Package 'introgress'

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R topics documented:
introgress-package 2 AdmixDataSim1 3 AdmixDataSim2 4 AdmixDom 5 calc.intersp.het 6 clines.plot 7 compare.clines 9 composite.clines 11 delta 12

2 introgress-package

	est.h fit.c.clines				
	fit.invariant.clines .				
	fixup.combos.touse				
	genomic.clines				
	h.func				
	like.h				
	LociD		 	 	 21
	LociDataSim1				
	LociDataSim2		 	 	 22
	mk.image		 	 	 23
	p1D				
	p1DataSim2				
	p2D		 	 	 26
	p2DataSim2		 	 	 27
	per.locus.like		 	 	 27
	prepare.data		 	 	 28
	s.wrapper		 	 	 31
	support.limit		 	 	 31
	test.combinations .		 	 	 31
	test.data.objects		 	 	 32
	test.genotypes		 	 	 32
	triangle.plot		 	 	 32
Index					35
	ogress-package	introgress			

Description

introgress provides functions for analyzing introgression of genotypes between divergent, hybridizing lineages, including estimating genomic clines from multi-locus genotype data and testing for deviations from neutral expectations. Functions are also provided for maximum likelihood estimation of molecular hybrid index and graphical analysis.

Details

introgress includes several core functions that are needed to implement the genomic clines method of Gompert and Buerkle (2009a). prepare.data estimates the counts of alleles inherited from each of two parental population at each locus for admixed individuals. These estimates are based on genotype data from admixed population(s) and specified parental populations. The function est.h uses the list output returned from prepare.data and the raw genotype data for the admixed population(s) to compute maximum likelihood estimates of hybrid index. The list output returned by prepare.data and the data.frame output returned by est.h are used to estimate genomic clines, which is accomplished with the function genomic.clines. The genomic.clines function includes arguments specifying whether significance testing is performed and the procedure used to generate null expectations for significance testing. The clines.plot function provides graphical

AdmixDataSim1 3

output for genomic clines analysis similar to Gompert and Buerkle (2009a, 2009b). In addition, the introgress package includes the compare.clines function to contrast patterns of introgression between hybrid zones.

introgress implements additional functions for graphical analysis of hybrid zones. triangle.plot plots the relationship between hybrid index and inter-class heterozygosity (calc.intersp.het) for an admixed population. The mk.image function produces a graphical representation of marker ancestry allowing visual inspection of variation in patterns of introgression among markers.

For further information regarding the above functions and additional introgress functions, please see the appropriate function help pages.

Author(s)

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References

Gompert Z. and Buerkle C. A. (2009) A powerful regression-based method for admixture mapping of isolation across the genome of hybrids. *Molecular Ecology*, **18**, 1207-1224.

Gompert Z. and Buerkle C. A. (2009) *introgress*: a software package for mapping components of isolation in hybrids. *Molecular Ecology Resources*, in preparation.

AdmixDataSim1

Admixed Population Genotype Data from Simulation 1

Description

This data set contains genotypes for a simulated admixed population. The simulated admixed population consisted of 500 diploid hermaphroditic individuals with ten pairs of chromosomes, each one Morgan in length. The admixed population resulted from an intitial hybridization event between two parental populations (combined in equal proportions) and mating within the admixed population continued for five additional generations. Fitness of hybrids was determined based on a marker at the center of chromosome 1; individuals homozygous at this location had a fitness of 1, while heterozygotes had of fitness of 0.1. Two hundred admixed individuals were sampled at the completion of the simulation and scored for 110 co-dominant markers spaced evenly across all 10 linkage groups (at 10 cM intervals).

The data are provided as a matrix with rows and columns corresponding to markers and individuals, respectively. Alleles inherited from parental population 1 are recorded as P1 and alleles inherited from parental population 2 are recorded as P2.

Usage

data(AdmixDataSim1)

Format

A matrix with 110 rows and 200 columns.

4 AdmixDataSim2

Source

From simulations conducted by CAB and ZG.

References

Gompert Z. and Buerkle C. A. (2009) A powerful regression-based method for admixture mapping of isolation across the genome of hybrids. *Molecular Ecology*, **18**, 1207-1224.

Gompert Z. and Buerkle C. A. (2009) *introgress*: a software package for mapping components of isolation in hybrids. *Molecular Ecology Resources*, in preparation.

See Also

LociDataSim1

AdmixDataSim2

Admixed Population Genotype Data from Simulation 2

Description

This data set contains genotypes for a simulated admixed population. The admixed population consists of 100 individuals scored for 90 co-dominant markers and 10 dominant markers. Admixed individuals were simulated by sampling genotypes from parental populations (p1DataSim2 and p2DataSim2). The first and second rows of this matrix data object give population and individual identifications for each admixed individual. The following rows contain the genotype data; rows correspond to markers and columns correspond to individuals.

Usage

data(AdmixDataSim2)

Format

A matrix with 102 rows and 100 columns.

Source

From simulations conducted by CAB and ZG.

See Also

LociDataSim2, p1DataSim2, p2DataSim2

AdmixDom 5

AdmixDom

Admixed Population Dominant Genotype Data from Simulation 1

Description

This data set contains genotypes for a simulated admixed population. The simulated admixed populations conisted of 500 diploid hermaphroditic individuals with ten pairs of chromosomes, each one Morgan in length. The admixed population resulted from an intitial hybridization event between two parental populations (combined in equal proportions) and mating within the admixed population continued for five additional generations. Fitness of hybrids was determined based on a marker at the center of chromosome 1; individuals homozygous at this location had a fitness of 1, while heterozygotes had of fitness of 0.1. Two hundred admixed individuals were sampled at the completion of the simulation and scored for 110 dominant markers spaced evenly across all 10 linkage groups (at 10 cM intervals). Alleles inherited from parental population 1 were treated as the dominant alleles.

The data are provided as a matrix with rows and columns corresponding to markers and individuals, respectively. For each marker an individuals genotype is given by a 1 (homozygous for population 1 alleles or heterozygous) or 0 (homozygous for population 2 alleles).

Usage

data(AdmixDom)

Format

A matrix with 110 rows and 200 columns.

Source

From simulations conducted by CAB and ZG.

References

Gompert Z. and Buerkle C. A. (2009) A powerful regression-based method for admixture mapping of isolation across the genome of hybrids. *Molecular Ecology*, **18**, 1207-1224.

Gompert Z. and Buerkle C. A. (2009) *introgress*: a software package for mapping components of isolation in hybrids. *Molecular Ecology Resources*, in preparation.

See Also

LociD

6 calc.intersp.het

calc.intersp.het

Calculate Interspecific Heterozygosity

Description

This function calculates interspecific heterozygosity of individuals from a matrix of allele counts.

Usage

```
calc.intersp.het(introgress.data=NULL)
```

Arguments

```
introgress.data
```

a list produced by prepare. data or a matrix with allele counts.

Details

This function calculates an admixed individual's interspecific heterozygosity (i.e. the proportion of the individual's genome with alleles inherited from both parental populations) based on allele counts. This function should only be used for co-dominant markers.

Value

A numerical vector with an estimate of interspecific heterozygosity for each individual.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

See Also

```
prepare.data
```

clines.plot 7

```
## Estimate inter-specific heterozygosity
int.het<-calc.intersp.het(introgress.data=introgress.data)
## End(Not run)</pre>
```

clines.plot Clines Plot

Description

This function produces graphical plots of genomic clines using the output from the function genomic.clines.

Usage

Arguments

cline.data	a list that is the product of the genomic.clines function.
marker.order	an optional numeric or character vector specifying the order to plot marker results in; if marker.order = NULL markers are plotted in the order they were originally provided.
rplots	numerical value specifying the number of plots per row in the output.
cplots	numerical value specifying the number of plots per column in the output.
pdf	logical specifying whether to print the plots to a pdf file; if pdf=FALSE plots are printed to the current graphical device.
out.file	a character string for the filename for the output if pdf=TRUE.
colors	a vector of two colors to be used for cline plots.
quantiles	logical specifying whether to include genotype specific quantile information on the plots.
lb.cd	numeric vector of three proportions specifying the lower bounds for co-dominant markers that is used to determine whether each genotype is under-represented.
ub.cd	numeric vector of three proportions specifying the upper bounds for co-dominant markers that is used to determine whether each genotype is over-represented.
lb.dh	numeric vector of two proportions specifying the lower bounds for dominant and haploid markers that is used to determine whether each genotype is underreprsented.
ub.dh	numeric vector of two proportions specifying the upper bounds for dominant and haploid markers that is used to determine whether each genotype is over-reprsented.

8 clines.plot

cd	vector with three characters used for labeling genotypes of co-dominant markers
	in cline plots.
dh	vector with two characters used for labeling genotypes of dominant and haploid
	markers in cline plots.

Details

This function produces graphical plots based on the data object produced by the genomic.clines function. A separate plot is produced for each marker. Plots depict the probability of a given genotype as a function of hybrid index. Plots for the observed data are shown with solid (homozygous population 1 genotype for co-dominant markers, or population 1 allele for dominant or haploid markers) and dashed lines (inter-specific heterozygotes for co-dominant markers, not shown for dominant or haploid markers). If significance testing was conducted with the genomic.clines function, the corresponding 95% confidence intervals are shown in dark and light green. Circles indicate individuals that are homozygous for alleles from population 1 (co-dominant) or population 1 alleles (dominant or haploid) on the top line, interspecific heterozygotes (co-dominant only) in the middle, and homozygotes for alleles from population 2 (co-dominant) or population 2 alleles (dominant or haploid) on the bottom line. The number of individuals with each genotype is printed on the right vertical axis. The locus name and P-value are printed in each plot. If quantiles = TRUE and genotype-specific quantiles were computed with the genomic.clines function by setting classification = TRUE, a title is given for each individual plot that includes whether each genotype (as labeled by cd or dh) was over- (+) or under-represented (-) compared to neutral expectation using 1b.cd, ub.cd, 1b.dh, ub.dh as thresholds.

See Gompert and Buerkle (2009a, 2009b) for additional details and examples.

Value

A plot is produced, but a data object is not returned.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

References

Gompert Z. and Buerkle C. A. (2009) A powerful regression-based method for admixture mapping of isolation across the genome of hybrids. *Molecular Ecology*, **18**, 1207-1224.

Gompert Z. and Buerkle C. A. (2009) *introgress*: a software package for mapping components of isolation in hybrids. *Molecular Ecology Resources*, in preparation.

See Also

```
genomic.clines
```

```
## this code assumes the data object clines.out2 has been produced using
## the sample code for the "genomic.clines" function
```

compare.clines 9

```
## produce plots of genomic clines
## Not run:
clines.plot(cline.data=clines.out2)
## End(Not run)
```

compare.clines

Compare Clines

Description

This function contrasts patterns of introgression between two hybrid zones.

Usage

Arguments

cline.data1 a list that is the product of the genomic.clines function.
cline.data2 a list that is the product of the genomic.clines function.
sig.test a logical specifying whether to perform significance testing.

n.reps numeric value specifying the number of permutations to conduct for signficance

testing.

Details

This function estimates that likelihood of the count data from cline.data2 given the regression models from cline.data1 and cline.data2 and returns the log ratio of the latter to the former. cline.data1 and cline.data2 are lists returned by genomic.clines each based on a different hybrid zone between the same parental populations or species; the molecular markers and parental allele frequencies should be the same for both hybrid zones. The range of hybrid index estimates for individuals comprising cline.data2 should exceed the range of hybrid index estimated for individuals comprising cline.data1 to avoid predicting allele counts using the regression model from cline.data1 beyond the range of hybrid indexes that were included in the original model. The log likelihood ratios returned by this function can be used to determine the degree of congruence for marker specific patterns of introgression between the analyzed hybrid zones. This function includes a permutation procedure for testing whether log likelihood ratios are significantly greater than expected by chance, which is invoked by setting sig.test = TRUE. This option should only be employed when both hybrid zones contain many individuals with low and high hybrid index estimates to minimized the problem described above.

See Gompert and Buerkle (2009a, 2009b) for additional details and examples.

Value

A matrix with log likelihood ratios for each marker and P-values from significance testing if sisg.test = TRUE.

10 compare.clines

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

References

Gompert Z. and Buerkle C. A. (2009) A powerful regression-based method for admixture mapping of isolation across the genome of hybrids. *Molecular Ecology*, **18**, 1207-1224.

Gompert Z. and Buerkle C. A. (2009) *introgress*: a software package for mapping components of isolation in hybrids. *Molecular Ecology Resources*, in preparation.

See Also

```
genomic.clines, prepare.data, est.h
```

```
## Not run:
## load simulated data
## markers have fixed differences, with
## alleles coded as 'P1' and 'P2'
data(AdmixDataSim1)
data(LociDataSim1)
## use prepare.data to produce introgress.data
introgress.data<-prepare.data(admix.gen=AdmixDataSim1,
                               loci.data=LociDataSim1,
                               parental1="P1", parental2="P2",
                               pop.id=FALSE, ind.id=FALSE, fixed=TRUE)
## estimate hybrid index
hi.index<-est.h(introgress.data=introgress.data,
                loci.data=LociDataSim1, p1.allele="P1",
                p2.allele="P2")
## random sampling to divide data into two sets of 100 individuals,
## this creates two admixed populations (hybrid zones)
numbs<-sample(1:200,200,replace=FALSE)
sam1<-numbs[1:100]
sam2<-numbs[101:200]
## estimate genomic clines for each data set,
## significance testing is not conducted
clines.out1<-genomic.clines(introgress.data=introgress.data,</pre>
                            hi.index=hi.index,loci.data=LociDataSim1,
                            sig.test=FALSE, ind.touse=sam1)
clines.out2<-genomic.clines(introgress.data=introgress.data,</pre>
                            hi.index=hi.index,loci.data=LociDataSim1,
                            sig.test=FALSE, ind.touse=sam2)
## compare clines between data sets, with significance testing
```

composite.clines 11

composite.clines

Composite Clines Plot

Description

This function produces an overlayed graphical plot of genomic clines using the output from the function genomic.clines.

Usage

Arguments

cline.data a list that is the product of the genomic.clines function.

pdf logical specifying whether to print the plots to a pdf file; if pdf=FALSE plots are

printed to the current graphical device.

out.file a character string for the filename for the output if pdf=TRUE.

colors a vector of two colors to be used for cline plots.

labels vector with two characters used for labeling marker genotypes on the plots.

Details

This function produces graphical plots based on the data object produced by the <code>genomic.clines</code> function. Plots depict the probability of a given genotype as a function of hybrid index. Unlike the <code>clines.plot</code> function, plots for each marker are overlayed. If significance testing was performed the null distribution of the first marker is shown (which should be the same as the null distribution for all markers if the permutation method was used). This function only works with co-dominant markers. See Teeter et al. 2010 for an example of the plot produced by this function. Also, compare this function to <code>clines.plot</code>.

Value

A plot is produced, but a data object is not returned.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

12 delta

References

Gompert Z. and Buerkle C. A. (2009) A powerful regression-based method for admixture mapping of isolation across the genome of hybrids. *Molecular Ecology*, **18**, 1207-1224.

Teeter K. C., Thibodeau L. M., Gompert Z., Buerkle C. A., Nachman M. W., and Tucker, P. K. (2010) The variable genomic architecture of isolation between hybridizing species of house mice. *Evolution*, **64**, 472-485.

See Also

```
genomic.clines, clines.plot
```

Examples

```
## this code assumes the data object clines.out2 has been produced using
## the sample code for the "genomic.clines" function

## produce plots of genomic clines
## Not run:
composite.clines(cline.data=clines.out2)

## End(Not run)
```

delta

Delta

Description

This function calculates delta (δ), the differential between allelic frequencies in two populations. It is called by the function prepare.data.

Usage

```
delta(SpA, SpB)
```

Arguments

SpA a vector of population allele frequencies.

SpB a vector of population allele frequencies.

Details

This function calculates the allele frequency differential for a pair of species or populations (δ , Gregorius and Roberds 1986) for a single locus.

$$\delta = \sum_{i} \frac{|f_{i1} - f_{i2}|}{2}$$

where f_{i1} and f_{i2} denote the frequency of the *i*th allele in populations one and two, respectively. δ ranges from 0, for identical populations, to 1, for populations that share no alleles in common.

est.h

Value

This function returns a vector of length one with the value of δ .

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

References

Gregorius, H. R. and Roberds, J. H. (1986) Measurement of genetical differentiation among subpopulations. *Theoretical and Applied Genetics*, **71**, 826-834.

See Also

```
prepare.data
```

Examples

```
## allele frequencies for two populations
pop.a<-c(0.3,0.5,0.2)
pop.b<-c(0.1,0.1,0.8)
## delta calculation
delta(pop.a,pop.b)</pre>
```

est.h

Estimate Hybrid Index

Description

This function finds maximum likelihood estimates of hybrid index as described by Buerkle (2005).

Usage

```
est.h(introgress.data=NULL, loci.data=NULL, ind.touse=NULL,
    fixed=FALSE, p1.allele=NULL, p2.allele=NULL)
```

Arguments

introgress.data

a list produced by prepare. data or a matrix with allele counts.

loci.data a matrix or array providing marker information.

ind. touse vector of individual identifications, numeric indexes, or logicals that specify a

subset of individuals for analysis, if NULL all individuals are included.

fixed a logical specifying whether different alleles are fixed for each parental popula-

tion for all markers.

14 est.h

p1.allele if fixed=TRUE provides the character used to specify parental population 1 alle-

les.

p2.allele if fixed=TRUE provides the character used to specify parental population 2 alle-

les.

Details

introgress.data may either be the list that is returned by the function prepare.data, or, if fixed=TRUE, introgress.data may simply be a matrix or array providing counts of the number of alleles derived from parental population 1 for each admixed individual. If introgress.data is a matrix or array, rows and columns correspond to loci and individuals, respectively.

loci.data is a matrix or array where each row provides information on one locus. The first column gives a unique locus name (e.g. "locus3"), and the second column specifies whether the locus is co-dominant ("C" or "c"), haploid ("H" or "h"), or dominant ("D" or "d"). These first two columns in loci.data are required. The third column, which is optional, is a numeric value specifying the linkage groups for the marker. The fourth column, which is also optional, is a numeric value specifying both the linkage group and location on the linkage group (e.g. 3.70, for a marker at 70 cM on linkage group 3). These optional columns can be used for ordering markers for the mk.image, genomic.clines, and clines.plot functions.

If the parental populations exhibit fixed allelic differences for all markers scored (i.e. fixed=TRUE) then p1.allele and p2.allele should give the character used to specify alleles derived from parental populations one and two, respectively (e.g. p1.allele="p1" and p2.allele="p2").

est.h uses a maximum likelihood method to estimate the hybrid index for each admixed individual. This estimate is simply the proportion of alleles derived from population 2 if fixed=TRUE. In contrast, if populations share alleles (i.e. fixed=FALSE), the estimate accounts for uncertainty in the ancestry of alleles, but the estimate of hybrid index is still an estimate of the proportion of the genome that is inherited from population 2. For each individual, est.h returns a point estimate and 95% confidence interval of hybrid index.

See Buerkle (2005) for additional details.

Value

A data frame with point estimates of hybrid index and upper and lower limits of 95% confidence intervals (interval of hybrid index that falls within two support units of the ML estimate):

lower Lower limit of 95% confidence interval.

h Maximum-likelihood estimate of hybrid index.

upper Upper limit of 95% confidence interval.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

References

Buerkle C. A. (2005) Maximum-likelihood estimation of a hybrid index based on molecular markers. *Molecular Ecology Notes*, **5**, 684-687.

fit.c.clines 15

Gompert Z. and Buerkle C. A. (2009) A powerful regression-based method for admixture mapping of isolation across the genome of hybrids. *Molecular Ecology*, **18**, 1207-1224.

Gompert Z. and Buerkle C. A. (2009) *introgress*: a software package for mapping components of isolation in hybrids. *Molecular Ecology Resources*, in preparation.

See Also

```
prepare.data
```

Examples

```
## Not run:
## load simulated data
## markers have fixed differences, with
## alleles coded as 'P1' and 'P2'
data(AdmixDataSim1)
data(LociDataSim1)
## use prepare.data to produce introgress.data
introgress.data<-prepare.data(admix.gen=AdmixDataSim1,</pre>
                               loci.data=LociDataSim1,
                               parental1="P1", parental2="P2",
                               pop.id=FALSE, ind.id=FALSE,
                               fixed=TRUE)
## estimate hybrid index
hi.index<-est.h(introgress.data=introgress.data,</pre>
                loci.data=LociDataSim1, ind.touse=NULL, fixed=TRUE,
                p1.allele="P1", p2.allele="P2")
write.table(hi.index, file="hindex.txt", quote=FALSE, sep=",")
## End(Not run)
```

fit.c.clines

Fit Co-dominant Clines

Description

This is an internal function called by genomic.clines.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

See Also

```
genomic.clines
```

fit.invariant.clines Fit Invariant Clines

Description

This is an internal function called by genomic.clines.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

See Also

```
genomic.clines
```

fixup.combos.touse

Fix Combos To Use

Description

This is an internal function called by prepare.data.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

See Also

test.combinations, prepare.data

genomic.clines

Genomic Clines

Description

This function fits genomic clines to genotypic data using the method described by Gompert and Buerkle (2009a). Significance testing is included, but optional.

Usage

Arguments

introgress.data

a list produced by prepare. data or a matrix with allele counts.

hi.index a data frame produced by est.h or a numeric vector of hybrid index estimates.

loci.data a matrix or array providing marker information.

sig. test a logical specifying whether to perform significance testing.

method method to generate null distribution; either "permutation" or "parametric".

n.reps numeric value specifying number of neutral simulations.

classification a logical specifying whether to calculate genotype specific quantiles (ignored if

sig.test=FALSE).

het.cor a logical specifying whether to correct for deviations from expected heterozy-

gosity when conducting neutral simulations using the parametric method (ig-

nored with permutation method).

loci.touse vector of loci names, numeric indexes, or logicals that specify a subset of loci

for analysis, if NULL all loci are included.

ind. touse vector of individual identifications, numeric indexes, or logicals that specify a

subset of individuals for analysis, if NULL all individuals are included.

Details

introgress.data may either be the list that is returned by the function prepare.data, or, if fixed=TRUE, introgress.data may simply be a matrix or array providing counts of the number of alleles derived from parental population 1 for each admixed individual. If introgress.data is a matrix or array, rows and columns correspond to loci and individuals, respectively.

loci.data is a matrix or array where each row provides information on one locus. The first column gives a unique locus name (e.g. "locus3"), and the second column specifies whether the locus is co-dominant ("C" or "c"), haploid ("H" or "h"), or dominant ("D" or "d"). These first two columns in loci.data are required. The third column, which is optional, is a numeric value specifying the linkage groups for the marker. The fourth column, which is also optional, is a numeric value specifying both the linkage group and location on the linkage group (e.g. 3.70, for a marker at 70 cM on linkage group 3). These optional columns can be used for ordering markers for the mk.image, genomic.clines, and clines.plot functions.

This function (genomic.clines) estimates genomic clines in genotype frequency for admixed populations using the genomic clines method described by Gompert and Buerkle (2009a). If sig.test = FALSE, genomic clines are estimated for the admixed population, but no significance testing is done. If sig.test = TRUE, the genomic cline for each locus is evaluated for deviations from neutral expectations. Either the permutation method (method = "permutation") or the parametric method (method = "parametric") described by Gompert and Buerkle (2009a) can be used to generate the neutral distribution for significance testing. The permutation method cannot be used if both co-dominant and dominant (or haploid) data are included in the analysis. If classification = TRUE this function also returns the proportion of neutral simulations/permutations yielding a model with a higher total probability of a given genotype for a given marker than the model from the observed data

The function will issue a warning if an invariant locus is included (all individuals have the same genotype). In this case the probability of one of the genotypes does not vary with hybrid index.

See Gompert and Buerkle (2009a, 2009b) for additional details.

Value

A list with the following components:

Summary.data	a matrix with the locus data including log likelihood ratios and P-values from significance testing if $sig.test = TRUE$.
Fitted.AA	a matrix with fitted values for the population 1 homozygote for each locus (row) and individual (column).
Fitted.Aa	a matrix with fitted values for inter-population heterozygotes for each locus (row) and individual (column).
Fitted.aa	a matrix with fitted values for the population 2 homozygote for each locus (row) and individual (column).
Neutral.AA	a matrix with upper and lower bounds for the empirical 95% confidence interval for the expected population 1 homozygote genomic clines under neutrality for each locus (row) and individual (column); these confidence intervals are based on the neutral simulations/permutations.
Neutral.Aa	a matrix with upper and lower bounds for the empirical 95% confidence interval for the expected inter-population heterozygote genomic clines under neutrality for each locus (row) and individual (column); these confidence intervals are based on the neutral simulations/permutations.
Neutral.aa	a matrix with upper and lower bounds for the empirical 95% confidence interval for the expected population 2 homozygote genomic clines under neutrality for each locus (row) and individual (column); these confidence intervals are based on the neutral simulations/permutations.
Count.matrix	the user supplied count.matrix.
hybrid.index	the user supplied hi.index.
Loci.data	the user supplied loci.data.
Quantiles	a matrix with the proportion of neutral simulations/permutations yielding a model with a higher total probability of a given genotype (column) than the model from the observed data; proportions are provided for each locus (row).

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

References

Gompert Z. and Buerkle C. A. (2009) A powerful regression-based method for admixture mapping of isolation across the genome of hybrids. *Molecular Ecology*, **18**, 1207-1224.

Gompert Z. and Buerkle C. A. (2009) *introgress*: a software package for mapping components of isolation in hybrids. *Molecular Ecology Resources*, in preparation.

See Also

prepare.data, est.h

```
## Not run:
## Example 1, genomic clines analysis without significance testing, or
## with significance testing on a subset of the data
## load simulated data
## markers do not have fixed differences
data(AdmixDataSim2)
data(LociDataSim2)
data(p1DataSim2)
data(p2DataSim2)
## use prepare.data to produce introgress.data
introgress.data1<-prepare.data(admix.gen=AdmixDataSim2,</pre>
                              loci.data=LociDataSim2,
                              parental1=p1DataSim2, parental2=p2DataSim2,
                              pop.id=TRUE, ind.id=TRUE, fixed=FALSE)
## estimate hybrid index
hi.index1<-est.h(introgress.data=introgress.data1,loci.data=LociDataSim2,
                fixed=FALSE)
## estimate genomic clines without significance testing
clines.out1<-genomic.clines(introgress.data=introgress.data1,</pre>
                           hi.index=hi.index1,
                           loci.data=LociDataSim2, sig.test=FALSE)
## for a subset of loci, estimate genomic clines with significance testing
clines.out1b<-genomic.clines(introgress.data=introgress.data1,</pre>
                            hi.index=hi.index1,
                            loci.data=LociDataSim2, sig.test=TRUE,
                            method="parametric", loci.touse=1:10)
## Example 2, genomic clines analysis with significance testing
## load simulated data
## markers have fixed differences, with
## alleles coded as 'P1' and 'P2'
data(AdmixDataSim1)
data(LociDataSim1)
## use prepare.data to produce introgress.data
introgress.data2<-prepare.data(admix.gen=AdmixDataSim1,</pre>
                              loci.data=LociDataSim1,
                              parental1="P1", parental2="P2",
                              pop.id=FALSE, ind.id=FALSE, fixed=TRUE)
## estimate hybrid index
hi.index2<-est.h(introgress.data=introgress.data2,
               loci.data=LociDataSim1, fixed=TRUE, p1.allele="P1",
               p2.allele="P2")
```

20 like.h

h.func

Hybrid Index Function

Description

This is an internal function called by est.h.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

See Also

est.h

like.h

Likelihood Hybrid Index

Description

This is an internal function called by est.h.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

See Also

est.h

LociD 21

LociD

Dominant Marker Information for Simulation 1

Description

This data object provides the marker information associated with AdmixDom. Rows correspond to markers (110 markers spaced evenly across 10 linkage groups at 10 cM intervals). The first column gives the locus name, (c1.f is the marker at the location of the genomic region that determined each indvidual's fitness, see AdmixDom). The second column (type) indicates that all of the markers are dominant (D). The third and fourth columns specify each markers linkage group (between 1 and 10) and relative location on each linkage group, respectively.

Usage

data(LociD)

Format

A matrix with 110 rows and 4 columns.

Source

From simulations conducted by CAB and ZG.

References

Gompert Z. and Buerkle C. A. (2009) A powerful regression-based method for admixture mapping of isolation across the genome of hybrids. *Molecular Ecology*, **18**, 1207-1224.

Gompert Z. and Buerkle C. A. (2009) *introgress*: a software package for mapping components of isolation in hybrids. *Molecular Ecology Resources*, in preparation.

See Also

AdmixDom

LociDataSim1

Marker Information for Simulation 1

Description

This data object provides the marker information associated with AdmixSimData1. Rows correspond to markers (110 markers spaced evenly across 10 linkage groups at 10 cM intervals). The first column gives the locus name, (c1.f is the marker at the location of the genomic region that determined each indvidual's fitness, see AdmixSimData1). The second column (type) indicates that all of the markers are co-dominant (C). The third and fourth columns specify each markers linkage group (between 1 and 10) and relative location on each linkage group, respectively.

22 LociDataSim2

Usage

data(LociDataSim1)

Format

A matrix with 110 rows and 4 columns.

Source

From simulations conducted by CAB and ZG.

References

Gompert Z. and Buerkle C. A. (2009) A powerful regression-based method for admixture mapping of isolation across the genome of hybrids. *Molecular Ecology*, **18**, 1207-1224.

Gompert Z. and Buerkle C. A. (2009) *introgress*: a software package for mapping components of isolation in hybrids. *Molecular Ecology Resources*, in preparation.

See Also

AdmixDataSim1

LociDataSim2

Marker Information for Simulation 2

Description

This data object provides the marker information associated with AdmixDataSim2. Rows correspond to markers (100 markers total). The first column gives the locus name and the second column gives the locus type; co-dominant (C) for the first 90 markers, dominant (D) for the last 10 markers. Map information is not provided for these markers.

Usage

data(LociDataSim2)

Format

A matrix with 100 rows and 2 columns.

Source

From simulations conducted by CAB and ZG.

See Also

AdmixDataSim2, p1DataSim2, p2DataSim2

mk.image 23

Description

This function produces a graphical representation of marker ancestry across individuals and facilitates visual inspection of variation in patterns of introgression among markers.

Usage

```
mk.image(introgress.data=NULL, loci.data=NULL,
         marker.order=NULL, hi.index=NULL, ind.touse=NULL,
         loci.touse=NULL, ylab.image="Individuals", main.image="",
         xlab.h="population 2 ancestry", col.image=NULL,
         pdf=TRUE, out.file="image.pdf")
```

Arg

Į	guments	
	introgress.data	
		a list produced by prepare.data or a matrix with allele counts.
	loci.data	a matrix or array providing marker information.
	marker.order	a numeric or character vector specifying the order in which to plot markers, if marker.order=NULL the markers will be plotted in the order in which they occur in the introgress.data.
	hi.index	a data frame produced by est.h or a numeric vector of hybrid index estimates.
	ind.touse	vector specifying a subset of individuals to plot, if ind. to use=NULL all individuals will be included.
	loci.touse	vector specifying a subset of markers to plot, if loci.touse=NULL all markers will be included.
	ylab.image	character string giving the label for the y-axis.
	main.image	character string giving the main label for the plot.
	xlab.h	character string giving the x-axis label for the hybrid index portion of the plot.
	col.image	vector of three colors to be used for the image plot, if ${\tt col.image=NULL}$ default colors will be used.
	pdf	a logical specifying whether to print the plot to a pdf, if pdf=FALSE the current graphical output device will be used.
	out.file	character string specifying the name of the output file for the image, if pdf=TRUE.

Details

introgress.data may either be the list that is returned by the function prepare.data, or, if fixed=TRUE, introgress.data may simply be a matrix or array providing counts of the number of alleles derived from parental population 1 for each admixed individual. If introgress.data is a matrix or array, rows and columns correspond to loci and individuals, respectively.

24 mk.image

loci.data is a matrix or array where each row provides information on one locus. The first column gives a unique locus name (e.g. "locus3"), and the second column specifies whether the locus is co-dominant ("C" or "c"), haploid ("H" or "h"), or dominant ("D" or "d"). These first two columns in loci.data are required. The third column, which is optional, is a numeric value specifying the linkage groups for the marker. The fourth column, which is also optional, is a numeric value specifying both the linkage group and location on the linkage group (e.g. 3.70, for a marker at 70 cM on linkage group 3). If present, the third column will be used to draw breaks between and label linkage groups. The fourth column can be used to generate an order in which to plot markers (specified in marker.order).

This function (mk.image) produces a plot of marker specific ancestry for each individual. Each row corresponds to an individual and each column to a marker. Each marker/individual combination is colored dark green for homozygotes for alleles from parental population 1 (allele count of 2), medium green for interspecific heterozygotes (allele count of 1), light green for homozygotes for alleles from parental population 2 (allele count of 0), or white (missing data). Individuals are ordered according to hybrid index estimates, which are plotted to the right of the main plot.

Value

A plot is produced, but no value is returned.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

References

Gompert Z. and Buerkle C. A. (2009) *introgress*: a software package for mapping components of isolation in hybrids. *Molecular Ecology Resources*, in preparation.

See Also

```
prepare.data, est.h
```

p1D 25

p1D

Parental Population 1 Dominant Genotype Data from Simulation 1

Description

This data set contains genotype data for parental population 1 associated with AdmixDom. This data set consists of 110 dominant markers scored for 10 individuals. All individuals were given a genotype of 1, meaning they possessed the dominant allele at each marker.

Usage

data(p1D)

Format

A matrix with 110 rows and 10 columns.

Source

From simulations conducted by CAB and ZG.

See Also

AdmixDom

p1DataSim2

Parental Population 1 Dominant Genotype Data from Simulation 2

Description

This data set contains genotype data for parental population 1 associated with AdmixDataSim2. This data set consists of 90 co-dominant and 10 dominant markers scored for 50 individuals. The 220 allele occurs at a high frequency for the 90 co-dominant markers in this population, as does the 1 allele (phenotype) for the 10 dominant markers.

26 p2D

Usage

```
data(p1DataSim2)
```

Format

A matrix with 100 rows and 50 columns.

Source

From simulations conducted by CAB and ZG.

See Also

AdmixDataSim2

p2D

Parental Population 2 Dominant Genotype Data from Simulation 1

Description

This data set contains genotype data for parental population 2 associated with AdmixDom. This data set consists of 110 dominant markers scored for 10 individuals. All individuals were given a genotype of 0, meaning that they are homozygous for the recessive allele at each marker.

Usage

data(p2D)

Format

A matrix with 110 rows and 10 columns.

Source

From simulations conducted by CAB and ZG.

See Also

AdmixDom

p2DataSim2 27

p2DataSim2

Parental Population 2 Genotype Data from Simulation 2

Description

This data set contains genotype data for parental population 2 associated with AdmixDataSim2. This data set consists of 90 co-dominant and 10 dominant markers scored for 50 individuals. The 224 and 230 alleles occurs at high frequency for the 90 co-dominant markers in this population, as does the 0 (recessive) allele for the 10 dominant markers.

Usage

data(p2DataSim2)

Format

A matrix with 100 rows and 50 columns.

Source

From simulations conducted by CAB and ZG.

See Also

AdmixDataSim2

per.locus.like

Per Locus Likelihood

Description

This is an internal function called by est.h.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

See Also

est.h

28 prepare.data

Description

This function is meant to be used with individuals from an admixed population. The function determines the number of alleles inherited from each of two parental populations at each locus. The counts are based on genotype data from specified parental populations, which must be supplied. This function works with both co-dominant and dominant (or haploid) data.

Usage

Arguments

admix.gen	a matrix, array or data frame with genotype data
loci.data	a matrix or array providing marker information.
parental1	a matrix or two-dimensional array if $fixed=FALSE$, a single character if $fixed=TRUE$.
parental2	a matrix or two-dimensional array if $fixed=FALSE$, a single character if $fixed=TRUE$.
pop.id	a logical specifying whether admix.gen includes a row specifying sampling localities.
ind.id	a logical specifying whether admix.gen includes a row specifying individual identifications.
fixed	a logical specifying whether all loci scored exhibit fixed differences between the parental populations.
sep.rows	a logical specifying whether genotypes at a locus are recorded using two rows.
sep.columns	a logical specifying whether genotypes at a locus are recorded using two columns.

Details

Genotypic data for individuals are provided in admix.gen, a data object with genotypes for each individual at each locus in the format 'A/D' or '110/114' for co-dominant data, 'A' or 'hap1b' for haploid data, and '0' or '1' for dominant data. In other words, for co-dominant and haploid data alleles can be encoded by any simple character string. Each row should contain data for a locus and columns should correspond to individuals. Missing data should be entered as 'NA/NA' or 'NA' for co-dominant and haploid / dominant data, respectively.

Alternatively, in admix.gen genotypic data for an individual can be split between two rows (sep.rows = TRUE) or two columns (sep.columns = TRUE). These options are similar to those of the data format for the program *structure* (Pritchard et al. 2000, Falush et al. 2003), with the difference that admix.gen is transposed relative to the input for *structure*. Thus, after reading in a *structure* file, the data matrix

prepare.data 29

can be transposed with rawdata <- t(rawdata) before passing the matrix to prepare.data. If genotype data are split across columns or rows, and they include haploid or dominant markers, the second allele for these markers should be recorded as NA.

If pop.id = TRUE and ind.id = TRUE the first row of admix.gen should give the population identification (i.e. sampling locality) of each individual and the second row should provide a unique individual identification; genotype information would then begin on row three.

loci.data is a matrix or array data object where each row provides information on one locus. The first column gives a unique locus name (e.g. "locus3"), and the second column specifies whether the locus is co-dominant ("C" or "c"), haploid ("H" or "h"), or dominant ("D" or "d"). These first two columns in loci.data are required. The third column, which is optional, is a numeric value specifying the linkage groups for the marker. If present, this column is used in the mk.image function for plotting. The fourth column, which is also optional, is a numeric value specifying both the linkage group and location on the linkage group (e.g. 3.70, for a marker at 70 cM on linkage group 3). This last column could be used to generate a different order in which to utilize marker data from admix.gen in other functions in the package (specified in the marker.order argument to mk.image and clines.plot). Each column in loci.data should have a heading (the second column should be named "type").

If the parental populations exhibit fixed differences for all markers scored (i.e. fixed = TRUE) then parental1 and parental2 should give the character used to specify alleles derived from parental populations one and two, respectively (e.g. parental1 = "p1" and parental2 = "p2"). If parental populations exhibit fixed differences at all loci, the count matrix produced by prepare.data is simply a count of the number of alleles inherited from parental population 1 for each individual at each locus (0, 1, or 2 for co-dominant marker data; 0 or 1 for dominant or haploid marker data).

If the parental populations do not exhibit fixed differences at all loci scored (i.e. fixed = FALSE) then parental 1 and parental 2 should be matrix data objects providing genotype data for individuals sampled from each of the parental populations. These data objects should be in the same format as the genotype data data object, with the difference that they should not contain rows for individual and population identifications at the top. prepare data uses the parental data objects to calculate allele frequencies at each locus for both of the parental populations. Alleles are then binned into allelic classes with maximum (equal to the observed) frequency differentials between parental populations (δ , Gregorius and Roberds 1986). These allelic classes serve as the basis for estimating the count matrix, which is in the same format as described above. In the absence of fixed differences the counts are of alleles from the allelic class associated with population 1 and the frequency of allelic classes in the parental species can be used to account for uncertainty in the ancestry of particular alleles.

See Gompert and Buerkle (2009a, 2009b) for additional details.

Value

A list with the following components:

Individual.data

a matrix with pop.id and ind.id data if they were supplied.

Count.matrix the count matrix; each row corresponds to a locus and each column represents

an individual.

Combos.to.use NULL if fixed = TRUE, otherwise this provides the allelic class data needed for

genomic.clines.

30 prepare.data

Parental1.allele.freq

matrix of allele frequencies calculated for parental population 1 where each row is a locus and each column is an allele.

Parental2.allele.freq

matrix of allele frequencies calculated for parental population 2 where each row

is a locus and each column is an allele.

Alleles a matrix specifying the names of the alleles in the same order as they are given

in Parental1.allele.freq and Parental2.allele.freq for each locus.

Admix.gen the matrix of genotype data for the admixed population; each row corresponds

to a locus and each column represents an individual.

Author(s)

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References

Falush D., Stephens M., and Pritchard J. K. (2003) Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics, **164**, 1567-1587.

Gompert Z. and Buerkle C. A. (2009) A powerful regression-based method for admixture mapping of isolation across the genome of hybrids. *Molecular Ecology*, **18**, 1207-1224.

Gompert Z. and Buerkle C. A. (2009) *introgress*: a software package for mapping components of isolation in hybrids. *Molecular Ecology Resources*, in preparation.

Gregorius H. R. and Roberds J. H. (1986) Measurement of genetical differentiation among subpopulations. *Theoretical and Applied Genetics*, **71**, 826-834.

Pritchard J. K., Stephens M., and Donnelly P. (2000) Inference of population structure using multi-locus genotype data. Genetics, **155**, 945-959.

See Also

```
delta, mk.image, genomic.clines, clines.plot
```

s.wrapper 31

s.wrapper

Sign Wrapper

Description

This is an internal function called by est.h.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

See Also

est.h

support.limit

Support Limit

Description

This is an internal function called by est.h.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

See Also

est.h

test.combinations

Test Combinations

Description

This is an internal function called by prepare.data.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

See Also

delta, prepare.data

32 triangle.plot

test.data.objects

Test Data Objects

Description

This is an internal function called by prepare.data.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

See Also

prepare.data

test.genotypes

Test Genotypes

Description

This is an internal function called by prepare.data.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

See Also

prepare.data

triangle.plot

Triangle Plot

Description

This function makes a plot of interspecific heterozygosity as a function of hybrid index.

Usage

triangle.plot 33

Arguments

hi.index	a data frame produced by est.h or a numeric vector of hybrid index estimates.
int.het	a vector of numeric interspecific heterozygosity estimates.
pdf	a logical specifying whether results should be output to a pdf file.
out.file	a character string specifying the name of the output file if pdf=TRUE.

Details

This function plots interspecific heterozygosity as a function of hybrid index for individuals from an admixed population. Individuals that are the progeny of at least one parent from one of the pure parental populations should have maximal heterozygosity for the observed hybrid index. The plot has lines that correspond to these theoretical maximum values. Individuals that fall on the maximal line are likely F1s or backcross progeny. Evidence for individuals of this type will be more likely if the data set consists of loci with no alleles in common between parental species (delta=1), whereas shared alleles will lead to ambiguity in inferring ancestry. Hybrid index estimates can be obtained from the est.h function and interspecific heterozygosity estimates can be obtained from the calc.intersp.het function.

Value

A plot is produced, but there is no return value.

Author(s)

Zachariah Gompert <zgompert@uwyo.edu>, C. Alex Buerkle <buerkle@uwyo.edu>

See Also

```
est.h, calc.intersp.het, delta
```

```
## produce triangle plots
## load simulated data
## markers have fixed differences, with
## alleles coded as 'P1' and 'P2'
data(AdmixDataSim1)
data(LociDataSim1)
## use prepare.data to produce introgress.data
introgress.data<-prepare.data(admix.gen=AdmixDataSim1,</pre>
                              loci.data=LociDataSim1,
                              parental1="P1", parental2="P2",
                              pop.id=FALSE, ind.id=FALSE,
                              fixed=TRUE)
## estimate hybrid index
hi.index<-est.h(introgress.data=introgress.data,
                loci.data=LociDataSim1, fixed=TRUE, p1.allele="P1",
                p2.allele="P2")
```

34 triangle.plot

```
## Estimate interspecific heterozygosity
int.het<-calc.intersp.het(introgress.data=introgress.data)
## make plot
triangle.plot(hi.index=hi.index, int.het=int.het, pdf=FALSE)</pre>
```

Index

```
*Topic datasets
                                                   p1D, 25
    AdmixDataSim1, 3
                                                   p1DataSim2, 4, 22, 25
    AdmixDataSim2, 4
                                                   p2D, 26
    AdmixDom, 5
                                                   p2DataSim2, 4, 22, 27
    LociD, 21
                                                   per.locus.like, 27
    LociDataSim1, 21
                                                   prepare.data, 2, 6, 10, 13, 15, 16, 18, 24, 28,
                                                            31, 32
    LociDataSim2, 22
    p1D, 25
                                                   s.wrapper, 31
    p1DataSim2, 25
                                                   support.limit, 31
    p2D, 26
    p2DataSim2, 27
                                                   test.combinations, 16, 31
                                                   test.data.objects, 32
AdmixDataSim1, 3, 22
                                                   test.genotypes, 32
AdmixDataSim2, 4, 22, 26, 27
                                                   triangle.plot, 3, 32
AdmixDom, 5, 21, 25, 26
calc.intersp.het, 3, 6, 33
clines.plot, 2, 7, 12, 30
compare.clines, 3, 9
composite.clines, 11
delta, 12, 30, 31, 33
est.h, 2, 10, 13, 18, 20, 24, 27, 31, 33
fit.c.clines, 15
fit.invariant.clines, 16
fixup.combos.touse, 16
genomic.clines, 2, 8, 10, 12, 15, 16, 16, 30
h. func, 20
introgress-package, 2
like.h, 20
LociD, 5, 21
LociDataSim1, 4, 21
LociDataSim2, 4, 22
mk.image, 3, 23, 30
```