

Package ‘pegas’

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ZipData no

Description Functions for reading, writing, plotting, analysing, and manipulating allelic and haplotypic data, including from VCF files, and for the analysis of population nucleotide sequences and micro-satellites including coalescent analyses, linkage disequilibrium, population structure (Fst, Amova) and equilibrium (HWE), haplotype networks, minimum spanning tree and network, and median-joining networks.

License GPL (>= 2)

URL <https://emmanuelparadis.github.io/pegas.html>

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pegas-package	<i>Population and Evolutionary Genetics Analysis System</i>
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Description

pegas provides functions for the analysis of allelic data and of haplotype data from DNA sequences. It requires and complements two other R-packages: **ape** and **adegenet**.

The complete list of functions can be displayed with `library(help = pegas)`.

More information on **pegas** can be found at <https://emmanuelparadis.github.io/pegas.html>.

Author(s)

Emmanuel Paradis, Thibaut Jombart, Zhian N. Kamvar, Brian Knaus, Alastair Potts, Klaus Schliep, David Winter

Maintainer: Emmanuel Paradis

all.equal.haploNet	<i>Compare Two Haplotype Networks</i>
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Description

This function compares two haplotype networks and returns either TRUE or a description of the differences.

Usage

```
## S3 method for class 'haploNet'
all.equal(target, current, use.steps = TRUE, ...)
```

Arguments

target, current two objects of class "haplotype".
 use.steps a logical value: whether to consider the number of steps (or length) in each link.
 ... (unused).

Details

This function should return TRUE if the two networks are identical even if the links are ordered differently. In all other situations, a vector of character strings describing the differences is returned.

As usual with the [all.equal](#) function, this cannot be used directly to return a TRUE/FALSE value (see examples).

Value

either a logical value (TRUE), or a vector of mode character.

Author(s)

Emmanuel Paradis

See Also

[haploNet](#), [mst](#)

Examples

```
data(woodmouse)
d <- dist.dna(woodmouse, "n")
nt1 <- mst(d)
nt2 <- msn(d)
(comp <- all.equal(nt1, nt2)) # clearly different

## how to use all.equal to return TRUE/FALSE:
isTRUE(comp) # FALSE
```

alleles2loci

Build Loci Object From Matrix of Alleles

Description

These functions transform a matrix of alleles into an object of class "loci", or the reverse operation.

Usage

```
alleles2loci(x, ploidy = 2, rownames = NULL, population = NULL,
             phased = FALSE)
loci2alleles(x)
```

Arguments

x	a matrix or a data frame where each column is an allele, or an object of class "loci".
ploidy	an integer specifying the level of ploidy.
rownames	an integer giving the column number to be used as rownames of the output.
population	an integer giving the column number to be used as population (if any).
phased	a logical specifying whether the genotypes should be output as phased. By default, they are unphased.

Details

Genetic data matrices are often arranged with one allele in each column of the matrix (particularly for micro-satellites), so that the number of columns is equal to the number of loci times the level of ploidy. `alleles2loci` transforms such matrices into a "loci" object.

If the rownames of the input matrix are already set, they are used in the output. Alternatively, it is possible to specify which column to use as rownames (this column will be deleted before creating the genotypes).

If the input matrix has colnames, then the names of the first column of each genotype is used as names of the output loci (see examples).

`loci2alleles` checks that all individuals have the ploidy for a given locus (if not an error occurs), but ploidy can vary among loci.

Value

an object of class "loci" or a matrix.

Author(s)

Emmanuel Paradis

See Also

[read.loci](#), [as.loci](#)

The vignette "ReadingFiles" explains how to read such a data set from Dryad (<https://datadryad.org/>).

Examples

```
x <- matrix(c("A", "A", "A", "a"), 2)
colnames(x) <- c("Loc1", NA)
y <- alleles2loci(x)
print(y, details = TRUE)
loci2alleles(y)
```

allelicrichness

Allelic Richness and Rarefaction Plots

Description

These functions analyse allelic richness.

Usage

```
allelicrichness(x, pop = NULL, method = "extrapolation", min.n = NULL)
rarefactionplot(x, maxn = nrow(x), type = "l", xlab = "Sample size",
               ylab = "Expected number of alleles", plot = TRUE, ...)
rhost(x, pop = NULL, method = "extrapolation")
```

Arguments

x	an object of class "loci".
pop	a vector or factor giving the population assignment of each row of x, or a single numeric value specifying which column of x to use as population indicator. By default, the column labelled "population" is used.
method	a character string which should be one of "extrapolation", "rarefaction", "raw" or an unambiguous abbreviation of these.
min.n	the value of n used in the rarefaction method; by default, the smallest observed number of genotypes within a population.
maxn	the largest sample size used to calculate the rarefaction curve.
type, xlab, ylab	arguments passed to plot.
plot	a logical value specifying whether to do the rarefaction plot (TRUE by default).
...	arguments passed to and from methods.

Details

allelicrichness computes for each locus in x the estimated allelic richness. Three methods are available: the extrapolation method (Foulley and Ollivier 2006), the rarefaction method (Hurlbert 1971), and the raw numbers of alleles.

rarefactionplot computes the rarefaction curves of the number of alleles with respect to sample size using Hurlbert's (1971) method. A plot is made by default.

Value

allelicrichness returns a numeric matrix.

rarefactionplot returns invisibly a list of matrices with the coordinates of the rarefaction plots for each locus.

rhost returns a numeric vector.

Author(s)

Emmanuel Paradis

References

El Mousadik, A. and Petit, R. J. (1996) High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L. Skeels)] endemic to Morocco. *Theoretical and Applied Genetics*, **92**, 832–836.

Foulley, J. L. and Ollivier, L. (2006) Estimating allelic richness and its diversity. *Livestock Science*, **101**, 150–158.

Hurlbert, S. H. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, **52**, 577–586.

Examples

```
data(jaguar)
rarefactionplot(jaguar)
allelicrichness(jaguar)
rhost(jaguar)
```

amova

Analysis of Molecular Variance

Description

This function performs a hierarchical analysis of molecular variance as described in Excoffier et al. (1992). This implementation accepts any number of hierarchical levels.

Usage

```
amova(formula, data = NULL, nperm = 1000, is.squared = FALSE)
## S3 method for class 'amova'
print(x, ...)
getPhi(sigma2)
write.pegas.amova(x, file = "")
```

Arguments

formula	a formula giving the AMOVA model to be fitted with the distance matrix on the left-hand side of the ~, and the population, region, etc, levels on its right-hand side (see details).
data	an optional data frame where to find the hierarchical levels; by default they are searched for in the user's workspace.
nperm	the number of permutations for the tests of hypotheses (1000 by default). Set this argument to 0 to skip the tests and simply estimate the variance components.
is.squared	a logical specifying whether the distance matrix has already been squared.

x	an object of class "amova".
sigma2	a named vector of variance components.
file	a file name.
...	unused (here for compatibility).

Details

The formula must be of the form $d \sim A/B/\dots$ where d is a distance object, and A, B, etc. are the hierarchical levels from the highest to the lowest one. Any number of levels is accepted, so specifying $d \sim A$ will simply test for population differentiation.

It is assumed that the rows of the distance matrix are in the same order than the hierarchical levels (which may be checked by the user).

The function `getPhi()` is a convenience function for extracting a table of hierarchical Phi-statistics for reporting. This will be an $N+1$ by N matrix where N is the number of hierarchical levels and GLOBAL is always the first row of the matrix. The matrix can read as COLUMN in ROW.

If the variance components passed to `getPhi()` are not named, they will be reported as "level 1", "level 2", etc.

Value

An object of class "amova" which is a list with a table of sums of square deviations (SSD), mean square deviations (MSD), and the number of degrees of freedom, and a vector of variance components.

Note

If there are more than three levels, approximate formulae are used to estimate the variance components.

If there is an error message like this:

```
Error in FUN(X[[1L]], ...) : 'bin' must be numeric or a factor
```

it may be that the factors you use in the formula were not read correctly. You may convert them with the function `factor`, or, before reading your data files, do this command (in case this option was modified):

```
options(stringsAsFactors = TRUE)
```

Author(s)

Emmanuel Paradis, Zhian N. Kamvar, and Brian Knaus

References

Excoffier, L., Smouse, P. E. and Quattro, J. M. (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics*, **131**, 479–491.

See Also

amova in **ade4** for an implementation of the original Excoffier et al.'s model; adonis in **vegan** for a general (multivariate) implementation of an ANOVA framework with distances.

Examples

```
### All examples below have 'nperm = 100' for faster execution times.
### The default 'nperm = 1000' is recommended.
require(ape)
data(woodmouse)
d <- dist.dna(woodmouse)
g <- factor(c(rep("A", 7), rep("B", 8)))
p <- factor(c(rep(1, 3), rep(2, 4), rep(3, 4), rep(4, 4)))
(d_gp <- amova(d ~ g/p, nperm = 100)) # 2 levels
sig2 <- setNames(d_gp$varcomp$sigma2, rownames(d_gp$varcomp))
getPhi(sig2) # Phi table
amova(d ~ p, nperm = 100) # 1 level
amova(d ~ g, nperm = 100)

## 3 levels (quite slow):
## Not run:
pop <- gl(64, 5, labels = paste0("pop", 1:64))
region <- gl(16, 20, labels = paste0("region", 1:16))
conti <- gl(4, 80, labels = paste0("conti", 1:4))
dd <- as.dist(matrix(runif(320^2), 320))
(dd_crp <- amova(dd ~ conti/region/pop, nperm = 100))
sig2 <- setNames(dd_crp$varcomp$sigma2, rownames(dd_crp$varcomp))
getPhi(sig2)

## End(Not run)
```

as.loci

Conversion Among Allelic Data Classes

Description

These functions do conversion among different allelic data classes.

Usage

```
as.loci(x, ...)
## S3 method for class 'genind'
as.loci(x, ...)
genind2loci(x)
## S3 method for class 'data.frame'
as.loci(x, allele.sep = "/", col.pop = NULL, col.loci = NULL, ...)
loci2genind(x, ploidy = 2, na.alleles = c("0", "."), unphase = TRUE)
## S3 method for class 'factor'
as.loci(x, allele.sep = "/", ...)
```

```
## S3 method for class 'character'
as.loci(x, allele.sep = "/", ...)
loci2SnpMatrix(x, checkSNP = TRUE)
```

Arguments

x	an object of class "loci" or "genind", a data frame, a factor, or a vector of mode character.
allele.sep	the character(s) separating the alleles for each locus in the data file (a forward slash by default).
col.pop	specifies whether one of the column of the data file identifies the population; default NULL, otherwise an integer or a character giving the number or the name of the column.
col.loci	a vector of integers or of characters specifying the indices or the names of the columns that are loci. By default, all columns are taken as loci except the one labelled "population", if present or specified.
ploidy	the ploidy level (see details).
na.alleles	a vector of character strings giving the alleles to be treated as missing data.
unphase	a logical value; by default, the genotypes are unphased before conversion (this should not be changed).
...	further arguments to be passed to or from other methods.
checkSNP	a logical value. If you are sure that all data in the "loci" object are SNPs, using checkSNP = FALSE makes it faster.

Details

The main objectives of these functions is to provide easy conversion between the data structures of **adegenet** and **pegas**, so both packages can be used together smoothly. In addition, it is possible to create a "loci" object directly from a data frame, a vector, or a factor.

genind2loci(x) and as.loci(x) are the same if x is of class "genind".

The ploidy level specified in loci2genind can be a vector in which case it should be of length equal to the number of individuals and will be interpreted as giving the ploidy of each of them. Note that this is different from [getPloidy](#) which returns the ploidy level of each locus.

Value

An object of class c("loci", "data.frame") for as.loci and genind2loci; an object of class "genind" for loci2genind; an object of class "SnpMatrix" for loci2SnpMatrix.

Author(s)

Emmanuel Paradis

See Also

[read.loci](#), [genind](#), [df2genind](#) for converting data frames to "genind", [alleles2loci](#)

Examples

```
x <- c("A-A", "A-a", "a-a")
as.loci(x, allele.sep = "-")
## Not run:
if (require(adeget)) {
  data(nancycats)
  x <- as.loci(nancycats)
  y <- loci2genind(x) # back to "genind"
  identical(nancycats@tab, y@tab)
  identical(nancycats@pop, y@pop)
}
## End(Not run)
```

bind.loci

*Bind Loci Objects***Description**

These functions combine objects of class "loci" by binding their rows or their columns.

Usage

```
## S3 method for class 'loci'
rbind(...)
## S3 method for class 'loci'
cbind(...)
```

Arguments

... some object(s) of class "loci", separated with commas.

Details

These two methods call `[rc]bind.data.frame` and take care to respect the attribute "locicol" of the returned object.

You can pass a data frame in the ..., but then you should bypass the generic by calling `cbind.loci` directly. Do not try to pass a vector: this will mess the "locicol" attribute. Instead, make a data frame with this vector (see examples).

Value

An object of class "loci".

Author(s)

Emmanuel Paradis

See Also

[.loci

Examples

```

a <- as.loci(data.frame(x = "A/a", y = 1), col.loci = 1)
b <- as.loci(data.frame(y = 2, x = "A/A"), col.loci = 2)
## rbind.loci reorders the columns if necessary:
str(rbind(a, b))
## cbind sets "locicol" correctly:
str(cbind(a, b))
str(cbind(b, a))
## Unexpected result...
str(cbind(a, data.frame(z = 10)))
## ... bypass the generic:
str(pegas::cbind.loci(a, data.frame(z = 10)))
## ... or much better: a$z <- 10
## Here "locicol" is not correct...
str(pegas::cbind.loci(z = 10, a))
## ... instead
str(pegas::cbind.loci(data.frame(z = 10), a))

```

by.loci

*Summary by Population or Other Factor***Description**

This is an implementation of the generic `by` function which applies a function to some data for a each level of a categorical factor.

Usage

```

## S3 method for class 'loci'
by(data, INDICES = data$population, FUN = NULL, ..., simplify = TRUE)

```

Arguments

<code>data</code>	an object of class "loci".
<code>INDICES</code>	a vector of the same length as the number of rows in data.
<code>FUN</code>	a function
<code>...</code>	(currently unused).
<code>simplify</code>	(currently unused).

Details

The default `FUN = NULL` calculates allele frequencies for each population in data.

Value

a list by default indexed by locus.

Author(s)

Emmanuel Paradis

See Also

[by](#)

Examples

```
data(jaguar)
by(jaguar)
by(na.omit(jaguar))
```

cophenetic.haploNet	<i>Cophenetic Matrix on Haplotype Networks</i>
---------------------	--

Description

This function calculates the cophenetic distance on a network. The output can be used to find nodes with short distances to most nodes.

Usage

```
## S3 method for class 'haploNet'
cophenetic(x)
```

Arguments

x an object of class "haploNet".

Details

The results of the function are likely to be approximate in most cases with reticulations in the network. In the case of MSTs, the results are exact.

Value

a numeric matrix with colnames and rownames set to the labels of the network nodes.

Author(s)

Emmanuel Paradis

See Also

[cophenetic.phylo](#) in **ape**, [cophenetic](#) for the generic function

Examples

```
example(mst)
coph <- cophenetic(r)
rowSums(coph)
```

diffHaplo

Comparison Between Two Haplotypes

Description

This function compares two haplotypes and returns a summary of the differences.

Usage

```
diffHaplo(h, a = 1, b = 2, strict = FALSE, trailingGapsAsN = TRUE)
```

Arguments

<code>h</code>	an object of class "haplotype".
<code>a, b</code>	two integers (or character strings) giving the indices (or labels) of the two haplotypes to be compared.
<code>strict</code>	a logical value; if TRUE, ambiguities and gaps in the sequences are ignored and treated as separate characters.
<code>trailingGapsAsN</code>	a logical value; if TRUE (the default), the leading and trailing alignment gaps are considered as unknown bases (i.e., N). This option has no effect if <code>strict = TRUE</code> .

Details

The options `strict` and `trailingGapsAsN` are passed to [seg.sites](#).

Value

a data frame with three columns named `pos` (position of the differences) and the labels of the two haplotypes compared.

Author(s)

Emmanuel Paradis

See Also

[haploNet](#), [haplotype](#)

Examples

```
data(woodmouse)
h <- haplotype(woodmouse)
diffHaplo(h) # compares the 1st and 2nd haplotypes
diffHaplo(h, 1, 3)
diffHaplo(h, "I", "III") # same than above but using labels
```

dist.asd

*Allelic Sharing Distance***Description**

This function computes the allelic sharing distance (ASD) for diploid genotypes.

Usage

```
dist.asd(x, scaled = TRUE, pairwise.deletion = FALSE)
```

Arguments

x an object of class "loci".

scaled a logical value specifying whether the distances should be scaled by the number of loci.

pairwise.deletion a logical value: whether to check for missing values for each pairwise comparison (see details).

Details

The ASD between two diploid genotypes is (Gao and Martin, 2009):

$$\frac{1}{L} \sum_{j=1}^L d_j$$

where L is the number loci, d_j is the value for the j th locus: 0 if both genotypes are identical, 1 if they have one allele in common, or 2 if they have no allele in common.

dist.asd works for all diploid genotypes (phased or unphased, with two alleles or more). Note that the required conditions are not checked by the present function: see the functions below.

The pairwise deletion is done with respect to missing values coded as [NA](#), not on the 'null alleles' ('0' or '.'). You may need to use the function [nullAlleles2NA](#) first if your data has genotypes with null alleles that you want to treat as missing values.

Value

an object of class "dist".

Author(s)

Emmanuel Paradis

References

Gao, X. and Martin, E. R. (2009) Using allele sharing distance for detecting human population stratification. *Human Hederity*, **68**, 182–191.

See Also

[is.snp](#), [is.phased](#), [getPloidy](#), [nullAlleles2NA](#)

Examples

```
data(jaguar)
## ASD for micro-satellites:
d <- dist.asd(jaguar)
co <- rainbow(nlevels(jaguar$pop))
plot(nj(d), "u", tip.color = co[jaguar$pop], font = 2, lab4 = "a")
legend("topleft", legend = levels(jaguar$pop), text.col = co, text.font = 2)
```

dist.hamming

Hamming Distance

Description

This function implements a general purpose Hamming distance.

Usage

```
dist.hamming(x)
```

Arguments

x a matrix or a data frame.

Details

This function should work for a wide range of data types. A typical usage would be with an object of class c("haplotype", "character").

For objects of class c("haplotype", "DNABin"), it is better to use `dist.dna(x, "n")` to compute the Hamming distances.

Value

an object of class "dist".

Author(s)

Emmanuel Paradis

See Also

[haplotype](#), [dist.haplotype.loci](#)

`edit.loci`*Edit Allelic Data with R's Data Editor*

Description

This allows to edit a data frame of class "loci" with R's spreadsheet-like data editor.

Usage

```
## S3 method for class 'loci'
edit(name, edit.row.names = TRUE, ...)
```

Arguments

<code>name</code>	an object of class "loci".
<code>edit.row.names</code>	a logical specifying to allow editing the rownames, TRUE by default (by contrast to data frames).
<code>...</code>	further arguments to be passed to or from other methods.

Details

This 'method' of the generic `edit` respects the class and the attribute "locicol" of the allelic data frame.

Value

A data frame with class `c("loci", "data.frame")`.

Author(s)

Emmanuel Paradis

See Also

[read.loci](#), [summary.loci](#)

Description

These functions compute the F -statistics developed by Patterson et al. (2012).

Usage

```
F2(x, allele.freq = NULL, population = NULL, check.data = TRUE,
   pops = NULL, jackknife.block.size = 10, B = 1e4)
F3(x, allele.freq = NULL, population = NULL, check.data = TRUE,
   pops = NULL, jackknife.block.size = 10, B = 1e4)
F4(x, allele.freq = NULL, population = NULL, check.data = TRUE,
   pops = NULL, jackknife.block.size = 10, B = 1e4)
```

Arguments

<code>x</code>	an object of class "loci".
<code>allele.freq</code>	alternatively, a list of allele (absolute) frequencies as output by <code>by.loci</code> (if this is used, <code>x</code> is ignored).
<code>population</code>	a column name or number giving which column of <code>x</code> should be treated as the population variable. By default, the column named "population" is used.
<code>check.data</code>	if FALSE, it is assumed that the user checked that all loci are strict SNPs. By default, the data are checked for the number of alleles and the non-SNP loci are dropped with a warning.
<code>pops</code>	a vector giving two, three, or four population names depending on the function. The order of these names is important (see Patterson et al. 2012). By default, the populations in <code>x</code> are taken in the order they appear, and an error is returned if the number of populations does not match the number required by the function.
<code>jackknife.block.size</code>	the size of the block used in the jackknife to assess the significance of the F -statistic (this should be around one thousandth of the number of loci, or not less than 10).
<code>B</code>	the number of replications of the bootstrap used to assess the significance of the F -statistic.

Details

These functions are provisional versions.

It is much better to compute the allele frequencies, and then use `allele.freq` with different combinations of `pops`.

Value

A vector with names.

Author(s)

Emmanuel Paradis

References

Patterson, N., Moorjani, P., Luo, Y., Mallick, S., Rohland, N., Zhan, Y., Genschoreck, T., Webster, T. and Reich, D. (2012) Ancient admixture in human history. *Genetics*, **192**, 1065–1093.

See Also

[by.loci](#), [Fst](#), the package **admixturegraph** that can draw graphs from the output of this function.

Fst	<i>F-Statistics</i>
-----	---------------------

Description

Fst computes the F_{IT} , F_{ST} and F_{IS} for each locus in the data. Rst computes the R_{ST} for microsatellites.

Usage

```
Fst(x, pop = NULL, quiet = TRUE, na.alleles = "")
Rst(x, pop = NULL, quiet = TRUE, na.alleles = "")
```

Arguments

x	an object of class "loci".
pop	a vector or factor giving the population assignment of each row of x, or a single numeric value specifying which column of x to use as population indicator. By default, the column labelled "population" is used.
quiet	a logical value: should calculations be quiet?
na.alleles	by default, only genotypes coded as NA are considered as missing data. This option is to specify if some alleles code for missing data.

Details

Fst uses the formulae in Weir and Cockerham (1984) for each allele, and then averaged within each locus over the different alleles as suggested by these authors.

Rst uses the formulae in Slatkin (1995).

Value

A matrix with genes (loci) as rows and the three *F*-statistics as columns.

Author(s)

Emmanuel Paradis

References

- Slatkin, M. (1995) A measure of population subdivision based on microsatellite allele frequencies. *Genetics*, **139**, 457–462.
- Weir, B. S. and Cockerham, C. C. (1984) Estimating F -statistics for the analysis of population structure. *Evolution*, **38**, 1358–1370.
- Weir, B. S. and Hill, W. G. (2002) Estimating F -statistics. *Annual Review of Genetics*, **36**, 721–750.

See Also

`fstat` in package **hierfstat**; package **dirmult** on CRAN that implements various estimators of the Dirichlet-multinomial distribution, including maximum likelihood and the moments estimator of Weir and Hill (2002); `Fst` in **Biodem** that calculates F_{ST} from a “kinship matrix”.

Examples

```
data(jaguar)
Fst(jaguar)
Rst(jaguar)

## no Fst but Fit and Fis in case of single population:
jaguar_corridor <- jaguar[jaguar$population == "Green Corridor", ]
Fst(jaguar_corridor)
```

geod

Geodesic Distances

Description

This function calculates geodesic (or great-circle) distances between pairs of points with their longitudes and latitudes given in (decimal) degrees.

Usage

```
geod(lon, lat = NULL, R = 6371)
```

Arguments

- | | |
|------------------|---|
| <code>lon</code> | either a vector of numeric values with the longitudes in degrees, or, if <code>lat = NULL</code> , a matrix giving the longitudes (first column) and the latitudes (second column). |
| <code>lat</code> | a vector with the latitudes. |
| <code>R</code> | the mean radius of the Earth (see details). |

Details

The default value of R is the mean radius of the Earth which is slightly smaller than the radius at the equator (6378.1 km).

Value

a numeric symmetric matrix with the distances between pairs of points in kilometres.

Author(s)

Emmanuel Paradis

References

https://en.wikipedia.org/wiki/Great-circle_distance

<https://en.wikipedia.org/wiki/Earth>

See Also

[geoTrans](#), [as.dist](#)

Examples

```
## the distance between 0N 0E and 0N 180E...
geod(c(0, 180), c(0, 0)) # ~ 20015.09 km
## ... the same using the radius of the Earth at the equator:
geod(c(0, 180), c(0, 0), 6378.1) # ~ 20037.39 km
## The same comparison for two points 5 degrees apart:
geod(c(0, 5), c(0, 0)) # ~ 555.9746 km
geod(c(0, 5), c(0, 0), 6378.1) # ~ 556.5942 km
```

geoTrans

Manipulate Geographical Coordinates

Description

geoTrans transforms geographical coordinates in degrees, minutes and seconds input as characters (or a factor) into numerical values in degrees. geoTrans2 does the reverse operation.

Usage

```
geoTrans(x, degsym = NULL, minsym = "'", secsym = "\\")
geoTrans2(lon, lat = NULL, degsym = NULL, minsym = "'",
           secsym = "\\\"", dropzero = FALSE, digits = 3,
           latex = FALSE)
```

Arguments

<code>x</code>	a vector of character strings storing geographical coordinates; this can be a factor with the levels correctly set.
<code>degSYM, minSYM, secSYM</code>	a single character giving the symbol used for degrees, minutes and seconds, respectively.
<code>lon</code>	either a vector of numeric values with the longitudes in degrees, or, if <code>lat = NULL</code> , a matrix (or a data frame) giving the longitudes in the first column and the latitudes in the second column.
<code>lat</code>	a vector with the latitudes.
<code>dropzero</code>	a logical value: if TRUE, the number of arc-seconds is dropped if it is zero; similarly for the number of arc-minutes if the number of arc-seconds is also zero.
<code>digits</code>	an integer used for rounding the number of arc-seconds.
<code>latex</code>	a logical value: if TRUE, the returned character is formatted with LaTeX code.

Details

geoTrans should be robust to any pattern of spacing around the values and the symbols (see examples). If the letter S, W, or O is found in the coordinate, the returned value is negative. Note that longitude and latitude should not be mixed in the same character strings.

geoTrans2 can be used with [cat](#) (see examples).

The default for `degSYM` (NULL) is because the degree symbol (°) is coded differently in different character encodings. By default, the function will use the appropriate character depending on the system and encoding used.

Value

geoTrans returns a numeric vector with the coordinates in degrees (eventually as decimal values).
geoTrans2 returns a character vector.

Author(s)

Emmanuel Paradis

See Also

[geod](#)

Examples

```
coord <- c("N 43°27'30\"", "N43°27'30\"", "43°27'30"N",
           "43° 27' 30\" N", "43 ° 27 ' 30 \" N",
           "43°27'30\"", "43°27.5'")
cat(coord, sep = "\n")
geoTrans(coord)
geoTrans("43 D 27.5'", degSYM = "D")
```

```

geoTrans("43° 27' 30\" S")

XL <- c(100.6417, 102.9500)
YL <- c(11.55833, 14.51667)
cat(geoTrans2(XL, YL, dropzero = TRUE), sep = "\n")
cat(geoTrans2(XL, YL, latex = TRUE), sep = "\\n")

```

getHaploNetOptions *Options to Plot haploNet Objects*

Description

These functions change the graphical options to plot haplotype networks.

Usage

```

getHaploNetOptions()
setHaploNetOptions(...)

```

Arguments

... option(s) and value(s) to be changed (separated by commas if several).

Details

The options are listed below with their default values. Most of these values use the standard R graphical parameters (see [par](#)).

- bg = "transparent": the background colour of the plot.
- labels = TRUE: whether to show the haplotype labels.
- labels.cex = 1: size of the haplotype labels.
- labels.font = 2: font of the haplotype labels.
- labels.color = "black": colour of the haplotype labels.
- link.color = "black": colour of the links.
- link.type = 1: type of line for the links.
- link.type.alt = 2: type of lines for the alternative links.
- link.width = 1: line width for the links.
- link.width.alt = 1: line width for the alternative links.
- haplotype.inner.color = "white": colour used inside the haplotype symbols.
- haplotype.outer.color = "black": colour used for the border of the haplotype symbols.
- mutations.cex = 1: size of the mutation annotations.
- mutations.font = 1: font of the mutation annotations.
- mutations.frame.background = "#0000FF4D": background colour (transparent blue).

- mutations.frame.border = "black": colour of the frame.
- mutations.text.color = 1: colour of the mutation annotations.
- mutations.arrow.color = "black": colour of the arrow pointing to the link.
- mutations.arrow.type = "triangle": type of the previous arrow.
- mutations.sequence.color = "#BFBFBF4D": colour of the sequence (transparent grey).
- mutations.sequence.end = "round": possible choices: "round", "butt", or "square" (or alternatively 0, 1, or 2).
- mutations.sequence.length = 0.3: the length of the segment showing the sequence as fraction of the graphical window.
- mutations.sequence.width = 5: thickness of this segment.
- pie.outer.color = "black": colour of the circle around pie charts.
- pie.inner.segments.color = "black": colour of the segments separating the shares of the pies.
- pie.colors.function = rainbow: function used to define colours for the frequencies.
- scale.ratio = 1: the scale ratio between links and symbol sizes.
- show.mutation = 1: option used to show mutation or not (0).

Value

getHaploNetOptions returns a list of options. The other function returns nothing.

Author(s)

Emmanuel Paradis

See Also

[plot.haploNet](#), [mutations](#)

Examples

```
getHaploNetOptions()
```

hap.div

Haplotype Diversity

Description

This function computes haplotype diversity from DNA sequences. This is a generic function.

Usage

```
hap.div(x, ...)
## S3 method for class 'haplotype'
hap.div(x, variance = FALSE, method = "Nei", ...)
## S3 method for class 'DNABin'
hap.div(x, variance = FALSE, method = "Nei", ...)
```


Arguments

x	an object with DNA data.
variance	a logical value specifying whether to calculate the variance of the estimated haplotype diversity.
method	(unused, see details).
...	further arguments passed to and from methods.

Details

Currently, only Nei and Tajima's (1981) method is available.

Value

a numeric vector with one or two values (if variance = TRUE).

Author(s)

Emmanuel Paradis

References

Nei, M. and Tajima, F. (1981) DNA polymorphism detectable by restriction endonuclease. *Genetics*, **97**, 145–163.

See Also

[nuc.div](#)

Examples

```
data(woodmouse)
hap.div(woodmouse) # all haplotypes are unique

## neuraminidase sequences from the 2009 H1N1 data (with adegenet):
if (requireNamespace("adegenet", quietly = TRUE)) {
  fl <- system.file("files/pdH1N1-NA.fasta", package = "adegenet")
  H1N1.NA <- read.dna(fl, "fasta")
  hap.div(H1N1.NA, TRUE)
}
```

haploFreq*Haplotype Frequencies With a Covariate*

Description

This utility function extracts the absolute frequencies of haplotypes with respect to a categorical variable (a factor). The output is useful when plotting haplotype networks.

Usage

```
haploFreq(x, fac, split = "_", what = 2, haplo = NULL)
```

Arguments

x	a set of DNA sequences (as an object of class "DNABin").
fac	a factor giving the categorical variable (can be missing).
split	a single character (see details).
what	a single integer (see details).
haplo	an object of class "haplotype".

Details

The frequencies of each haplotype in x are counted with respect to a factor which is either specified with fac, or extracted from the labels of x. In the second case, these labels are split with respect to the character specified in split and the what'th substrings are extracted and taken as the categorical variable (see example).

If haplo is specified, the haplotype frequencies are taken from it, otherwise they are calculated from x.

Value

a matrix of counts.

Author(s)

Klaus Schliep and Emmanuel Paradis

See Also

[haplotype](#), [haploNet](#)

Examples

```
## generate some artificial data from 'woodmouse':
data(woodmouse)
x <- woodmouse[sample(15, size = 50, replace = TRUE), ]
## labels IdXXX_PopXXX_LocXXX
rownames(x) <- paste("Id", 1:50, "_Pop", 1:2, "_Loc", 1:5, sep = "")
head(labels(x))
h <- haplotype(x)
## frequencies of haplotypes wrt 'Pop':
f.pop <- haploFreq(x, haplo = h)
## frequencies of haplotypes wrt 'Loc':
f.loc <- haploFreq(x, what = 3, haplo = h)
nt <- haploNet(h)
fq <- attr(nt, "freq")
op <- par(mfcol = c(1, 2))
plot(nt, size = fq, pie = f.pop, labels = FALSE)
plot(nt, size = fq, pie = f.loc, labels = FALSE)
par(op)
```

haploNet

Haplotype Networks

Description

haploNet computes a haplotype network. There is a plot method and two conversion functions towards other packages.

Usage

```
haploNet(h, d = NULL, getProb = TRUE)
## S3 method for class 'haploNet'
print(x, ...)
## S3 method for class 'haploNet'
plot(x, size = 1, col, bg, col.link, lwd, lty,
     shape = "circles", pie = NULL, labels, font, cex, col.lab, scale.ratio,
     asp = 1, legend = FALSE, fast = FALSE, show.mutation,
     threshold = c(1, 2), xy = NULL, ...)
## S3 method for class 'haploNet'
as.network(x, directed = FALSE, altlinks = TRUE, ...)
## S3 method for class 'haploNet'
as.igraph(x, directed = FALSE, use.labels = TRUE,
         altlinks = TRUE, ...)
## S3 method for class 'haploNet'
as.phylo(x, quiet, ...)
## S3 method for class 'haploNet'
as.evonet(x, ...)
```

Arguments

<code>h</code>	an object of class "haplotype".
<code>d</code>	an object giving the distances among haplotypes (see details).
<code>getProb</code>	a logical specifying whether to calculate Templeton's probabilities (see details).
<code>x</code>	an object of class "haploNet".
<code>size</code>	a numeric vector giving the diameter of the circles representing the haplotypes: this is in the same unit than the links and eventually recycled.
<code>col</code>	a character vector specifying the colours of the circles; eventually recycled.
<code>bg</code>	a character vector (or a function) specifying either the colours of the background of the symbols (if <code>pie = NULL</code>), or the colours of the slices of the pies (could be a function); eventually recycled.
<code>col.link</code>	a character vector specifying the colours of the links; eventually recycled.
<code>lwd</code>	a numeric vector giving the width of the links; eventually recycled.
<code>lty</code>	idem for the line types.
<code>shape</code>	the symbol shape used for the haplotypes (eventually recycled): "circles", "squares", "diamonds" (can be abbreviated).
<code>pie</code>	a matrix used to draw pie charts for each haplotype; its number of rows must be equal to the number of haplotypes.
<code>labels</code>	a logical specifying whether to identify the haplotypes with their labels (the default).
<code>font</code>	the font used for these labels (bold by default); must be an integer between 1 and 4.
<code>cex</code>	a numerical specifying the character expansion of the labels.
<code>col.lab</code>	the color of the labels.
<code>scale.ratio</code>	the ratio of the scale of the links representing the number of steps on the scale of the circles representing the haplotypes. It may be needed to give a value greater than one to avoid overlapping circles.
<code>asp</code>	the aspect ratio of the plot. Do not change the default unless you want to distort your network.
<code>legend</code>	a logical specifying whether to draw the legend, or a vector of length two giving the coordinates where to draw the legend; FALSE by default. If TRUE, the user is asked to click where to draw the legend.
<code>fast</code>	a logical specifying whether to optimize the spacing of the circles; FALSE by default.
<code>show.mutation</code>	an integer value: if 0, nothing is drawn on the links; if 1, the mutations are shown with small segments on the links; if 2, they are shown with small dots; if 3, the number of mutations are printed on the links.
<code>threshold</code>	a numeric vector with two values (or 0) giving the lower and upper numbers of mutations for alternative links to be displayed. If <code>threshold = 0</code> , alternative links are not drawn at all.
<code>directed</code>	a logical specifying whether the network is directed (FALSE by default).

<code>use.labels</code>	a logical specifying whether to use the original labels in the returned network.
<code>altlinks</code>	whether to output the alternative links when converting to another class; TRUE by default.
<code>quiet</code>	whether to give a warning when reticulations are dropped when converting a network into a tree.
<code>xy</code>	the coordinates of the nodes (see replot).
<code>...</code>	further arguments passed to plot.

Details

By default, the haplotype network is built using an infinite site model (i.e., uncorrected or Hamming distance) of DNA sequences and pairwise deletion of missing data (see [dist.dna](#)). Users may specify their own distance with the argument `d`. There is no check of labels, so the user must make sure that the distances are ordered in the same way than the haplotypes.

The probabilities calculated with Templeton et al.'s (1992) method may give non-finite values with very divergent sequences, resulting in an error from haploNet. If this happens, it may be better to use `getProb = FALSE`.

If two haplotypes are very different, haploNet will likely fail (error during integration due to non-finite values).

Value

haploNet returns an object of class "haploNet" which is a matrix where each row represents a link in the network, the first and second columns give the numbers of the linked haplotypes, the third column, named "step", gives the number of steps in this link, and the fourth column, named "Prob", gives the probability of a parsimonious link as given by Templeton et al. (1992). There are three additional attributes: "freq", the absolute frequencies of each haplotype, "labels", their labels, and "alter.links", the alternative links of the network.

`as.network` and `as.igraph` return objects of the appropriate class.

Note

Plotting haplotype networks is a difficult task. There is a vignette in **pegas** (see `vignette("PlotHaploNet")`) giving some information on this issue. You may also see two posts on *r-sig-genetics* (July 2022) that give some tricks in the situation when one haplotype is abundant and the others are in low frequencies (the symbols are likely to overlap a lot by default):

<https://stat.ethz.ch/pipermail/r-sig-genetics/2022-July/000237.html>

<https://stat.ethz.ch/pipermail/r-sig-genetics/2022-July/000238.html>

The first post explains how to use the package **network** in combination with **pegas**, and the second one gives a trick that works with **pegas** only for a similar result.

Author(s)

Emmanuel Paradis, Klaus Schliep

References

Templeton, A. R., Crandall, K. A. and Sing, C. F. (1992) A cladistic analysis of phenotypic association with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics*, **132**, 619–635.

See Also

[haplotype](#), [haploFreq](#), [replot](#), [diffHaplo](#), [mst](#), [mjn](#)

Examples

```
## generate some artificial data from 'woodmouse':
data(woodmouse)
x <- woodmouse[sample(15, size = 110, replace = TRUE), ]
h <- haplotype(x)
(net <- haploNet(h))
plot(net)
## symbol sizes equal to haplotype sizes:
plot(net, size = attr(net, "freq"), fast = TRUE)
plot(net, size = attr(net, "freq"))
plot(net, size = attr(net, "freq"), scale.ratio = 2, cex = 0.8)
```

haplotype

Haplotype Extraction and Frequencies

Description

haplotype extracts the haplotypes from a set of DNA sequences. The result can be plotted with the appropriate function.

Usage

```
haplotype(x, ...)
## S3 method for class 'DNABin'
haplotype(x, labels = NULL, strict = FALSE,
          trailingGapsAsN = TRUE, ...)
## S3 method for class 'character'
haplotype(x, labels = NULL, ...)
## S3 method for class 'numeric'
haplotype(x, labels = NULL, ...)
## S3 method for class 'haplotype'
plot(x, xlab = "Haplotype", ylab = "Number", ...)
## S3 method for class 'haplotype'
print(x, ...)
## S3 method for class 'haplotype'
summary(object, ...)
## S3 method for class 'haplotype'
sort(x,
```

```

    decreasing = ifelse(what == "frequencies", TRUE, FALSE),
    what = "frequencies", ...)
## S3 method for class 'haplotype'
x[...]

```

Arguments

<code>x</code>	a set of DNA sequences (as an object of class "DNABin"), or an object of class "haplotype".
<code>object</code>	an object of class "haplotype".
<code>labels</code>	a vector of character strings used as names for the rows of the returned object. By default, Roman numerals are given.
<code>strict</code>	a logical value; if TRUE, ambiguities and gaps in the sequences are ignored and treated as separate characters.
<code>trailingGapsAsN</code>	a logical value; if TRUE (the default), the leading and trailing alignment gaps are considered as unknown bases (i.e., N). This option has no effect if <code>strict = TRUE</code> .
<code>xlab, ylab</code>	labels for the x- and y-axes.
<code>...</code>	further arguments passed to <code>barplot</code> (unused in <code>print</code> and <code>sort</code>).
<code>decreasing</code>	a logical value specifying in which order to sort the haplotypes; by default this depends on the value of <code>what</code> .
<code>what</code>	a character specifying on what feature the haplotypes should be sorted: this must be "frequencies" or "labels", or an unambiguous abbreviation of these.

Details

The way ambiguities in the sequences are taken into account is explained in a post to r-sig-phylo (see the examples below):

<https://www.mail-archive.com/r-sig-phylo@r-project.org/msg05541.html>

The sort method sorts the haplotypes in decreasing frequencies (the default) or in alphabetical order of their labels (if `what = "labels"`). Note that if these labels are Roman numerals (as assigned by `haplotype`), their alphabetical order may not be their numerical one (e.g., IX is alphabetically before VIII).

From **pegas** 0.7, `haplotype` extracts haplotypes taking into account base ambiguities (see Note below).

Value

`haplotype` returns an object of class `c("haplotype", "DNABin")` which is an object of class "DNABin" with two additional attributes: `"index"` identifying the index of each observation that share the same haplotype, and `"from"` giving the name of the original data.

`sort` returns an object of the same class respecting its attributes.

Note

The presence of ambiguous bases and/or alignment gaps in DNA sequences can make the interpretation of haplotypes difficult. It is recommended to check their distributions with [image.DNAbin](#) and [base.freq](#) (using the options in both functions).

Comparing the results obtained playing with the options `strict` and `trailingGapsAsN` of `haplotype.DNAbin` may be useful. Note that the **ape** function [seg.sites](#) has the same two options (as from **ape** 5.4) which may be useful to find the relevant sites in the sequence alignment.

Note

There are cases where the algorithm that pools the different sequences into haplotypes has difficulties, although it seems to require a specific configuration of missing/ambiguous data. The last example below is one of them.

Author(s)

Emmanuel Paradis

See Also

[haploNet](#), [haploFreq](#), [subset.haplotype](#), [DNAbin](#) for manipulation of DNA sequences in R.

The haplotype method for objects of class "loci" is documented separately: [haplotype.loci](#).

Examples

```
## generate some artificial data from 'woodmouse':
data(woodmouse)
x <- woodmouse[sample(15, size = 110, replace = TRUE), ]
(h <- haplotype(x))
## the indices of the individuals belonging to the 1st haplotype:
attr(h, "index")[[1]]
plot(sort(h))
## get the frequencies in a named vector:
setNames(lengths(attr(h, "index")), labels(h))

fl <- tempfile(fileext = ".fas")

## data posted by Hirra Farooq on r-sig-phylo (see link above):
cat(">[A]\nCCCGATTTTATATCAACATTTATTT-----",
    ">[D]\nCCCGATTTT-----",
    ">[B]\nCCCGATTTTATATCAACATTTATTT-----",
    ">[C]\nCCCGATTTTATATCACCATTTATTTTGATT",
    file = fl, sep = "\n")
x <- read.dna(fl, "f")
unlink(fl)

## show the sequences and the distances:
alview(x)
dist.dna(x, "N", p = TRUE)
```



```
## by default there are 3 haplotypes with a warning about ambiguity:
haplotype(x)

## the same 3 haplotypes without warning:
haplotype(x, strict = TRUE)

## if we remove the last sequence there is, by default, a single haplotype:
haplotype(x[-4, ])

## to get two haplotypes separately as with the complete data:
haplotype(x[-4, ], strict = TRUE)

## a simpler example:
y <- as.DNABin(matrix(c("A", "A", "A", "A", "R", "-"), 3))
haplotype(y) # 1 haplotype
haplotype(y, strict = TRUE) # 3 haplotypes
haplotype(y, trailingGapsAsN = FALSE) # 2 haplotypes

## a tricky example with 4 sequences and 1 site:
z <- as.DNABin(matrix(c("Y", "A", "R", "N"), 4))
alview(z, showpos = FALSE)

## a single haplotype is identified:
haplotype(z)
## 'Y' has zero-distance with (and only with) 'N', so they are pooled
## together; at a later iteration of this pooling step, 'N' has
## zero-distance with 'R' (and ultimately with 'A') so they are pooled

## if the sequences are ordered differently, 'Y' and 'A' are separated:
haplotype(z[c(4, 1:3), ])
```

haplotype.loci

Haplotype Extraction and Frequencies From Allelic Data

Description

This function extracts haplotypes from phased genotypes.

Usage

```
## S3 method for class 'loci'
haplotype(x, locus = 1:2, quiet = FALSE, compress = TRUE,
          check.phase = TRUE, ...)
## S3 method for class 'haplotype.loci'
plot(x, ...)
dist.haplotype.loci(x)
```

Arguments

<code>x</code>	an object of class "loci" or of class "haplotype.loci".
<code>locus</code>	a vector of integers giving the loci to analyse.
<code>quiet</code>	a logical value specifying whether to not print the progress of the analysis (FALSE by default).
<code>compress</code>	by default only the unique haplotypes are returned with their frequencies. If <code>compress = FALSE</code> , a matrix with all observed haplotypes is returned (with the number of columns equals to the number of individuals times the ploidy level).
<code>check.phase</code>	a logical value specifying whether to check if the individual genotypes are phased.
<code>...</code>	arguments passed to and from methods.

Details

The individuals with at least one unphased genotype are ignored with a warning.

`dist.haplotype.loci` computes pairwise distances among haplotypes by counting the number of different alleles.

Checking whether the genotypes are phased can be time consuming with very big data sets. It may be useful to set `check.phase = FALSE` if several analyses are done on the same data and no warning was issued after the first scan, or you are sure that the genotypes are phased.

Value

`haplotype` returns a matrix of mode character with the loci as rows and the haplotypes as columns. The attribute "freq" gives the counts of each haplotype and the class is "haplotype.loci".

`dist.haplotype.loci` returns an object of class "dist".

Note

`haplotype` is a generic function with methods for objects of class "DNABin" and of class "loci".

Note that the class returned by these methods is different: `c("haplotype", "DNABin")` and `"haplotype.loci"`, respectively. This and other details are likely to change in the future.

Author(s)

Emmanuel Paradis

See Also

[haplotype](#), [LD](#)

heterozygosity

*Heterozygosity at a Locus Using Gene Frequencies***Description**

These functions compute the mean heterozygosity(ies) from gene frequencies, and return optionally the associated variance(s).

Usage

```
H(x, ...)
## S3 method for class 'loci'
H(x, variance = FALSE, observed = FALSE, ...)
## Default S3 method:
H(x, variance = FALSE, ...)

heterozygosity(x, variance = FALSE)
```

Arguments

<code>x</code>	an object of class "loci", or vector or a factor.
<code>variance</code>	a logical indicating whether the variance of the estimated heterozygosity should be returned (TRUE), the default being FALSE.
<code>observed</code>	a logical specifying whether to calculate the observed heterozygosity.
<code>...</code>	unused.

Details

The argument `x` can be either a factor or a vector. If it is a factor, then it is taken to give the individual alleles in the population. If it is a numeric vector, then its values are taken to be the numbers of each allele in the population. If it is a non-numeric vector, it is coerced as a factor.

The mean heterozygosity is estimated with:

$$\hat{H} = \frac{n}{n-1} \left(1 - \sum_{i=1}^k p_i^2 \right)$$

where n is the number of genes in the sample, k is the number of alleles, and p_i is the observed (relative) frequency of the i th allele.

Value

For the default method: a numeric vector of length one with the estimated mean heterozygosity (the default), or of length two if the variance is returned.

For the "loci" method: a numeric matrix with one, two, or three columns with a row for each locus and the values of heterozygosity as columns.

Author(s)

Emmanuel Paradis

References

Nei, M. (1987) *Molecular evolutionary genetics*. New York: Columbia University Press.

See Also

[theta.s](#)

Examples

```
data(jaguar)
H(jaguar, TRUE, TRUE)
## use the (old) default method:
## convert the data and compute frequencies:
S <- summary(jaguar)
## compute H for all loci:
sapply(S, function(x) H(x$allele))
## ... and its variance
sapply(S, function(x) H(x$allele, variance = TRUE))
```

hw.test

Test of Hardy–Weinberg Equilibrium

Description

This function tests, for a series of loci, the hypothesis that genotype frequencies follow the Hardy–Weinberg equilibrium. `hw.test` is a generic with methods for the classes "[loci](#)" and `genind`. Note that the latter replaces `HWE.test.genind` in the **adegenet** package.

Usage

```
hw.test(x, B = 1000, ...)
## S3 method for class 'loci'
hw.test(x, B = 1000, ...)
## S3 method for class 'genind'
hw.test(x, B = 1000, ...)
```

Arguments

<code>x</code>	an object of class " loci " or <code>genind</code> .
<code>B</code>	the number of replicates for the Monte Carlo procedure; for the regular HW test, set <code>B = 0</code> (see details).
<code>...</code>	further arguments to be passed.

Details

This test can be performed with any level of ploidy. Two versions of the test are available: the classical χ^2 -test based on the expected genotype frequencies calculated from the allelic frequencies, and an exact test based on Monte Carlo permutations of alleles (Guo and Thompson 1992). For the moment, the latter version is available only for diploids. Set $B = 0$ if you want to skip the second test.

Value

A matrix with three or four columns with the χ^2 -value, the number of degrees of freedom, the associated P -value, and possibly the P -value from the Monte Carlo test. The rows of this matrix are the different loci in x .

Author(s)

Main code by Emmanuel Paradis; wrapper for `genind` objects by Thibaut Jombart.

References

Guo, S. W. and Thompson, E. A. (1992) Performing the exact test of Hardy–Weinberg proportion for multiple alleles. *Biometrics*, **48**, 361–372.

Examples

```
## Not run:
if (require(adegenet)) {

  ## load data
  data(nancycats)

  ## test on genind object, no permutation
  hw.test(nancycats, B=0)

  ## test on loci object
  x <- as.loci(nancycats)
  hw.test(x)
}
## End(Not run)
data(jaguar)
hw.test(jaguar)
```

jaguar

Jaguar Micro-Satellites

Description

Fifty nine jaguars (*Panthera onca*) from four populations genotyped at thirteen micro-satellites by Haag et al. (2010).

Usage

```
data(jaguar)
```

Format

An object of class "loci" with 59 rows and 14 columns.

Source

Haag, T., Santos, A. S., Sana, D. A., Morato, R. G., Cullen, Jr., L., Crawshaw, Jr., P. G., De Angelo, C., Di Bitetti, M. S., Salzano, F. M. and Eizirik, E. (2010) The effect of habitat fragmentation on the genetic structure of a top predator: loss of diversity and high differentiation among remnant populations of Atlantic Forest jaguars (*Panthera onca*). *Molecular Ecology*, **22**, 4906–4921.

Haag, T., Santos, A. S., Sana, D. A., Morato, R. G., Cullen, Jr., L., Crawshaw, Jr., P. G., De Angelo, C., Di Bitetti, M. S., Salzano, F. M. and Eizirik, E. (2010) Data from: The effect of habitat fragmentation on the genetic structure of a top predator: loss of diversity and high differentiation among remnant populations of Atlantic Forest jaguars (*Panthera onca*). Dryad Digital Repository. [doi:10.5061/dryad.1884](https://doi.org/10.5061/dryad.1884)

See Also

[loci](#), [alleles2loci](#)

The vignette “ReadingFiles” explains how to read data like these from Dryad (<https://datadryad.org/>).

Examples

```
data(jaguar)
str(jaguar)
s <- summary(jaguar)
## Not run:
## works if the device is large enough:
plot(s, layout = 30, las = 2)

## End(Not run)
```

 LD

Linkage Disequilibrium

Description

These two functions analyse linkage disequilibrium in the case of phased (LD) or unphased (LD2) genotypes.

Usage

```
LD(x, locus = c(1, 2), details = TRUE)
LD2(x, locus = c(1, 2), details = TRUE)
```

Arguments

x	an object of class "loci".
locus	a vector of two integers giving the loci to analyse.
details	a logical value indicating whether to print the correlation matrix among alleles.

Details

These functions consider a pair of loci and compute the correlations among pairs of alleles.

LD first scans the data for unphased genotypes: all individuals with at least one unphased genotype are dropped with a warning. It is based on the observed frequencies of haplotypes (Zaykin et al. 2008). LD2 is based on the observed frequencies of different genotypes (Schaid 2004).

Both functions accept any number of alleles. LD can work with any level of ploidy; LD2 works with diploid data.

The present version does not test the significance of the T_2 test (Zaykin et al. 2008) with permutations. These authors present simulation results suggesting that the chi-squared approximation has similar type I error rates and power than the test based on permutations even for small sample sizes. Furthermore, this test has better statistical properties than alternatives such as those reported here (LRT and Pearson's test).

Value

For both functions, if `details = FALSE`, only the T_2 test is returned.

For LD: if `details = TRUE`, a named list with the following elements:

Observed frequencies	the counts of haplotypes in the data.
Expected frequencies	the expected frequencies of haplotypes computed from the observed proportions of alleles under the assumption of no linkage disequilibrium.
Correlations among alleles	the observed correlations among alleles from both loci.
LRT (G-squared)	the likelihood-ratio test of the null hypothesis of no linkage disequilibrium.
Pearson's test (chi-squared)	the chi-squared test based on haplotypes counts.
T_2	the T_2 test with its number of degrees of freedom (df).

For LD2: if `details = TRUE`, a named list with two elements:

Delta	the correlations among alleles (denoted <i>Delta</i> in Schaid 2004).
T_2	the T_2 test with its number of degrees of freedom (df).

Author(s)

Emmanuel Paradis

References

- Schaid, D. J. (2004) Linkage disequilibrium testing when linkage phase is unknown. *Genetics*, **166**, 505–512.
- Zaykin, D. V., Pudovkin, A. and Weir, B. S. (2008) Correlation-based inference for linkage disequilibrium with multiple alleles. *Genetics*, **180**, 533–545.

See Also

[haplotype.loci](#), [is.phased](#), [LDscan](#)

Examples

```
data(jaguar)
LD2(jaguar, details = FALSE)
LD2(jaguar, locus = 8:9, details = FALSE)
```

LDscan

Multi-Locus Linkage Disequilibrium

Description

LDscan computes a matrix of pairwise linkage disequilibrium (LD) coefficients ($|r|$) from a set of loci (which must be bi-allelic; if not, the results are not guaranteed to be meaningful). The genotypes must be phased.

LDmap plots a matrix of LD coefficients, optionally with the positions of the loci.

Usage

```
LDscan(x, ...)

## S3 method for class 'DNABin'
LDscan(x, quiet = FALSE, what = c("r", "Dprime"), ...)
## S3 method for class 'loci'
LDscan(x, depth = NULL, quiet = FALSE,
       what = c("r", "Dprime"), ...)

LDmap(d, POS = NULL, breaks = NULL, col = NULL, border = NA,
      angle = 0, asp = 1, cex = 1, scale.legend = 0.8, ...)
```

Arguments

<code>x</code>	an object of class "loci" with phased genotypes.
<code>depth</code>	a vector of integers giving the the depth(s) (or lags) at which the r 's are calculated. By default, all possible depths are considered.
<code>quiet</code>	a logical: should the progress of the operation be printed?

what	the quantity to be computed. Two choices are possible: "r" (the default) for the absolute value of the correlation between alleles and "Dprime" for the (scaled) coefficients.
d	a correlation matrix (can be an object of class "dist").
POS	an optional vector of locus positions (e.g., from a VCF file; see examples).
breaks	a vector of break intervals to count the values in d; by default, ten equally-sized intervals are used.
col	an optional vector of colours; a scale from lightyellow to red is used by default.
border	the border of the rectangles: the default is to have no border (this is not the same than default in rect ; see examples).
angle	value (in degrees) to rotate the graphic.
asp	the aspect ratio of the graphic; one by default so the elements are squares (not rectangles).
cex	the scaling of the labels and text.
scale.legend	the scaling of the legend rectangles.
...	further arguments passed to methods (LDscan) or to plot.default (LDmap).

Details

The LD coefficient r is well defined when the two loci have only two alleles. In other cases, LD is well defined (see [LD](#)) but the definition of r is not clear.

All levels of ploidy are accepted, but all loci should have the same ploidy level.

If depth is used, the r 's are calculated only for the pairs of loci that are distant by these values in x, but necessarily on the chromosome. The returned list has names set with the values of depth.

The value returned is actually $|r|$ (not r^2).

Value

LDscan returns an object of class "dist" by default, or a list if depth is used.

Author(s)

Emmanuel Paradis

See Also

[LD](#), [read.vcf](#)

Examples

```
data(woodmouse)
d <- LDscan(woodmouse)
LDmap(d, seg.sites(woodmouse), seq(0, 1, .1))

## Not run:
## Download the VCF file from Dryad:
```

```
## https://doi.org/10.5061/dryad.446sv.2

## the VCF file should have this name:
fl <- "global.pop.GATK.SNP.hard.filters.V3.phased_all.pop.maf.05.recode.vcf.gz"

info.fly <- VCFloci(fl)

## LD map from the first 100 loci:
x <- read.vcf(fl, to = 100) # read only 100 loci
res <- LDscan(x)
bks <- seq(0, 1, 0.2)
LDmap(res, info.fly$POS[1:100], bks, scale.legend = 3)

## check the chromosomes:
table(info.fly$CHROM)

## LD map from 100 loci randomly distributed on the chromosome:
s <- ceiling(seq(1, 224253, length.out = 100))
xs <- read.vcf(fl, which.loci = s)
res2 <- LDscan(xs)
LDmap(res2, info.fly$POS[s], bks, scale.legend = 3)

## something simpler with 10 loci:
x10 <- x[, 1:10]
## the VCF file has no locus IDs, so we give some here:
names(x10) <- paste0("Loc", 1:10)
res10 <- LDscan(x10, quiet = TRUE)
LDmap(res10, angle = 45, border = NULL)

## End(Not run)
```

mjn

Median-Joining Network

Description

This function computes the median-joining network (MJN) as described by Bandelt et al. (1999).

Usage

```
mjn(x, epsilon = 0, max.n.cost = 10000, prefix = "median.vector_",
    quiet = FALSE)
## S3 method for class 'mjn'
plot(x, shape = c("circles", "diamonds"),
     bg = c("green", "slategrey"), labels = FALSE, ...)
```

Arguments

x a matrix (or data frame) of DNA sequences or binary 0/1 data; an object of class "mjn" for plot.

epsilon	tolerance parameter.
max.n.cost	the maximum number of costs to be computed.
prefix	the prefix used to label the median vectors.
quiet	a logical value; by default, the progress of the calculations is printed.
shape, bg	the default shapes and colours for observed haplotypes and median vectors.
labels	by default, the labels of the haplotypes are printed.
...	other arguments passed to plot.haploNet .

Details

MJN is a network method where unobserved sequences (the median vectors) are reconstructed and included in the final network. Unlike [mst](#), [rmst](#), and [msn](#), [mjn](#) works with the original sequences, the distances being calculated internally using a Hamming distance method (with `dist(x, "manhattan")` for binary data or `dist.dna(x, "N")` for DNA sequences).

The parameter `epsilon` controls how the search for new median vectors is performed: the larger this parameter, the wider the search (see the example with binary data).

If the sequences are very divergent, the search for new median vectors can take a very long time. The argument `max.n.cost` controls how many such vectors are added to the network (the default value should avoid the function to run endlessly).

The arguments `shape` and `bg` must be of length two (unlike in [plot.haploNet](#)). It is possible to have more flexibility when plotting the MJN by changing its class, for instance with the output in the examples below: `class(nt0) <- "haploNet"`.

Value

an object of class `c("mjn", "haploNet")` with an extra attribute (`data`) containing the original data together with the median vectors.

Note

Since **pegas** 1.0, [mjn](#) is expected to run in reasonable times (less than 15 sec with 100 sequences). Bandelt et al. (1999) reported long computing times because of the need to compute a lot of median vectors. Running times also depend on the level of polymorphism in the data (see above).

Author(s)

Emmanuel Paradis

References

Bandelt, H. J., Forster, P. and Rohl, A. (1999) Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*, **16**, 37–48.

See Also

[haploNet](#), [mst](#)

Examples

```
## data in Table 1 of Bandelt et al. (1999):
x <- c(0, 0, 0, 0, 0, 0, 0, 0, 0, 0,
      1, 1, 1, 1, 0, 0, 0, 0, 0, 0,
      1, 0, 0, 0, 1, 1, 1, 0, 0, 0,
      0, 1, 1, 1, 1, 1, 1, 0, 1, 1)
x <- matrix(x, 4, 9, byrow = TRUE)
rownames(x) <- LETTERS[1:4]
(nt0 <- mjn(x))
(nt1 <- mjn(x, 1))
(nt2 <- mjn(x, 2))
plot(nt0)

## Not run:
## same like in Fig. 4 of Bandelt et al. (1999):
plotNetMDS(nt2, dist(attr(nt2, "data"), "manhattan"), 3)

## End(Not run)

## data in Table 2 of Bandelt et al. (1999):
z <- list(c("g", "a", "a", "a", "a", "a", "a", "a", "a", "a", "a", "a"),
         c("a", "g", "g", "a", "a", "a", "a", "a", "a", "a", "a", "a"),
         c("a", "a", "a", "g", "a", "a", "a", "a", "a", "a", "g", "g"),
         c("a", "a", "a", "a", "g", "g", "a", "a", "a", "a", "g", "g"),
         c("a", "a", "a", "a", "a", "a", "a", "a", "g", "g", "c", "c"),
         c("a", "a", "a", "a", "a", "a", "g", "g", "g", "g", "a", "a"))
names(z) <- c("A1", "A2", "B1", "B2", "C", "D")
z <- as.matrix(as.DNABin(z))
(ntz <- mjn(z, 2))

## Not run:
## same like in Fig. 5 of Bandelt et al. (1999):
plotNetMDS(ntz, dist.dna(attr(ntz, "data"), "N"), 3)

## End(Not run)
```

MMD

Mismatch Distribution

Description

This function draws a histogram of the frequencies of pairwise distances from a set of DNA sequences.

Usage

```
MMD(x, xlab = "Distance", main = "", rug = TRUE, legend = TRUE,
    lcol = c("blue", "red"), lty = c(1, 1), bw = 2, ...)
```

Arguments

<code>x</code>	a set of DNA sequences (object of class "DNABin").
<code>xlab</code>	the label for the x-axis.
<code>main</code>	the title (none by default).
<code>rug</code>	a logical specifying whether to add a rug of the pairwise distances on the horizontal axis (see rug).
<code>legend</code>	a logical specifying whether to draw a legend.
<code>lcol</code>	the colours used for the curves.
<code>lty</code>	the line types for the curves
<code>bw</code>	the bandwidth used for the empirical density curve (passed to density).
<code>...</code>	further arguments passed to hist .

Details

The histogram shows the observed distribution of pairwise distances. The lines show an empirical density estimate (in blue) and the expected distribution under stable population (Rogers and Harpending 1992).

Value

an invisible list with three elements:

<code>histogram</code>	the output of the hist call.
<code>empirical.density</code>	the empirical density as estimated by density .
<code>expected.curve</code>	the values of the curve expected under stable population.

Author(s)

Emmanuel Paradis and David Winter

References

Rogers, A. R. and Harpending, H. (1992) Population growth makes waves in the distribution of pairwise genetic-differences. *Molecular Biology and Evolution*, **9**, 552–569.

Examples

```
data(woodmouse)
mmd.woodm <- MMD(woodmouse)
str(mmd.woodm)
MMD(woodmouse, breaks = 20, legend = FALSE)
MMD(woodmouse, lty = 1:2, lcol = rep("black", 2), col = "lightgrey")
```

mst

*Minimum Spanning Tree and Network***Description**

Computes a minimum spanning tree (MST) using Kruskal's algorithm, the minimum spanning network using Bandelt et al.'s algorithm, or the randomized minimum spanning tree (Paradis 2018).

Usage

```
mst(d)
msn(d)
rmst(d, B = NULL, stop.criterion = NULL, iter.lim = 1000,
      quiet = FALSE, random = FALSE)
```

Arguments

d	a distance matrix, either as an object of class "dist", or a (square symmetric) matrix.
B	number of randomizations (ignored if random = FALSE).
stop.criterion	the stopping criterion if B is not given (see details; ignored if random = FALSE).
iter.lim	the maximum number of iterations (ignored if random = FALSE).
quiet	a logical value specifying whether to indicate progress of calculations.
random	the default is to find all MSTs compatible with the data. If TRUE, the random algorithm described in Paradis (2018) is used.

Details

The new default implementation of `rmst` uses an algorithm which finds all possible MSTs compatible with the data. This gives the same results than `random = TRUE` if the number of iterations is sufficiently large.

If `random = TRUE`, the calculations stop when no new links are found after a number of successive iterations specified by `stop.criterion`. By default, this number is `ceiling(sqrt(n))` where `n` is the number of observations. This criterion is ignored if `B` is given, or if `n < 6` in which case complete enumeration is done. In all cases, no more than `iter.lim` iterations are done.

The method implemented in `rmst` is not directly related to the algorithm of the same name summarized by Ramachandran (2008).

Value

an object of class "[haploNet](#)".

Note

ape has a function named `mst` which is older (and used by other packages) and returns its results in a different form. The present version is more efficient. If you want to use the older version after loading **pegas**, use `ape::mst` since **ape** will be loaded before **pegas**.

Author(s)

Emmanuel Paradis

References

- Bandelt, H. J., Forster, P. and Rohl, A. (1999) Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*, **16**, 37–48.
- Kruskal, J. B., Jr. (1956) On the shortest spanning subtree of a graph and the traveling salesman problem. *Proceedings of the American Mathematical Society*, **7**, 48–50.
- Paradis, E. (2018) Analysis of haplotype networks: the randomized minimum spanning tree method. *Methods in Ecology and Evolution*, **9**, 1308–1317.
- Paradis, E. (2025) An efficient algorithm to find all minimum spanning trees. *Journal of Complex Networks*, **13**, cnaf004.
- Ramachandran, V. (2008) Randomized Minimum Spanning Tree. *In*: Kao, M. Y. (ed) Encyclopedia of Algorithms. Pages 1747–1750. Springer, Boston, MA.

See Also[haploNet](#), [mjn](#)**Examples**

```
data(woodmouse)
d <- dist.dna(woodmouse, "n")
(r <- mst(d))
plot(r)

## a case where the RMST and the MJN are identical:
x <- c(">A", "TAAGTGCAT", ">B", "TAAATGCAT", ">C", "TAGGTGCAT", ">D", "TAAGTACAT",
      ">E", "TAAGTGTAT", ">F", "TAAGTACAC", ">G", "TAAGTACGT", ">H", "CAAGTACAC",
      ">I", "CAAGCACAC", ">J", "CAAGTACAT", ">K", "CGAGTACAT", ">L", "TAAGTACGC",
      ">M", "CAAGCACAT")
fl <- tempfile()
cat(x, file = fl, sep = "\n")
x <- read.dna(fl, "f")
tr <- rmst(dist.dna(x, "n"))
ts <- mjn(x)
stopifnot(all.equal(tr, ts))
unlink(fl)
```

mutations

*Plot Mutations on Networks***Description**

`mutations` draws annotations about mutations related to the link of a haplotype network.

Usage

```
mutations(haploNet, link, x, y, data = NULL, style = "table", POS, SELEN, ...)
```

Arguments

haploNet	an object of class "haploNet" which should be plotted beforehand.
link	the link number; can be left missing in which case the list of links in the network is printed and the function exits.
x, y	the coordinates where to draw the annotations; can be left missing: the user is then asked to click where to draw them and the chosen coordinates are printed.
data	the sequence data; can be left missing if the data are attached to the network (for a MJN network output by mjn .)
style	the type annotations. There two possible choices: "table" (default) and "sequence" (can be abbreviated).
POS, SELEN	a vector of genomic positions and the sequence length in case data is of class "haplotype.loci".
...	options

Details

The easiest way to use this function is with an output from [mjn](#) since the data are attached to the network. In other cases, the sequence data must given to the argument data or attached to the network as an attribute named "data".

Value

none

Author(s)

Emmanuel Paradis

See Also

[plot.haploNet](#), [haplotype.loci](#)

Examples

```
## simple example
x <- as.DNABin(matrix(c("a", "g"), 2, 1))
rownames(x) <- paste("Ind", 1:2, sep = "_")
nt <- mst(dist.dna(x, "N"))
plot(nt)
mutations(nt, link = 1, x = 2, y = 2, data = x)

example(mjn)
plot(nty, xlim = c(-5, 20))
mutations(nty, 6, 10, 0, style = "s")
mutations(nty, 8, 10, -2, style = "s")
```

na.omit.loci	<i>Missing Allelic Data</i>
--------------	-----------------------------

Description

The first function is a method of the generic function [na.omit](#).

`nullAlleles2NA` changes all genotypes with at least one ‘null’ allele (that is among the values in `na.alleles`) into NA.

Usage

```
## S3 method for class 'loci'  
na.omit(object, na.alleles = c("0", "."), ...)  
  
nullAlleles2NA(object, na.alleles = c("0", "."))
```

Arguments

<code>object</code>	an object of class "loci".
<code>na.alleles</code>	a vector of character strings giving the alleles to be treated as missing data.
<code>...</code>	(unused)

Details

The side effect of `na.omit` is to drop the rows (individuals) with unclearly identified genotypes, i.e., with at least one allele among `na.alleles`.

Other variables in the data table are eventually checked and levels with no observation (e.g., population) are dropped.

`nullAlleles2NA` does not remove any observation but changes these genotypes into [NA](#).

Value

an object of class "loci".

Author(s)

Emmanuel Paradis

Examples

```
data(jaguar)  
nrow(jaguar)  
nrow(na.omit(jaguar))  
nrow(nullAlleles2NA(jaguar))
```

nuc.div

*Nucleotide Diversity***Description**

This function computes the nucleotide diversity from a sample of DNA sequences or a set of haplotypes.

Usage

```
nuc.div(x, ...)
## S3 method for class 'DNABin'
nuc.div(x, variance = FALSE, pairwise.deletion = FALSE, ...)
## S3 method for class 'haplotype'
nuc.div(x, variance = FALSE, pairwise.deletion = FALSE, ...)
```

Arguments

x	a matrix or a list which contains the DNA sequences.
variance	a logical indicating whether to compute the variance of the estimated nucleotide diversity.
pairwise.deletion	a logical indicating whether to delete the sites with missing data in a pairwise way. The default is to delete the sites with at least one missing data for all sequences.
...	further arguments to be passed.

Details

This is a generic function with methods for classes "DNABin" and "haplotype". The first method uses the sum of the number of differences between pairs of sequences divided by the number of comparisons (i.e. $n(n-1)/2$, where n is the number of sequences). The second method uses haplotype frequencies. It could be that both methods give (slightly) different results because of missing or ambiguous nucleotides: this is generally solved by setting `pairwise.deletion = TRUE`.

The variance of the estimated diversity uses formula (10.9) from Nei (1987). This applies only if all sequences are of the same lengths, and cannot be used if `pairwise.deletion = TRUE`. A bootstrap estimate may be in order if you insist on using the latter option.

Value

A numeric vector with one or two values if `variance = TRUE`.

Author(s)

Emmanuel Paradis

References

Nei, M. (1987) *Molecular evolutionary genetics*. New York: Columbia University Press.

See Also

[base.freq](#), [GC.content](#), [theta.s](#), [seg.sites](#)

Examples

```
data(woodmouse)
nuc.div(woodmouse)
nuc.div(woodmouse, TRUE)
nuc.div(woodmouse, FALSE, TRUE)
```

plotNetMDS

Plot Networks With MDS Layout

Description

This function plots a haplotype network using a layout calculated from an MDS performed on the pairwise distance matrix. The haplotypes have always the same positions for different networks.

Usage

```
plotNetMDS(net, d, k = 2, show.mutation = FALSE, col = NULL, font = 2, cex = 1)
```

Arguments

net	an object of class "haploNet".
d	an object of class "dist" (or a matrix).
k	the number of dimensions of the plot (2 or 3).
show.mutation	a logical value: if TRUE, the number of steps is printed on the links.
col	the colours of the links; by default, semi-transparent green.
font	the font used to print the labels; bold by default.
cex	the character expansion of the labels.

Value

NULL

Author(s)

Emmanuel Paradis

References

Paradis, E. (2017) Analysis of haplotype networks: the randomized minimum spanning tree method. Manuscript.

See Also

[haploNet](#)

Examples

```
data(woodmouse)
d <- dist.dna(woodmouse, "n")
net <- rmst(d)
plotNetMDS(net, d)
```

R2.test

Ramos-Onsins–Rozas Test of Neutrality

Description

This function computes Ramos-Onsins and Rozas's test of neutrality for a set of DNA sequences.

Usage

```
R2.test(x, B = 1000, theta = 1, plot = TRUE, quiet = FALSE, ...)
```

Arguments

<code>x</code>	a DNA matrix (object of class "DNABin").
<code>B</code>	the number of replicates used for the simulation procedure.
<code>theta</code>	the value of the θ population parameter used in the simulation.
<code>plot</code>	a logical value specifying whether to plot the results (TRUE by default).
<code>quiet</code>	a logical value specifying whether to not display the progress of the simulations. The default is FALSE meaning that a progress bar is displayed by default.
<code>...</code>	further arguments passed to <code>hist</code> .

Value

a list with two elements: `R2` the value of the test statistic R_2 , and `P.val` the associated P -value. If `B = 0` a single value, the test statistic, is returned

Note

The simulation procedure probably needs to be tested and improved. However the results make sense so far.

Author(s)

Emmanuel Paradis

References

- Ramos-Onsins, R. and Rozas, R. (2002) Statistical properties of new neutrality tests against population growth. *Molecular Biology and Evolution*, **19**, 2092–2100.
- Sano, J. and Tachida, G. (2005) Gene genealogy and properties of test statistics of neutrality under population growth. *Genetics*, **169**, 1687–1697.

See Also

[read.dna](#), [dist.dna](#)

Examples

```
data(woodmouse)
R2.test(woodmouse, quiet = TRUE)
```

read.gtx

Read Genetix Data Files

Description

This function reads allelic data from a Genetix file (.gtx).

Usage

```
read.gtx(file)
```

Arguments

file a file name specified by either a variable of mode character or a quoted string.

Value

A data frame with class `c("loci", "data.frame")`.

Note

The package **adegenet** has a similar function, [read.genetix](#), but it returns an object of class "genind".

Author(s)

Emmanuel Paradis

References

Belkhir, K., Borsa, P., Chikhi, L., Raufaste, N. and Bonhomme, F. (1996–2004) GENETIX 4.05, logiciel sous Windows(TM) pour la genetique des populations. Laboratoire Genome, Populations, Interactions, CNRS UMR 5000, Universite de Montpellier II, Montpellier (France). <https://kimura.univ-montp2.fr/genetix/>

See Also

[read.loci](#), [write.loci](#), [read.vcf](#), [read.genetix](#)

Examples

```
if (require(adegenet)) {
  (X <- read.gtx(system.file("files/nancycats.gtx", package = "adegenet")))
  ## compare with the example in ?read.genetix
}
```

read.loci

Read Allelic Data Files

Description

This function reads allelic data from a text file: rows are individuals, and columns are loci and optional variables. By default, the first line of the file gives the locus names. If one column is labelled ‘population’, it is taken as a population variable.

Usage

```
read.loci(file, header = TRUE, loci.sep = "", allele.sep = "/"|",
          col.pop = NULL, col.loci = NULL, ...)
```

Arguments

file	a file name specified by either a variable of mode character, or a quoted string.
header	a logical specifying whether the first line of the data file gives the names of the loci (TRUE by default).
loci.sep	the character(s) separating the loci (columns) in the data file (a white space by default).
allele.sep	the character(s) separating the alleles for each locus in the data file (a forward slash by default).
col.pop	specifies whether one of the column of the data file identifies the population. By default, if one column is labelled ‘population’ (case-insensitive), it is taken as the population variable; otherwise an integer giving the number of the column or a character string giving its name. It is eventually renamed ‘population’ and transformed as a factor.

`col.loci` a vector of integers or characters specifying the indices or the names of the columns that are loci. By default, all columns are taken as loci except the population one, if present or specified.

`...` further arguments passed to `read.table` (e.g., `row.names`).

Details

The rownames of the returned object identify the individual genotypes; they are either taken from the data file if present, or given the values "1", "2", ... Similarly for the colnames: if absent in the file (in which case `header = FALSE` must be set), they are given the values "V1", "V2", ...

In the returned genotypes, alleles are separated by "/", even if it is not the case in the data file.

The vignette "Reading Genetic Data Files Into R with **adegenet** and **pegas**" explains how to read various file formats including Excel files (type `vignette("ReadingFiles")` in R).

Value

A data frame with class `c("loci", "data.frame")`. It is a data frame with an attribute "locicol" specifying the columns that must be treated as loci. The latter are factors. The other columns can be of any type.

Details on the structure can be found in <https://emmanuelparadis.github.io/pegas/DefinitionDataClassesPegas.pdf>

Author(s)

Emmanuel Paradis

See Also

[read.gtx](#), [read.vcf](#), [write.loci](#), [summary.loci](#)

read.vcf

Read Variant Calling Format Files

Description

`read.vcf` reads allelic data from VCF (variant calling format) files.

`write.vcf` writes allelic data from an object of class "loci" into a VCF file.

Usage

```
read.vcf(file, from = 1, to = 10000, which.loci = NULL, quiet = FALSE)
write.vcf(x, file, CHROM = NULL, POS = NULL, quiet = FALSE)
```

Arguments

file	a file name specified by either a variable of mode character, or a quoted string.
from, to	the loci to read; by default, the first 10,000.
which.loci	an alternative way to specify which loci to read is to give their indices (see link{VCFloci} how to obtain them).
quiet	a logical: should the progress of the operation be printed?
x	an object of class "loci".
CHROM, POS	two vectors giving the chromosomes and (genomic) positions of the loci (typically from the output of VCFloci).

Details

The VCF file can be compressed (*.gz) or not. Since pegas 0.11, compressed remote files can be read (see examples).

A TABIX file is not required (and will be ignored if present).

In the VCF standard, missing data are represented by a dot and these are read “as is” by the present function without trying to substitute by NA.

Value

an object of class `c("loci", "data.frame")`.

Note

Like for [VCFloci](#), the present function can read either compressed (*.gz) or uncompressed files. There should be no difference in performance between both types of files if they are relatively small (less than 1 Gb as uncompressed, equivalent to ~50 Mb when compressed). For bigger files, it is more efficient to uncompress them (if disk space is sufficient), especially if they have to be accessed several times during the same session.

Author(s)

Emmanuel Paradis

References

<https://www.internationalgenome.org/wiki/Analysis/vcf4.0>
<https://github.com/samtools/hts-specs>

See Also

[VCFloci](#), [read.loci](#), [read.gtx](#), [write.loci](#)

Examples

```
## Not run:
## Chr Y from the 1000 Genomes:
a <- "https://ftp-trace.ncbi.nih.gov/1000genomes/ftp/release/20130502"
b <- "ALL.chrY.phase3_integrated_v1b.20130502.genotypes.vcf.gz"
## WARNING: the name of the file above may change
url <- paste(a, b, sep = "/")
## Solution 1: download first
download.file(url, "chrY.vcf.gz")
## no need to uncompress:
(info <- VCFloci("chrY.vcf.gz"))
str(info) # show the modes of the columns
## Solution 2: read remotely (since pegas 0.11)
info2 <- VCFloci(url)
identical(info, info2)
rm(info2)

SNP <- is.snp(info)
table(SNP) # how many loci are SNPs?
## compare with:
table(getINFO(info, "VT"))

op <- par(mfcol = c(4, 1), xpd = TRUE)
lim <- c(2.65e6, 2.95e6)
## distribution of SNP and non-SNP mutations along the Y chr:
plot(info$POS, !SNP, "h", col = "red", main = "non-SNP mutations",
      xlab = "Position", ylab = "", yaxt = "n")
rect(lim[1], -0.1, lim[2], 1.1, lwd = 2, lty = 2)
plot(info$POS, SNP, "h", col = "blue", main = "SNP mutations",
      xlab = "Position", ylab = "", yaxt = "n")
rect(lim[1], -0.1, lim[2], 1.1, lwd = 2, lty = 2)
par(xpd = FALSE)
## same focusing on a smaller portion of the chromosome:
plot(info$POS, !SNP, "h", col = "red", xlim = lim, xlab = "Position",
      ylab = "", yaxt = "n")
plot(info$POS, SNP, "h", col = "blue", xlim = lim, xlab = "Position",
      ylab = "", yaxt = "n")
par(op)

## read both types of mutations separately:
X.SNP <- read.vcf("chrY.vcf.gz", which.loci = which(SNP))
X.other <- read.vcf("chrY.vcf.gz", which.loci = which(!SNP))

identical(rownames(X.SNP), VCFlabels("chrY.vcf.gz")) # TRUE
cat(VCFheader("chrY.vcf.gz"))

## get haplotypes for the first 10 loci:
h <- haplotype(X.SNP, 1:10)
## plot their frequencies:
op <- par(mar = c(3, 10, 1, 1))
plot(h, horiz=TRUE, las = 1)
par(op)
```

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

replot

Edit the Layout of a Haplotype Network

Description

This function makes possible to change the layout of a haplotype network interactively or with specified coordinates.

Usage

```
replot(xy = NULL, col.identifier = "purple", ...)
```

Arguments

<code>xy</code>	an optional list with vectors names <code>x</code> and <code>y</code> (or <code>xx</code> and <code>yy</code>) giving the coordinates of the nodes.
<code>col.identifier</code>	the colour used to identify the node to be moved.
<code>...</code>	further arguments passed to <code>plot</code> .

Details

This function can be used in two ways. By default (i.e., `replot()`), the user can edit a plotted haplotype network by clicking with the mouse on the graphical window: a message is printed asking to click once close to the node to move and then clicking again where this node should be placed (careful: two separate single clicks). Editing is stopped with a right click.

The second possible use is to specify the new coordinates of the nodes with the argument `xy`, typically, from a previous call to `replot` (see examples).

Since **pegas** 1.0, these coordinates can be used directly in `plot.haploNet` making possible to combine networks with other graphics (which not possible with `replot` because the network is replotted).

Value

a named list with two numeric vectors (`x` and `y`).

Note

For users of RStudio: the function does not work within this application. It seems the best is to run R from a shell (or maybe opening a new graphical device with [X11](#)).

Author(s)

Emmanuel Paradis

See Also

[haploNet](#), [haploFreq](#)

Examples

```
## a non-interactive example:
example(mjn)
layout(matrix(1:2, 1))
plot(ntz, labels = TRUE)
## it is possible plot this network with no line-crossing
## with these coordinates:
xy <- list(x = c(3.2, -2.6, -6.6, -7.2, 0, 3.5, 2.6, -2.9, -0.3, 3.4, -3.4),
           y = c(3.4, 4.4, 1.3, -3.9, -5.5, -10.9, 0.1, -0.8, -2.3, -7.9, -8.1))
replot(ntz, xy = xy) # or plot(ntz, xy = xy, labels = TRUE)
layout(1)

## an interactive example:
## Not run:
data(woodmouse)
net <- haploNet(haploptype(woodmouse))
plot(net)
o <- replot() # interactive
## click to rearrange the network at will...
## then do a different plot using the same coordinates:
plot(net, bg = "red", labels = FALSE, show.mutation = 2)
replot(o) # not interactive

## End(Not run)
```

rr.test

Tajima Relative Rate Test of Molecular Clock

Description

This function tests the hypothesis of a molecular evolutionary clock (i.e., a constant rate of molecular evolution) between two samples using an outgroup sample. It can be applied to both nucleotide and amino acid sequences.

Usage

```
rr.test(x, y, out)
```

Arguments

x, y	a single DNA sequence (object class "DNABin").
out	a single DNA sequence to be used as outgroup.

Value

a list with two numeric values: Chi (Chi-squared statistic) and Pval (the P-value).

Author(s)

Alastair Potts <potts.a@gmail.com>

References

Tajima, F. (1993) Simple methods for testing molecular clock hypothesis. *Genetics*, **135**, 599–607. (Equation 4)

Examples

```
require(ape)
data(woodmouse)
rr.test(x = woodmouse[2, ], y = woodmouse[3, ], out = woodmouse[1, ])

# Test all pairs in a sample:
outgroup <- woodmouse[1, ]
n <- nrow(woodmouse)
cc <- combn(2:n, 2)
FUN <- function(x)
  rr.test(woodmouse[x[1], ], woodmouse[x[2], ], outgroup)$Pval
OUT <- apply(cc, 2, FUN)
### two ways to arrange the output:
RES <- matrix(NA, n - 1, n - 1)
RES[row(RES) > col(RES)] <- OUT
RES <- t(RES)
RES[row(RES) > col(RES)] <- OUT
RES <- t(RES)
dimnames(RES) <- list(2:n, 2:n)
RES <- as.dist(RES)
### 2nd method:
class(OUT) <- "dist"
attr(OUT, "Labels") <- as.character(2:15)
attr(OUT, "Size") <- n - 1L
attr(OUT, "Diag") <- attr(OUT, "Upper") <- FALSE
### they are the same:
all(OUT == RES)
```

site.spectrum

Site Frequency Spectrum

Description

site.spectrum computes the (un)folded site frequency spectrum of a set of aligned DNA sequences or SNPs.

Usage

```

site.spectrum(x, ...)
## S3 method for class 'DNABin'
site.spectrum(x, folded = TRUE, outgroup = 1, ...)
## S3 method for class 'loci'
site.spectrum(x, folded = TRUE, ancestral = NULL, ...)
## S3 method for class 'spectrum'
plot(x, col = "red", main = NULL, ...)

```

Arguments

x	a set of DNA sequences (as an object of class "DNABin"), or an object of class "spectrum".
folded	a logical specifying whether to compute the folded site frequency spectrum (the default), or the unfolded spectrum if folded = FALSE.
outgroup	a single integer value giving which sequence is ancestral; ignored if folded = TRUE.
ancestral	a vector of ancestral alleles (required if folded = FALSE), typically from an output of VCFloci .
col	the colour of the barplot (red by default).
main	a character string for the title of the plot; a generic title is given by default (use main = "" to have no title).
...	further arguments passed to barplot , or to other methods.

Details

Under the infinite sites model of mutation, mutations occur on distinct sites, so every segregating (polymorphic) site defines a partition of the n sequences (see Wakeley, 2009). The *site frequency spectrum* is a series of values where the i th element is the number of segregating sites defining a partition of i and $n - i$ sequences. The *unfolded* version requires to define an ancestral state with an external (outgroup) sequence, so i varies between 1 and $n - 1$. If no ancestral state can be defined, the *folded* version is computed, so i varies between 1 and $n/2$ or $(n - 1)/2$, for n even or odd, respectively.

If folded = TRUE, sites with more than two states are ignored and a warning is returned giving how many were found.

If folded = FALSE, sites with an ambiguous state at the external sequence are ignored and a warning is returned giving how many were found. Note that it is not checked if some sites have more than two states.

If x is an object of class "loci", the loci which are not biallelic (e.g., SNPs) are dropped with a warning.

Value

site.spectrum returns an object of class "spectrum" which is a vector of integers (some values may be equal to zero) with the attributes "sample.size" and "folded" (a logical value) indicating which version of the spectrum has been computed.

Author(s)

Emmanuel Paradis

References

Wakeley, J. (2009) *Coalescent Theory: An Introduction*. Greenwood Village, CO: Roberts and Company Publishers.

See Also

[DNABin](#) for manipulation of DNA sequences in R, [haplotype](#)

Examples

```
require(ape)
data(woodmouse)
(sp <- site.spectrum(woodmouse))
plot(sp)
```

stairway

The Stairway Plot

Description

This function fits a model of population change using the site frequency spectrum (SFS). The default assumes $\Theta = 1$. A model of population change estimates the temporal changes in Θ with respect to the value of this parameter at present time. The model is specified by the user with the option `epoch`.

Usage

```
stairway(x, epoch = NULL, step.min = 1e-6, step.max = 1e-3)
## S3 method for class 'stairway'
plot(x, type = "S", xlab = "Coalescent intervals",
      ylab = expression(Theta), ...)
## S3 method for class 'stairway'
lines(x, type = "S", ...)
```

Arguments

<code>x</code>	an object of class site.spectrum or of class <code>stairway</code> .
<code>epoch</code>	an optional vector of integers giving the periods of time (or epochs) with distinct Θ .
<code>step.min</code>	a single numeric value giving the smallest step size used during optimization.
<code>step.max</code>	id. for the largest step size (see nlminb).
<code>type</code>	the type of lines.
<code>xlab, ylab</code>	the default labels on the axes.
<code>...</code>	further arguments passed to other methods.

Details

The basic method implemented in this function is similar to Polanski and Kimmel (2003). The temporal model with “epochs” is from Liu and Fu (2015).

Value

By default, a single numeric value with the null deviance. If epoch is used, a list with the following components:

estimates	the maximum likelihood estimates.
deviance	the deviance of the fitted model.
null.deviance	the deviance of the null model.
LRT	the likelihood-ratio test comparing the null and the fitted models.
AIC	the Akaike information criterion of the fitted model.

Author(s)

Emmanuel Paradis

References

- Liu, X. M. and Fu, Y. X. (2015) Exploring population size changes using SNP frequency spectra. *Nature Genetics*, **47**, 555–559.
- Polanski, A. and Kimmel, M. (2003) New explicit expressions for relative frequencies of single-nucleotide polymorphisms with application to statistical inference on population growth. *Genetics*, **165**, 427–436.

See Also

[site.spectrum](#), [nlminb](#)

Examples

```
data(woodmouse)
sp <- site.spectrum(woodmouse)
stairway(sp, c(1, 1, 1, 1, 1, 1, 1, 1, 2, 2, 2, 2, 2, 2))
```

subset.haplotype

Subsetting and Filtering Haplotypes

Description

This function selects haplotypes based on their (absolute) frequencies and/or proportions of missing nucleotides.

Usage

```
## S3 method for class 'haplotype'
subset(x, minfreq = 1, maxfreq = Inf, maxna = Inf, na = c("N", "?"), ...)
```

Arguments

x	an object of class c("haplotype", "DNABin").
minfreq, maxfreq	the lower and upper limits of (absolute) haplotype frequencies. By default, all haplotypes are selected whatever their frequency.
maxna	the maximum frequency (absolute or relative; see details) of missing nucleotides within a given haplotype.
na	a vector of mode character specifying which nucleotide symbols should be treated as missing data; by default, unknown nucleotide (N) and completely unknown site (?) (can be lower- or uppercase). There are two shortcuts: see details.
...	unused.

Details

The value of maxna can be either less than one, or greater or equal to one. In the former case, it is taken as specifying the maximum proportion (relative frequency) of missing data within a given haplotype. In the latter case, it is taken as the maximum number (absolute frequency).

na = "all" is a shortcut for all ambiguous nucleotides (including N) plus alignment gaps and completely unknown site (?).

na = "ambiguous" is a shortcut for only ambiguous nucleotides (including N).

Value

an object of class c("haplotype", "DNABin").

Author(s)

Emmanuel Paradis

See Also

[haplotype](#)

Examples

```
data(woodmouse)
h <- haplotype(woodmouse)
subset(h, maxna = 20)
subset(h, maxna = 20/ncol(h)) # same thing than above
```


summary.loci

*Print and Summaries of Loci Objects***Description**

These functions print and summarize table of alleles and loci (objects of class "loci").

Usage

```
## S3 method for class 'loci'
print(x, details = FALSE, ...)
## S3 method for class 'loci'
summary(object, ...)
## S3 method for class 'summary.loci'
print(x, ...)
## S3 method for class 'loci'
x[i, j, drop = FALSE]
## S3 method for class 'summary.loci'
plot(x, loci, what = "both", layout = 1, col = c("blue", "red"), ...)
```

Arguments

x, object	an object of class "loci" or "summary.loci".
details	a logical value: if TRUE the data are printed as a data frame; the default is FALSE.
i, j	indices of the rows and/or columns to select or to drop. They may be numeric, logical, or character (in the same way than for standard R objects).
drop	a logical specifying whether to returned an object of the smallest dimension possible, i.e., may return a vector or a factor if drop = TRUE (this is not the default).
loci	the loci (genes) to be plotted. By default, all loci are plotted.
what	the frequencies to be plotted. Three choices are possible: "alleles", "genotypes", and "both" (the default), or any unambiguous abbreviations.
layout	the number of graphs to be plotted simultaneously.
col	the colours used for the barplots.
...	further arguments to be passed to or from other methods.

Details

Genotypes not observed in the data frame are not counted.

When using the [method, if only one column is extracted and the option drop = TRUE, or if the returned data frame has no 'locus' column, then the class "loci" is dropped. The option drop = FALSE (default) keeps the class (see examples).

An object of class "loci" can be edited in the R data editor with, e.g., fix(x) or x <- edit(x).

summary.loci computes the absolute frequencies (counts); see the examples on how to compute the relative frequencies (proportions).

Value

`summary.loci` returns a list with the genes as names and each element made a list with two vectors "genotype" and "allele" with the frequencies (numbers) of genotypes and alleles, respectively. The names of these two vectors are the observed genotypes and alleles.

`print` and `plot` methods return `NULL`.

Author(s)

Emmanuel Paradis

See Also

[read.loci](#), [getAlleles](#), [edit.loci](#)

Examples

```
data(jaguar)
s <- summary(jaguar)
## Not run:
## works if the device is large enough:
plot(s, layout = 30, las = 2)
layout(1)

## End(Not run)
## compute the relative frequencies:
rapply(s, function(x) x/sum(x), how = "replace")
## extract a single locus:
jaguar[, 1]
jaguar[, 1, drop = TRUE] # returns a vector
jaguar[[1]]             # also returns a vector
```

SW

Sliding Windows

Description

Applies a function over a matrix or a vector using sliding windows. `sw` is a generic function with a method for "DNABin" matrices.

Usage

```
sw(x, width, step, ...)
## Default S3 method:
sw(x, width = 100, step = 50, POS = NULL,
   FUN = mean, out.of.pos = NA_real_, na.rm = TRUE, L = NULL, ...)
## S3 method for class 'DNABin'
sw(x, width = 100, step = 50, FUN = GC.content,
   rowAverage = FALSE, quiet = TRUE, ...)
```

```
## S3 method for class 'sw'
plot(x, type = "l", xlab = "Position", x.scaling = 1,
     show.ranges = FALSE, col.ranges = "blue",
     lty.ranges = 1, lwd.ranges = 1, ...)
```

Arguments

x	a vector or a matrix.
width	an integer giving the window width.
step	an integer giving the step separating successive windows.
POS	a numeric vector giving the positions of the sites.
FUN	the function to be applied to the windows.
rowAverage	a logical value: if TRUE, FUN is applied over all rows of x; if FALSE (the default) FUN is applied to each row of x.
out.of.pos	the values used for the sites which are not in POS.
na.rm	option passed to FUN.
L	the length of the chromosome (or sequence). If not given, this is largest value in POS or the length of x if POS is not given.
quiet	a logical value: if FALSE, the progress of the calculations is printed.
type	the type of plotting (see plot.default).
xlab	the label under the x-axis.
x.scaling	the scaling of the x-axis.
show.ranges	a logical value specifying whether to show the ranges of the windows with horizontal segments (ignored with a warning if x is a matrix).
col.ranges, lty.ranges, lwd.ranges	arguments to modify the appearance of the above segments (see segments).
...	further arguments passed to and from methods.

Details

FUN should return a single value.

x should be a matrix for the "DNABin" method, or a vector for the default one.

For the default method, the vector x is expanded into a vector of length L (see above on how this value is found) and the positions which are not in POS are filled with the value given in `out.of.pos`. The resulting vector is then analysed with the function FUN which must have an option `na.rm`. If the function you want to use does not have this option, you can use something like `FUN = function(x, na.rm = TRUE) foo(x[!is.na(x)])`, replacing 'foo' by the name of your function. You may also include more control on the handling of missing data.

Value

a matrix or a vector (if `rowAverage = TRUE`).

Author(s)

Emmanuel Paradis

Examples

```
data(woodmouse)
sw(woodmouse)
sw(woodmouse, 200, 200)
sw(woodmouse, 200, 200, rowAverage = TRUE)

## to get the proportions of G:
foo <- function(x) base.freq(x)["g"]
sw(woodmouse, 200, 200, FUN = foo, rowAverage = TRUE)

## a simulated example with the default method:
x <- runif(100)
pos <- sort(sample(1e6, 100))
resx <- sw(x, w = 2e4, s = 5e3, POS = pos, L = 1e6)
plot(resx, show.ranges = TRUE, x.scaling = 1e6, xlab = "Position (Mb)")
```

tajima.test	<i>Test of the Neutral Mutation Hypothesis</i>
-------------	--

Description

This function tests the neutral mutation hypothesis with Tajima’s *D*.

Usage

```
tajima.test(x)
```

Arguments

x a set of DNA sequences (object of class "DNABin").

Value

A list with three numeric values:

D	Tajima’s <i>D</i> statistic.
Pval.normal	the p-value assuming that <i>D</i> follows a normal distribution with mean zero and variance one.
Pval.beta	the p-value assuming that <i>D</i> follows a beta distribution after rescaling on [0, 1] (Tajima, 1989).

Note

Alignment gaps in the sequences are ignored when calculating pairwise distances.

Author(s)

Emmanuel Paradis

References

Tajima, F. (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*, **123**, 595–595.

Examples

```
require(ape)
data(woodmouse)
tajima.test(woodmouse)
```

theta.h

Population Parameter THETA using Homozygosity

Description

This function computes the population parameter THETA using the homozygosity (or mean heterozygosity) from gene frequencies.

Usage

```
theta.h(x, standard.error = FALSE)
```

Arguments

x a vector or a factor.

standard.error a logical indicating whether the standard error of the estimated theta should be returned (TRUE), the default being FALSE.

Details

The argument **x** can be either a factor or a vector. If it is a factor, then it is taken to give the individual alleles in the population. If it is a numeric vector, then its values are taken to be the numbers of each allele in the population. If it is a non-numeric vector, it is coerced as a factor.

The standard error is computed with an approximation due to Chakraborty and Weiss (1991).

Value

A numeric vector of length one with the estimated theta (the default), or of length two if the standard error is returned (**standard.error** = TRUE).

Author(s)

Emmanuel Paradis

References

Zouros, E. (1979) Mutation rates, population sizes and amounts of electrophoretic variation at enzyme loci in natural populations. *Genetics*, **92**, 623–646.

Chakraborty, R. and Weiss, K. M. (1991) Genetic variation of the mitochondrial DNA genome in American Indians is at mutation-drift equilibrium. *American Journal of Physical Anthropology*, **86**, 497–506.

See Also

[heterozygosity](#), [theta.s](#), [theta.k](#), [theta.tree](#)

Examples

```
data(jaguar)
## compute frequencies:
S <- summary(jaguar)
## compute THETA for all loci:
sapply(S, function(x) theta.h(x$allele))
```

theta.k

Population Parameter THETA using Expected Number of Alleles

Description

This function computes the population parameter THETA using the expected number of alleles.

Usage

```
theta.k(x, n = NULL, k = NULL)
```

Arguments

x	a vector or a factor.
n	a numeric giving the sample size.
k	a numeric giving the number of alleles.

Details

This function can be used in two ways: either with a vector giving the individual genotypes from which the sample size and number of alleles are derived (e.g., `theta.k(x)`), or giving directly these two quantities (e.g., `theta.k(n = 50, k = 5)`).

The argument `x` can be either a factor or a vector. If it is a factor, then it is taken to give the individual alleles in the population. If it is a numeric vector, then its values are taken to be the numbers of each allele in the population. If it is a non-numeric vector, it is coerced as a factor.

Both arguments `n` and `k` must be single numeric values.

Value

A numeric vector of length one with the estimated theta.

Note

For the moment, no standard-error or confidence interval is computed.

Author(s)

Emmanuel Paradis

References

Ewens, W. J. (1972) The sampling theory of selectively neutral alleles. *Theoretical Population Biology*, **3**, 87–112.

See Also

[theta.h](#), [theta.s](#), [theta.tree](#)

Examples

```
data(jaguar)
## compute frequencies:
S <- summary(jaguar)
## compute THETA for all loci:
sapply(S, function(x) theta.k(x$allele))
```

theta.msat

Population Parameter THETA From Micro-Satellites

Description

This function estimates the population parameter θ using micro-satellite data with three different estimators.

Usage

```
theta.msat(x)
```

Arguments

x an object of class "loci".

Details

The three estimators are based on (i) the variance of the number of repeats, (ii) the expected homozygosity (both described in Kimmel et al., 1998), and (iii) the mean allele frequencies (Haasl and Payseur, 2010).

The data must be micro-satellites, so the allele names must be the allele sizes (see the example). If the data are expressed in repeat counts, then only the first estimator is affected.

Value

a numeric matrix with loci as rows and the three estimates of θ as columns.

Author(s)

Emmanuel Paradis

References

Kimmel, M., Chakraborty, R., King, J. P., Bamshad, M., Watkins, W. S. and Jorde, L. B. (1998) Signatures of population expansion in microsatellite repeat data. *Genetics*, **148**, 1921–1930.

Haasl, R. J. and Payseur, B. A. (2010) The number of alleles at a microsatellite defines the allele frequency spectrum and facilitates fast accurate estimation of θ . *Molecular Biology and Evolution*, **27**, 2702–2715.

See Also

[theta.h](#), [theta.tree](#)

Examples

```
data(jaguar)
theta.msat(jaguar)
```

theta.s

Population Parameter THETA using Segregating Sites

Description

This function computes the population parameter THETA using the number of segregating sites s in a sample of n DNA sequences.

Usage

```
theta.s(x, ...)
## S3 method for class 'DNABin'
theta.s(x, variance = FALSE, ...)
## Default S3 method:
theta.s(x, n, variance = FALSE, ...)
```


Arguments

x	a numeric giving the number of segregating sites.
n	a numeric giving the number of sequences.
variance	a logical indicating whether the variance of the estimated THETA should be returned (TRUE), the default being FALSE.
...	arguments passed to methods.

Value

A numeric vector of length one with the estimated theta (the default), or of length two if the standard error is returned (variance = TRUE).

Author(s)

Emmanuel Paradis

References

- Watterson, G. A. (1975) On the number of segregating sites in genetical models without recombination. *Theoretical Population Biology*, **7**, 256–276.
- Tajima, F. (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*, **123**, 585–595.

See Also

[theta.h](#), [theta.k](#), [seg.sites](#), [nuc.div](#), [theta.tree](#)

Examples

```
data(woodmouse)
theta.s(woodmouse)
theta.s(woodmouse, variance = TRUE)
## using the default:
s <- length(seg.sites(woodmouse))
n <- nrow(woodmouse)
theta.s(s, n)
```

theta.tree

Population Parameter THETA Using Genealogy

Description

These functions estimate the population parameter Θ from a genealogy (coded as a phylogenetic tree) under the coalescent.

Usage

```
theta.tree(phy, theta, fixed = FALSE, analytical = TRUE, log = TRUE)
theta.tree.hetero(phy, theta, fixed = FALSE, log = TRUE)
```

Arguments

phy	an object of class "phylo".
theta	a numeric vector.
fixed	a logical specifying whether to estimate theta (the default), or to return the likelihoods for all values in theta.
analytical	a logical specifying whether to use analytical formulae to estimate theta and its standard-error. If FALSE, a numerical optimisation of the likelihood is performed (this option is ignored if fixed = TRUE)
.	.
log	a logical specifying whether to return the likelihoods on a log scale (the default); ignored if fixed = FALSE.

Details

With `theta.tree`, the tree `phy` is considered as a genealogy with contemporaneous samples, and therefore should be ultrametric. With `theta.tree.hetero`, the samples may be heterochronous so `phy` can be non-ultrametric. If `phy` is ultrametric, both functions return the same results.

By default, θ is estimated by maximum likelihood and the value given in `theta` is used as starting value for the minimisation function (if several values are given as a vector the first one is used). If `fixed = TRUE`, then the [log-]likelihood values are returned corresponding to each value in `theta`.

The present implementation does a numerical optimisation of the log-likelihood function (with `nlminb`) with the first partial derivative as gradient. It is possible to solve the latter and have a direct analytical MLE of θ (and its standard-error), but this does not seem to be faster.

Value

If `fixed = FALSE`, a list with two elements:

theta	the maximum likelihood estimate of Θ ;
logLik	the log-likelihood at its maximum.

If `fixed = TRUE`, a numeric vector with the [log-]likelihood values.

Author(s)

Emmanuel Paradis

References

- Kingman, J. F. C. (1982) The coalescent. *Stochastic Processes and their Applications*, **13**, 235–248.
- Kingman, J. F. C. (1982) On the genealogy of large populations. *Journal of Applied Probability*, **19A**, 27–43.
- Wakeley, J. (2009) *Coalescent Theory: An Introduction*. Greenwood Village, CO: Roberts and Company Publishers.

See Also

[theta.h](#), [theta.s](#), [theta.k](#)

Examples

```
tr <- rcoal(50)
(o <- theta.tree(tr))
theta.tree(tr, 10, analytical = FALSE) # uses nlminb()
## profile log-likelihood:
THETA <- seq(0.5, 2, 0.01)
logLikelihood <- theta.tree(tr, THETA, fixed = TRUE)
plot(THETA, logLikelihood, type = "l")
xx <- seq(o$theta - 1.96 * o$se, o$theta + 1.96 * o$se, 0.01)
yy <- theta.tree(tr, xx, fixed = TRUE)
polygon(c(xx, rev(xx)), c(yy, rep(0, length(xx))),
        border = NA, col = "lightblue")
segments(o$theta, 0, o$theta, o$logLik, col = "blue")
abline(v = 1, lty = 3)
legend("topright", legend = expression("log-likelihood",
    "True " * theta, hat(theta) * " (MLE)", "95%\ conf. interv."),
    lty = c(1, 3, 1, 1), lwd = c(1, 1, 1, 15),
    col = c("black", "black", "blue", "lightblue"))
```

utilities

Utily Functions for pegas

Description

The first three functions extract information on loci, `expand.genotype` creates a table of all possible genotypes given a set of alleles, `proba.genotype` calculates expected probabilities of genotypes under Hardy–Weinberg equilibrium, `is.snp` tests whether a locus is a SNP, `is.phased` tests whether a genotype is phased, and `unphase` unphase phased genotypes.

Usage

```
getPloidy(x)
getAlleles(x)
getGenotypes(x)
expand.genotype(n, alleles = NULL, ploidy = 2, matrix = FALSE)
proba.genotype(alleles = c("1", "2"), p, ploidy = 2)
```

```
is.snp(x)
## S3 method for class 'loci'
is.snp(x)
is.phased(x)
unphase(x)
```

Arguments

<code>x</code>	an object of class "loci".
<code>n</code>	an integer giving how many alleles to consider (ignored if <code>alleles</code> is used).
<code>alleles</code>	the allele names as a vector of mode character.
<code>ploidy</code>	an integer giving the ploidy level (either 2 or 4 for the moment).
<code>matrix</code>	a logical specifying whether to return the genotypes in a matrix or as a character vector.
<code>p</code>	a vector of allele probabilities; if missing, equal probabilities are assumed.

Details

`expand.genotype` and `proba.genotype` accept any level of ploidy and any number of alleles.

For `is.snp`, a locus is defined as a SNP if it has two alleles and their labels are made of a single character (e.g., A and T, or 1 and 2, but not A and AT).

Value

`getPloidy` returns the ploidy level of all genotypes as a matrix of integers with rownames and colnames taken from `x`.

`getAlleles` and `getGenotypes` return the alleles and genotypes, respectively, observed in all loci in an object of class "loci" as a list.

`expand.genotype` returns a character vector (the default) or a matrix where the rows are the genotypes and the columns are the alleles. The matrix is numeric by default, or character if the argument `alleles` is given.

`proba.genotype` returns a numeric vector with names set as the genotypes.

`is.snp` returns a logical vector specifying whether each locus is a SNP.

`is.phased` returns a matrix of the same size than the original data specifying whether each genotype is phased or not.

`unphase` unphases the genotypes and eventually pools those that become identical once unphased (e.g., A|T and T|A).

Author(s)

Emmanuel Paradis

Examples

```
data(jaguar)
X <- jaguar[, 1:2]
getAlleles(X)
getGenotypes(X)
expand.genotype(2)
expand.genotype(2, LETTERS[1:3])
expand.genotype(3, ploidy = 4)
proba.genotype() # classical HWE with 2 alleles
## an octoploid with a six-allele locus (1287 possible genotypes):
length(p <- proba.genotype(alleles = LETTERS[1:6], ploidy = 8))
max(p) # ~ 0.006
## back to the jaguar data:
s <- summary(X)
## allele counts from the first locus:
p <- s[[1]]$allele
## expected probabilities for the 136 possible genotypes...
proba.genotype(names(p), p/sum(p))
## ... to be compared with s[[1]]$genotype
```

VCFloci

Information From VCF Files

Description

These functions help to extract information from VCF files and to select which loci to read with [read.vcf](#).

Usage

```
VCFloci(file, what = "all", chunk.size = 1e9, quiet = FALSE)
## S3 method for class 'VCFinfo'
print(x, ...)
VCFheader(file)
VCFlabels(file)
## S3 method for class 'VCFinfo'
is.snp(x)
rangePOS(x, from, to)
selectQUAL(x, threshold = 20)
getINFO(x, what = "DP", as.is = FALSE)
```

Arguments

file	file name of the VCF file.
what	a character specifying the information to be extracted (see details).
chunk.size	the size of data in bytes read at once.
quiet	a logical: should the progress of the operation be printed?

<code>x</code>	an object of class "VCFinfo".
<code>from, to</code>	integer values giving the range of position values.
<code>threshold</code>	a numerical value indicating the minimum value of quality for selecting loci.
<code>as.is</code>	a logical. By default, <code>getINFO</code> tries to convert its output as numeric: if too many NA's are produced, the output is returned as character. Use <code>as.is = TRUE</code> to force the output to be in character mode.
<code>...</code>	further arguments passed to and from other methods.

Details

The variant call format (VCF) is described in details in the References. Roughly, a VCF file is made of two parts: the header and the genotypes. The last line of the header gives the labels of the genotypes: the first nine columns give information for each locus and are (always) "CHROM", "POS", "ID", "REF", "ALT", "QUAL", "FILTER", "INFO", and "FORMAT". The subsequent columns give the labels (identifiers) of the individuals; these may be missing if the file records only the variants. Note that the data are arranged as the transpose of the usual way: the individuals are as columns and the loci are as rows.

VCFloci is the main function documented here: it reads the information relative to each locus. The option `what` specifies which column(s) to read. By default, all of them are read. If the user is interested in only the locus positions, the option `what = "POS"` would be used.

Since VCF files can be very big, the data are read in portions of `chunk.size` bytes. The default (1 Gb) should be appropriate in most situations. This value should not exceed $2e9$.

VCFheader returns the header of the VCF file (excluding the line of labels). VCFlabels returns the individual labels.

The output of VCFloci is a data frame with as many rows as there are loci in the VCF file and storing the requested information. The other functions help to extract specific information from this data frame: their outputs may then be used to select which loci to read with [read.vcf](#).

`is.snp` tests whether each locus is a SNP (i.e., the reference allele, REF, is a single character and the alternative allele, ALT, also). It returns a logical vector with as many values as there are loci. Note that some VCF files have the information VT (variant type) in the INFO column.

`rangePOS` and `selectQUAL` select some loci with respect to values of position or quality. They return the indices (i.e., row numbers) of the loci satisfying the conditions.

`getINFO` extracts a specific information from the INFO column. By default, these are the total depths (DP) which can be changed with the option `what`. The meaning of these information should be described in the header of the VCF file.

Value

VCFloci returns an object of class "VCFinfo" which is a data frame with a specific print method.

VCFheader returns a single character string which can be printed nicely with `cat`.

VCFlabels returns a vector of mode character.

`is.snp` returns a vector of mode logical.

`rangePOS` and `selectQUAL` return a vector of mode numeric.

`getINFO` returns a vector of mode character or numeric (see above).

Note

VCFloci is able to read either compressed (*.gz) or uncompressed files.

Author(s)

Emmanuel Paradis

References

<https://www.internationalgenome.org/wiki/Analysis/vcf4.0>

<https://github.com/samtools/hts-specs>

See Also

[read.vcf](#)

Examples

```
## see ?read.vcf
```

write.loci	<i>Write Allelic Data Files</i>
------------	---------------------------------

Description

This function writes allelic data into a text file.

Usage

```
write.loci(x, file = "", loci.sep = " ", allele.sep = "/", ...)
```

Arguments

x	an object of class "loci".
file	a file name specified by either a variable of mode character, or a quoted string. By default, the data are printed on the console.
loci.sep	the character(s) use to separate the loci (columns) in the file (a space by default).
allele.sep	the character(s) used to separate the alleles for each locus in the file (a slash by default).
...	further arguments passed to write.table.

Value

NULL

Author(s)

Emmanuel Paradis

See Also

[read.loci](#), [write.table](#) for all its options

Examples

```
data(jaguar)
x <- jaguar[1:10, 1:3] # take a small subset
write.loci(x)
## use of '...':
write.loci(x, loci.sep = "\t", quote = FALSE, col.names = FALSE)
```


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