55

Usage

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

Arguments

Α

A projection matrix

Details

```
see section 4.5 in Caswell (2001).
```

Value

A vector containing the reproductive values scaled 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

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

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, ...)
```

56 resample

Arguments

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

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 sample 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

trices

Note

```
see section 12.1.5.2 on parametric bootsrap in Caswell (2001)
```

Author(s)

Chris Stubben

See Also

boot.transitions

```
data(hudsonia)
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)</pre>
```

secder 57

```
## 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 differnt 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) )</pre>
```

secder

secder

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, 1)
```

Arguments

A projection matrix

k row index for the specified transition

1 column index for the specified transition

Details

Function copied from demogR package since 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, $\partial^2 \lambda / \partial a_{ij} \partial a_{kl}$.

58 sensitivity

Note

The eigenvalue second derivatives are essential for calculating both perturbation analyses of the eigenvalue elasticities and stochastic sensitivities. secder is used in functions to calculate both these quantities.

Author(s)

James Holland Jones

References

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

Caswell, H. 2001. Matrix population models: Construction, analysis, and interpretation. 2nd ed. Sunderland, MA: Sinauer.

See Also

```
eigen.analysis
```

Examples

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)
```

sensitivity 59

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
```

```
data(teasel)
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)
## MATPLOT
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)</pre>
```

60 splitA

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 (and T is just A-F)

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 internally to split the matrix

stable.stage 61

Examples

```
data(whale)
splitA(whale)
# teasel -fertilitiles in last column
data(teasel)
splitA(teasel, r=1:6, c=6)
# hudsonia - fertilities in first two columns
data(hudsonia)
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")</pre>
```

stable.stage

Stable stage distribution

Description

Calculates the stable stage distribution of a projection matrix

Usage

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

Arguments

Α

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.

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Examples

stage.vector.plot

Plot stage vector projections

Description

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

Usage

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

A plot of stage or age class projections

Author(s)

Chris Stubben

References

see section 2.2 in Caswell 2001

stoch.growth.rate 63

See Also

```
see pop.projection
```

Examples

```
## matrix from Example 2.1 in Caswell
A<-matrix(c(
0, 0.3, 0,
1, 0, 0.5,
5, 0, 0
), nrow=3, dimnames=list(1:3,1:3))
n < -c(1,0,0)
p<-pop.projection(A,n,60)</pre>
## 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

Calculate 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.

64 stoch.projection

Value

A list with 3 items

approx log stochastic growth rate by Tuljapukar's approximation

sim log stochastic growth rate by simulation sim.CI confindence interval for simulation

Author(s)

Chris Stubben

Source

converted Matlab code from Box 7.4 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

stoch.projection to output population sizes from simulation

Examples

```
data(hudsonia)
sgr<-stoch.growth.rate(hudsonia)
sgr
exp(sgr$approx)</pre>
```

stoch.projection

Simulate stochastic growth from a sequence of matrices

Description

Simulates stochastic growth by projection using whole matrix selection techniques in an independently and identically distributed (iid) environment from a set of 2 or more projection matrices

Usage

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

stoch.projection 65

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.

Value

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

Author(s)

Chris Stubben

Source

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

References

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

```
data(hudsonia)
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),</pre>
```

66 stoch.quasi.ext

```
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

Calculate 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

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 vectorNx 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 ma-

trices.

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.

Value

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

stoch.sens 67

Author(s)

Chris Stubben

Source

converted Matlab code from Box 7.5 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.

See Also

```
stoch.projection
```

Examples

```
data(hudsonia)  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

stoch.sens

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 since it was removed from CRAN. See section 14.4.1 in Caswell 2001.

68 stretchbetaval

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. 2nd ed. Sunderland, MA: Sinauer.

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-Veralg.

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

See Also

```
eigen.analysis
```

Examples

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

stretchbetaval

Generate 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)
```

stretchbetaval 69

Arguments

mn	mean of a fertility rate
std	standard deviation
minb	minimum value
maxb	maximum value

fx Cumulative Distribution Function value

Details

This function calls function 'betaval'.

Value

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

Author(s)

Original MATLAB script by Morris & Doak (2002: 283). Adapted to R by Patrick Nantel, 11 July 2005.

Source

converted Matlab code from Box 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.

See Also

betaval

```
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)</pre>
```

70 teasel

```
{
    rndfert[i] <- stretchbetaval(f, sqrt(varF), fmin, fmax, runif(1))
}
hist(rndfert,20, main="Stretched beta-distributed random fertilities",
xlab="Fertility rate", , col="blue")</pre>
```

teasel

Projection matrix for teasel

Description

Projection matrix for the plant teasel

Usage

data(teasel)

Format

A projection matrix

Source

Example 5.2

References

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

```
data(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 71

test.census

Census data for hypothetical plant

Description

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

Usage

```
data(test.census)
```

Format

```
A data frame with 41 census observations on the following variables plant Plant id number year Year of census stage Stage class: seedling, vegetative, or reproductive fruits Total number of fruits
```

```
data(test.census)
stages <- c("seedling", "vegetative", "reproductive")</pre>
## Cross-tabulate stage vectors and order rows by stage
sv<- table(test.census$stage, test.census$year)[stages,]</pre>
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),</pre>
               year.x==year.y-1)
## Format column and row names
trans<-trans[,c(1:4,6)]
colnames(trans)[2:5] <- c("year", "stage", "fruits", "fate")</pre>
rownames(trans) <- 1:nrow(trans)</pre>
## Order stage and fate columns
trans$stage <- ordered(trans$stage, levels = stages)</pre>
```

72 tortoise

```
trans$fate <- ordered(trans$fate, levels = c(stages,"dead"))</pre>
## Select transitions for 2001-2002 and count offspring (seedlings)
trans01 <- subset(trans, year==2001)</pre>
seedlings<-nrow(subset(test.census, year==2002 & stage=="seedling"))</pre>
## 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$fruits) * seedlings</pre>
trans01
## Create transition frequency table and build T matrix
tf<-table( trans01$fate, trans01$stage )
tf
## remove "dead" fate from matrix
## T.mat<-prop.table(tf,2)[-4,]</pre>
T.mat<-prop.table(tf,2)[stages,]</pre>
## Summarize stage-specific fertility rates and build F matrix
fert<-tapply(trans01$seedling, trans01$stage, mean)</pre>
F.mat<-T.mat*0
F.mat[1,]<- fert
F.mat
## The final projection matrix is just
T.mat+F.mat
## OR use projection matrix function -
projection.matrix(trans01)
```

tortoise

Projection matrices for desert tortoise

Description

Projection matrices for the desert tortoise Gopherus agassizii

Usage

```
data(tortoise)
```

Format

A list of 4 projection matrices with 4 different fertility estimates (low, medium low, medium high, and high)

var2 73

Source

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

References

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

Doak, D., P. Kareiva, and B. Kleptetka. 1994. Modeling population viability for the desert tortoise in the Western Mojave Desert. Ecological Applications 4:446-460.

Examples

```
data(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)</pre>
```

var2

Calculate a variance matrix

Description

Calculates the variances from a list of matrices

Usage

var2(x)

Arguments

Χ

A list of two or more matrices

Details

Returns a matrix containing variances from a list of matrices using a combination of unlist and apply.

Value

A matrix containing variances

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Author(s)

Chris Stubben

Examples

data(hudsonia)
var2(hudsonia)

varEst

Estimate the variance of beta-binomial vital rates using approximation method of Akcakaya

Description

This function 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 aver-

age, 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

vitalsens 75

Examples

```
data(woodpecker)
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 expression with all matrix elements represented by zeros

or symbolic vital rates.

vitalrates A list of vital rates with names 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.

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References

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

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

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(</pre>
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)</pre>
vr < -seq(0,1,.1)
vrsen<-matrix(numeric(n*length(vr)), ncol=n, dimnames=list(vr, names(goose.vr)))</pre>
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]</pre>
     A < -matrix(sapply(goose.el, eval,goose.vr2 \ , NULL), \ nrow = sqrt(length(goose.el)), \ by row = TRUE) \\
      vrsen[i,h] <- max(Re(eigen(A)$values))</pre>
}
matplot(rownames(vrsen), vrsen, type='l', lwd=2, las=1,
ylab="Goose population growth", xlab="Value of vital rate",
main="Effects of changing goose vital rates")
vrn < -expression(s[0], s["">=1], f[2], f["">=3])
legend(.8, .4, vrn, lty=1:4, lwd=2, col=1:4, cex=1.2)
## then calculate sensitivities -- Table 9.1
x<-vitalsens(goose.el, goose.vr)
sum(x$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 kestral in Hiraldo et al 1996

vitalsim 77

```
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="Kestral vital rate sensitivity and elasticity") legend(1,1, rownames(t(x[,2:3])), fill=grey.colors(2)) abline(h=0)
```

vitalsim

Calculate stochastic growth rate and extinction time CDF using vital rates with within-year, auto-, and cross-correlations

Description

This function runs a series of stochastic PVA population projections 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, corrout, makemx, n0,
yrspan, Ne=500, tmax=50,runs=500, vrtypes=NULL,
vrmins=NULL, vrmaxs=NULL, sumweight=NULL)
```

Arguments

vrmeans	means of vital rates
vrvars	variance of vital rates
corrin	within year correlation
corrout	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 $1 = \text{beta}$, $2 = \text{stretched}$ beta, $3 = \text{lognormal}$, default is all ones
vrmins	minimum value for each vital rate; use zeros for rates that are not stretched betas, default is all zeros
vrmaxs	maximum value for each vital rate; use zeros for rates that are not stretched betas, default is all zeros

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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

The function 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 program by Morris and Doak (2002: 301 - 304). Adapted to R by Patrick Nantel, 12 July 2005.

Source

converted Matlab code from Box 8.10 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

hudmxdef, hudvrs and hudcorrs

whale 79

Examples

```
## load vital rates and correlation matrices
data(hudvrs)
data(hudcorrs)
## 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$corrin,</pre>
 hudcorrs$corrout, hudmxdef, vrtypes=hudvrtypes,
n0=c(4264,3,30,16,25,5), yrspan=20 , runs=100)
## deterministic and stochastic lambda
fullΓ1:27
## 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$corrin,</pre>
# diag(0,13), hudmxdef, vrtypes=hudvrtypes,
# n0=c(4264,3,30,16,25,5), yrspan=20 )
no.between <- list(CDFExt=c(rep(0,40),0.01,0.04,0.12,0.15,
0.20,0.31,0.49,0.58,0.72,0.78))
#NO correlations so corrout = diag(0,13) AND corrin=diag(13) - ones on diagonal
# no.corr<-vitalsim(hudvrs$mean, hudvrs$var, diag(13),</pre>
# diag(0,13), hudmxdef, vrtypes=hudvrtypes,
# n0=c(4264,3,30,16,25,5), yrspan=20 )
no.corr <- list(CDFExt=c(rep(0,39),0.03,0.03,0.06,0.12,0.20,</pre>
0.30,0.42,0.52,0.65,0.76,0.83))
## Figure 8.3 with corrected correlation matrices for full model
matplot(cbind(a=full$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

Projection matrix for killer whale

Description

Projection matrix for killer whales

Usage

data(whale)

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Format

A projection matrix.

Source

Projection matrix from Example 5.1 in Caswell (2001)

References

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

Examples

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

woodpecker

Survirvorship data for adult and juvenile Acorn Woodpeckers

Description

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

Usage

```
data(woodpecker)
```

Format

A data frame with 18 observations on the following 4 variables.

```
rate Adult or juvenile stage
year Year
start Total number of starting individuals
surv Number surviving to spring
```

woodpecker 81

Source

Stacey, P.B., and M. Taper. 1992. Environmentl 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

```
data(woodpecker)
woodpecker
with(subset(woodpecker, rate=='adult'),
  plot(year, 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</pre>
```

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