

# Package ‘inbreedR’

February 2, 2022

**Title** Analysing Inbreeding Based on Genetic Markers

**Version** 0.3.3

**Description** A framework for analysing inbreeding and heterozygosity-fitness correlations (HFCs) based on microsatellite and SNP markers.

**Depends** R (>= 3.2.1)

**License** GPL-2

**LazyData** true

**Imports** data.table (>= 1.9.6), parallel, stats, graphics

**Suggests** testthat (>= 0.10.0), knitr, rmarkdown, covr

**VignetteBuilder** knitr

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**NeedsCompilation** no

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bodyweight	<i>Oldfield mouse bodyweight data</i>
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### Description

Bodyweight data for 36 oldfield mice.

### Format

A vector with 36 elements.

### References

Hoffman, J.I., Simpson, F., David, P., Rijks, J.M., Kuiken, T., Thorne, M.A.S., Lacey, R.C. & Dasmahapatra, K.K. (2014) High-throughput sequencing reveals inbreeding depression in a natural population. *Proceedings of the National Academy of Sciences of the United States of America*, 111: 3775-3780. Doi: 10.1073/pnas.1318945111

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check_data	<i>Checks the data for consistency with the inbreedR working format.</i>
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### Description

The `inbreedR` working format is an  $i * l$  genotype matrix, whereby each individual is a row and each column is a locus. Heterozygosity at a given locus should be coded as 1, homozygosity as 0 and missing values should be coded as NA.

### Usage

```
check_data(genotypes, num_ind = NULL, num_loci = NULL)
```

### Arguments

genotypes	data.frame (or matrix) with individuals in rows and loci in columns, containing genotypes coded as 0 (homozygote), 1 (heterozygote) and NA (missing)
num_ind	Number of individuals
num_loci	Number of loci / markers

**Details**

Checks that (1) the genotype data just contains 3 elements, which is 0 for homozygote, 1 for heterozygote and NA for missing data, (2) the number of individuals corresponds to the number of rows and the number of loci corresponds to the number of columns, (3) the data type is numeric. .

**Value**

TRUE if the data format is correct, error message if any test failed

**Author(s)**

Martin A. Stoffel (martin.adam.stoffel@gmail.com)

**Examples**

```
data(mouse_msats)
# transform raw genotypes into 0/1 format
genotypes <- convert_raw(mouse_msats)
# check data
check_data(genotypes, num_ind = 36, num_loci = 12)
```

---

convert\_raw

*Genotype format converter*

---

**Description**

Turns raw genotype data into 0 (homozygote), 1 (heterozygote) and NA (missing), which is the working format for the `inbreedR` functions. A raw genotype matrix has individuals in rows and each locus in two adjacent columns. Individual ID's can be rownames. Type `data(mouse_msats)` for an example raw genotype data frame.

**Usage**

```
convert_raw(genotypes)
```

**Arguments**

`genotypes` Raw genotype data.frame or matrix. Rows represent individuals and each locus has two adjacent columns. Alleles within loci can be coded as numbers (e.g. microsatellite length) or characters (e.g. "A", "T") See `data(mouse_msats)` for an example. Missing values should be coded as NA.

**Value**

data.frame object with 0 (homozygote), 1 (heterozygote) and NA (missing data). Each locus is a column and each individual is a row.

**Author(s)**

Martin Stoffel (martin.adam.stoffel@gmail.com)

**Examples**

```
# Mouse microsatellite data with missing values coded as NA
data(mouse_msats)
genotypes <- convert_raw(mouse_msats)
head(genotypes)
```

---

g2\_microsats

*Estimating g2 from microsatellite data*


---

**Description**

Estimating g2 from microsatellite data

**Usage**

```
g2_microsats(genotypes, nperm = 0, nboot = 0, boot_over = "inds",
             CI = 0.95, verbose = TRUE)
```

**Arguments**

genotypes	data.frame with individuals in rows and loci in columns, containing genotypes coded as 0 (homozygote), 1 (heterozygote) and NA (missing)
nperm	Number of permutations for testing the hypothesis that the empirical g2-value is higher than the g2 for random associations between individuals and genotypes.
nboot	Number of bootstraps for estimating a confidence interval
boot_over	Bootstrap over individuals by specifying "inds" and over loci with "loci". Defaults to "ind".
CI	Confidence interval (default to 0.95)
verbose	If FALSE, nothing will be printed to show the status of bootstraps and permutations.

**Details**

Calculates g2 from smaller datasets. The underlying formula is computationally expensive due to double summations over all pairs of loci (see David et al. 2007). Use `convert_raw` to convert raw genotypes (with 2 columns per locus) into the required format.

**Value**

`g2_microsats` returns an object of class "inbreed". The functions 'print' and 'plot' are used to print a summary and to plot the distribution of bootstrapped g2 values and CI.

An 'inbreed' object from `g2_microsats` is a list containing the following components:

<code>call</code>	function call.
<code>g2</code>	g2 value
<code>p_val</code>	p value from permutation test
<code>g2_permut</code>	g2 values from permuted genotypes
<code>g2_boot</code>	g2 values from bootstrap samples
<code>CI_boot</code>	confidence interval from bootstraps
<code>se_boot</code>	standard error of g2 from bootstraps
<code>nobs</code>	number of observations
<code>nloc</code>	number of markers

**Author(s)**

Martin A. Stoffel (martin.adam.stoffel@gmail.com) & Mareike Esser (messer@techfak.uni-bielefeld.de)

**References**

David, P., Pujol, B., Viard, F., Castella, V. and Goudet, J. (2007), Reliable selfing rate estimates from imperfect population genetic data. *Molecular Ecology*, 16: 2474

**Examples**

```
data(mouse_msats)
# transform raw genotypes into 0/1 format
genotypes <- convert_raw(mouse_msats)
(g2_mouse <- g2_microsats(genotypes, nperm = 1000, nboot = 100, boot_over = "inds", CI = 0.95))
```

---

g2\_snps

*Estimating g2 from larger datasets, such as SNPs*


---

**Description**

Estimating g2 from larger datasets, such as SNPs

**Usage**

```
g2_snps(genotypes, nperm = 0, nboot = 0, boot_over = "inds", CI = 0.95,
        parallel = FALSE, ncores = NULL, verbose = TRUE)
```

**Arguments**

genotypes	data.frame with individuals in rows and loci in columns, containing genotypes coded as 0 (homozygote), 1 (heterozygote) and NA (missing)
nperm	number of permutations for to estimate a p-value
nboot	number of bootstraps to estimate a confidence interval
boot_over	Bootstrap over individuals by specifying "inds" and over loci with "loci". Defaults to "ind".
CI	confidence interval (default to 0.95)
parallel	Default is FALSE. If TRUE, bootstrapping and permutation tests are parallelized
ncores	Specify number of cores to use for parallelization. By default, all available cores are used.
verbose	If FALSE, nothing will be printed to show the status of bootstraps and permutations.

**Details**

Calculates g2 from SNP datasets. Use `convert_raw` to convert raw genotypes (with 2 columns per locus) into the required format

**Value**

`g2_snps` returns an object of class "inbreed". The functions 'print' and 'plot' are used to print a summary and to plot the distribution of bootstrapped g2 values and CI.

An 'inbreed' object from `g2_snps` is a list containing the following components:

call	function call.
g2	g2 value
p_val	p value from permutation test
g2_permut	g2 values from permuted genotypes
g2_boot	g2 values from bootstrap samples
CI_boot	confidence interval from bootstrap distribution
se_boot	standard error of g2 from bootstraps
nobs	number of observations
nloc	number of markers

**Author(s)**

Martin A. Stoffel (martin.adam.stoffel@gmail.com) & Mareike Esser (messer@techfak.uni-bielefeld.de)

**References**

Hoffman, J.I., Simpson, F., David, P., Rijks, J.M., Kuiken, T., Thorne, M.A.S., Lacey, R.C. & Dasmahapatra, K.K. (2014) High-throughput sequencing reveals inbreeding depression in a natural population. *Proceedings of the National Academy of Sciences of the United States of America*, 111: 3775-3780. Doi: 10.1073/pnas.1318945111

**Examples**

```
# load SNP genotypes in 0 (homozygous), 1 (heterozygous), NA (missing) format.
# low number of bootstraps and permutations for computational reasons.
data(mouse_snps)
(g2_mouse <- g2_snps(mouse_snps, nperm = 10, nboot = 10, CI = 0.95, boot_over = "loci"))

# parallelized version for more bootstraps or permutations
## Not run:
(g2_mouse <- g2_snps(mouse_snps, nperm = 1000, nboot = 1000,
                    CI = 0.95, parallel = TRUE, ncores = 4))

## End(Not run)
```

---

HHC	<i>Calculates heterozygosity-heterozygosity correlations with standardized multilocus heterozygosities (sMLH)</i>
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---

**Description**

Loci are randomly divided into two equal groups and the correlation coefficient between the resulting sMLH values is calculated.

**Usage**

```
HHC(genotypes, reps = 100, CI = 0.95)
```

**Arguments**

genotypes	data.frame with individuals in rows and loci in columns, containing genotypes coded as 0 (homozygote), 1 (heterozygote) and NA (missing)
reps	number of repetitions, i.e. splittings of the dataset
CI	size of the confidence interval around the mean het-het correlation (default is 0.95)

**Value**

call	function call.
HHC_vals	vector of HHC's obtained by randomly splitting the dataset
summary_exp_r2	r2 mean and sd for each number of subsetted loci
nobs	number of observations
nloc	number of markers

**Author(s)**

Martin A. Stoffel (martin.adam.stoffel@gmail.com)

## References

Balloux, F., Amos, W., & Coulson, T. (2004). Does heterozygosity estimate inbreeding in real populations?. *Molecular Ecology*, 13(10), 3021-3031.

## Examples

```
data(mouse_msats)
genotypes <- convert_raw(mouse_msats)
(out <- HHC(genotypes, reps = 100, CI = 0.95))
```

---

inbreedR

*inbreedR: Workflows for analysing variance in inbreeding and HFCs based on SNP or microsatellite markers.*

---

## Description

inbreedR contains the following functions:

[g2\\_microsats](#) [g2\\_snps](#) [convert\\_raw](#) [check\\_data](#) [r2\\_hf](#) [r2\\_Wf](#) [HHC](#) [sMLH](#) [MLH](#) [simulate\\_g2](#) [simulate\\_r2\\_hf](#) [plot.inbreed](#) [print.inbreed](#)

## Details

A correlation between heterozygosity ( $h$ ) and fitness ( $W$ ) requires a simultaneous effect of inbreeding level ( $f$ ) on both of them. A heterozygosity-fitness correlation (HFC) thus is the product of two correlations, which can be summarized in the following equation:

$$r(W, h) = r(W, f)r(h, f)$$

Estimating these parameters and their sensitivity towards the number and type of genetic markers used is the central framework of the inbreedR package. At the heart of measuring inbreeding based on genetic markers is the  $g_2$  statistic, which estimates the correlation of heterozygosity across markers, called identity disequilibrium (ID). ID is a proxy for inbreeding.

The package has three main goals:

- Assessing identity disequilibria and the potential to detect heterozygosity-fitness correlations
- Providing insights on the sensitivity of these measures based on the number/type of molecular markers used
- Implementing computationally efficient functions in a flexible environment for analysing inbreeding and HFC's with both small and large datasets.

For a short introduction to inbreedR start with the vignette: `browseVignettes(package = "inbreedR")`

## Author(s)

Martin Stoffel (martin.adam.stoffel@gmail.com), Mareike Esser (messer@uni-bielefeld.de)

## References

- Slate, J., David, P., Dodds, K. G., Veenliet, B. A., Glass, B. C., Broad, T. E., & McEwan, J. C. (2004). Understanding the relationship between the inbreeding coefficient and multilocus heterozygosity: theoretical expectations and empirical data. *Heredity*, 93(3), 255-265.
- Szulkin, M., Bierne, N., & David, P. (2010). HETEROZYGOSITY-FITNESS CORRELATIONS: A TIME FOR REAPPRAISAL. *Evolution*, 64(5), 1202-1217.
- David, P., Pujol, B., Viard, F., Castella, V. and Goudet, J. (2007), Reliable selfing rate estimates from imperfect population genetic data. *Molecular Ecology*, 16: 2474
- Hoffman, J.I., Simpson, F., David, P., Rijks, J.M., Kuiken, T., Thorne, M.A.S., Lacey, R.C. & Dasmahapatra, K.K. (2014) High-throughput sequencing reveals inbreeding depression in a natural population. *Proceedings of the National Academy of Sciences of the United States of America*, 111: 3775-3780.

MLH

*Calculate multilocus heterozygosity (MLH)*

## Description

MLH is defined as the total number of heterozygous loci in an individual divided by the number of loci typed in the focal individual. An MLH of 0.5 thus means that 50 percent of an individuals loci are heterozygous.

## Usage

```
MLH(genotypes)
```

## Arguments

genotypes	data.frame with individuals in rows and loci in columns, containing genotypes coded as 0 (homozygote), 1 (heterozygote) and NA (missing)
-----------	------------------------------------------------------------------------------------------------------------------------------------------

## Value

Vector of individual multilocus heterozygosities

## Author(s)

Martin A. Stoffel (martin.adam.stoffel@gmail.com)

## References

- Coltman, D. W., Pilkington, J. G., Smith, J. A., & Pemberton, J. M. (1999). Parasite-mediated selection against inbred Soay sheep in a free-living, island population. *Evolution*, 1259-1267.

**Examples**

```
data(mouse_msats)
genotypes <- convert_raw(mouse_msats)
het <- MLH(genotypes)
```

---

mouse\_msats

*Oldfield mouse microsatellite data*


---

**Description**

Dataset with each microsatellite locus in two adjacent columns (one per allele). Missing values are coded as NA.

**Format**

A data frame with 36 observations at 13198 loci.

**References**

Hoffman, J.I., Simpson, F., David, P., Rijks, J.M., Kuiken, T., Thorne, M.A.S., Lacey, R.C. & Dasmahapatra, K.K. (2014) High-throughput sequencing reveals inbreeding depression in a natural population. *Proceedings of the National Academy of Sciences of the United States of America*, 111: 3775-3780. Doi: 10.1073/pnas.1318945111

Dasmahapatra KK, Lacy RC, Amos W (2007) Estimating levels of inbreeding using AFLP markers. *Heredity* 100:286-295.

---

mouse\_snps

*Oldfield mouse SNP data*


---

**Description**

Mouse snp data in 0 (homozygous), 1(heterozygous) and NA (missing) format. Each row represents an individual and each column is a locus.

**Format**

A data.frame with 36 observations at 13198 loci.

**References**

Hoffman, J.I., Simpson, F., David, P., Rijks, J.M., Kuiken, T., Thorne, M.A.S., Lacey, R.C. & Dasmahapatra, K.K. (2014) High-throughput sequencing reveals inbreeding depression in a natural population. *Proceedings of the National Academy of Sciences of the United States of America*, 111: 3775-3780. Doi: 10.1073/pnas.1318945111

Dasmahapatra KK, Lacy RC, Amos W (2007) Estimating levels of inbreeding using AFLP markers. *Heredity* 100:286-295.

---

plot.inbreed	<i>Plot an inbreed object</i>
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---

**Description**

Plot an inbreed object

**Usage**

```
## S3 method for class 'inbreed'
plot(x, true_g2 = FALSE, plottype = c("boxplot",
  "histogram"), ...)
```

**Arguments**

x	An inbreed object.
true_g2	For plotting a simulate_g2 output. If TRUE, plots the real g2 (based on realized f) as a reference line.
plottype	deprecated. "boxplot" or "histogram" to plot the output of r2_hf() and to show either the boxplots through resampling of loci or the histogram from the bootstrapping of r2 over individuals.
...	Additional arguments to the hist() function for the g2 and HHC functions. Additional arguments to the boxplot() function for plotting the result of the r2_hf() function.

**Author(s)**

Martin Stoffel (martin.adam.stoffel@gmail.com)

**See Also**

[g2\\_snps](#), [g2\\_microsats](#)

---

print.inbreed	<i>Print an inbreed object</i>
---------------	--------------------------------

---

**Description**

Displays the results a inbreed object.

**Usage**

```
## S3 method for class 'inbreed'
print(x, ...)
```

**Arguments**

x                    An inbreed object from one of the inbreedR functions.  
 ...                Additional arguments; none are used in this method.

**Author(s)**

Martin Stoffel (martin.adam.stoffel@gmail.com)

**See Also**

[g2\\_snps](#), [g2\\_microsats](#), [plot](#)

---

r2_hf	<i>Expected r2 between standardized multilocus heterozygosity (h) and inbreeding level (f)</i>
-------	------------------------------------------------------------------------------------------------

---

**Description**

Expected r2 between standardized multilocus heterozygosity (h) and inbreeding level (f)

**Usage**

```
r2_hf(genotypes, type = c("msats", "snps"), nboot = NULL,
      parallel = FALSE, ncores = NULL, CI = 0.95)
```

**Arguments**

genotypes        data.frame with individuals in rows and loci in columns, containing genotypes coded as 0 (homozygote), 1 (heterozygote) and NA (missing)

type             specifies g2 formula to take. Type "snps" for large datasets and "msats" for smaller datasets.

nboot            number of bootstraps over individuals to estimate a confidence interval around r2(h, f)

parallel         Default is FALSE. If TRUE, bootstrapping and permutation tests are parallelized

ncores          Specify number of cores to use for parallelization. By default, all available cores but one are used.

CI                confidence interval (default to 0.95)

**Value**

call             function call.

r2\_hf\_full        expected r2 between inbreeding and sMLH for the full dataset

r2\_hf\_boot        expected r2 values from bootstrapping over individuals

CI\_boot          confidence interval around the expected r2

nobs             number of observations

nloc             number of markers

**Author(s)**

Martin A. Stoffel (martin.adam.stoffel@gmail.com)

**References**

Slate, J., David, P., Dodds, K. G., Veenliet, B. A., Glass, B. C., Broad, T. E., & McEwan, J. C. (2004). Understanding the relationship between the inbreeding coefficient and multilocus heterozygosity: theoretical expectations and empirical data. *Heredity*, 93(3), 255-265.

Szulkin, M., Bierne, N., & David, P. (2010). HETEROZYGOSITY-FITNESS CORRELATIONS: A TIME FOR REAPPRAISAL. *Evolution*, 64(5), 1202-1217.

**Examples**

```
data(mouse_msats)
genotypes <- convert_raw(mouse_msats)
(out <- r2_hf(genotypes, nboot = 100, type = "msats", parallel = FALSE))
plot(out)
```

---

r2\_Wf

*Expected r2 between inbreeding level (f) and fitness (W)*

---

**Description**

Expected r2 between inbreeding level (f) and fitness (W)

**Usage**

```
r2_Wf(genotypes, trait, family = "gaussian", type = c("msats", "snps"),
      nboot = NULL, parallel = FALSE, ncores = NULL, CI = 0.95)
```

**Arguments**

genotypes	A data.frame with individuals in rows and loci in columns, containing genotypes coded as 0 (homozygote), 1 (heterozygote) and NA (missing).
trait	vector of any type which can be specified in R's glm() function. Sequence of individuals has to match sequence of individuals in the rows of the genotypes data.frame.
family	distribution of the trait. Default is gaussian. For other distributions, just naming the distribution (e.g. binomial) will use the default link function (see ?family). Specifying another link function can be done in the same way as in the glm() function. A binomial distribution with probit instead of logit link would be specified with family = binomial(link = "probit")
type	specifies g2 formula to take. Type "snps" for large datasets and "msats" for smaller datasets.
nboot	number of bootstraps over individuals to estimate a confidence interval around r2(W, f).

parallel	Default is FALSE. If TRUE, bootstrapping and permutation tests are parallelized.
ncores	Specify number of cores to use for parallelization. By default, all available cores but one are used.
CI	confidence interval (default to 0.95)

**Value**

call	function call.
exp_r2_full	expected r2 between inbreeding and sMLH for the full dataset
r2_Wf_boot	expected r2 values from bootstrapping over individuals
CI_boot	confidence interval around the expected r2
nobs	number of observations
nloc	number of markers

**Author(s)**

Martin A. Stoffel (martin.adam.stoffel@gmail.com)

**References**

- Slate, J., David, P., Dodds, K. G., Veenliet, B. A., Glass, B. C., Broad, T. E., & McEwan, J. C. (2004). Understanding the relationship between the inbreeding coefficient and multilocus heterozygosity: theoretical expectations and empirical data. *Heredity*, 93(3), 255-265.
- Szulkin, M., Bierne, N., & David, P. (2010). HETEROZYGOSITY-FITNESS CORRELATIONS: A TIME FOR REAPPRAISAL. *Evolution*, 64(5), 1202-1217.

**Examples**

```
data(mouse_msats)
data(bodyweight)
genotypes <- convert_raw(mouse_msats)
```

```
(out <- r2_Wf(genotypes = genotypes, trait = bodyweight, family = "gaussian", type = "msats",
             nboot = 100, parallel = FALSE, ncores = NULL, CI = 0.95))
```

---

simulate\_g2

*Simulate g2*

---

**Description**

This function can be used to simulate genotype data, draw subsets of loci and calculate the respective  $g2$  values. Every subset of markers is drawn independently to give insights into the variation and precision of  $g2$  calculated from a given number of markers and individuals.

**Usage**

```
simulate_g2(n_ind = NULL, H_nonInb = 0.5, meanF = 0.2, varF = 0.03,
  subsets = NULL, reps = 100, type = c("msats", "snps"), CI = 0.95)
```

**Arguments**

n_ind	number of individuals to sample from the population
H_nonInb	true genome-wide heterozygosity of a non-inbred individual
meanF	mean realized inbreeding $f$
varF	variance in realized inbreeding $f$
subsets	a vector specifying the sizes of marker-subsets to draw. Specifying subsets = c(2, 5, 10, 15, 20) would draw marker sets of 2 to 20 markers. The minimum number of markers to calculate $g2$ is 2.
reps	number of resampling repetitions
type	specifies $g2$ formula. Type "snps" for large datasets and "msats" for smaller datasets.
CI	Confidence intervals to calculate (default to 0.95)

**Details**

The `simulate_g2` function simulates genotypes from which subsets of loci can be sampled independently. These simulations can be used to evaluate the effects of the number of individuals and loci on the precision and magnitude of  $g2$ . The user specifies the number of simulated individuals (`n_ind`), the subsets of loci (`subsets`) to be drawn, the heterozygosity of non-inbred individuals (`H_nonInb`) and the distribution of  $f$  among the simulated individuals. The  $f$  values of the simulated individuals are sampled randomly from a beta distribution with mean (`meanF`) and variance (`varF`) specified by the user (e.g. as in wang2011). This enables the simulation to mimic populations with known inbreeding characteristics, or to simulate hypothetical scenarios of interest. For computational simplicity, allele frequencies are assumed to be constant across all loci and the simulated loci are unlinked. Genotypes (i.e. the heterozygosity/homozygosity status at each locus) are assigned stochastically based on the  $f$  values of the simulated individuals. Specifically, the probability of an individual being heterozygous at any given locus ( $H$ ) is expressed as  $H = H0(1 - f)$ , where  $H0$  is the user-specified heterozygosity of a non-inbred individual and  $f$  is an individual's inbreeding coefficient drawn from the beta distribution.

**Value**

`simulate_g2` returns an object of class "inbreed". The functions 'print' and 'plot' are used to print a summary and to plot the  $g2$  values with means and confidence intervals

An 'inbreed' object from `simulate_g2` is a list containing the following components:

call	function call.
estMat	matrix with all $r2(h,f)$ estimates. Each row contains the values for a given subset of markers
true_g2	"true" $g2$ value based on the assigned realized inbreeding values
n_ind	specified number of individuals

subsets	vector specifying the marker sets
reps	repetitions per subset
H_nonInb	true genome-wide heterozygosity of a non-inbred individual
meanF	mean realized inbreeding $f$
varF	variance in realized inbreeding $f$
min_val	minimum $g^2$ value
max_val	maximum $g^2$ value
all_CI	confidence intervals for all subsets
all_sd	standard deviations for all subsets

**Author(s)**

Marty Kardos (marty.kardos@ebc.uu.se) & Martin A. Stoffel (martin.adam.stoffel@gmail.com)

**Examples**

```
data(mouse_msats)
genotypes <- convert_raw(mouse_msats)
sim_g2 <- simulate_g2(n_ind = 10, H_nonInb = 0.5, meanF = 0.2, varF = 0.03,
                    subsets = c(4,6,8,10), reps = 100,
                    type = "msats")
plot(sim_g2)
```

---

simulate_r2_hf	<i>Calculates the expected squared correlation between heterozygosity and inbreeding for simulated marker sets</i>
----------------	--------------------------------------------------------------------------------------------------------------------

---

**Description**

This function can be used to simulate genotype data, draw random subsamples and calculate the expected squared correlations between heterozygosity and fitness ( $r^2(h, f)$ ). Every subset of markers is drawn independently to give insights into the variation and precision of  $r^2(h, f)$  calculated from a given number of markers and individuals.

**Usage**

```
simulate_r2_hf(n_ind = NULL, H_nonInb = 0.5, meanF = 0.2, varF = 0.03,
              subsets = NULL, reps = 100, type = c("msats", "snps"), CI = 0.95)
```

**Arguments**

n_ind	number of individuals to sample from the population
H_nonInb	true genome-wide heterozygosity of a non-inbred individual
meanF	mean realized inbreeding $f$
varF	variance in realized inbreeding $f$
subsets	a vector specifying the sizes of marker-subsets to draw. Specifying subsets = c(2, 5, 10, 15, 20) would draw marker sets of 2 to 20 markers. The minimum number of markers is 2.
reps	number of resampling repetitions
type	specifies g2 formula. Type "snps" for large datasets and "msats" for smaller datasets.
CI	Confidence intervals to calculate (default to 0.95)

**Details**

The `simulate_r2_hf` function simulates genotypes from which subsets of loci can be sampled independently. These simulations can be used to evaluate the effects of the number of individuals and loci on the precision and magnitude of the expected squared correlation between heterozygosity and inbreeding ( $r^2(h, f)$ ). The user specifies the number of simulated individuals (`n_ind`), the subsets of loci (`subsets`) to be drawn, the heterozygosity of non-inbred individuals (`H_nonInb`) and the distribution of  $f$  among the simulated individuals. The  $f$  values of the simulated individuals are sampled randomly from a beta distribution with mean (`meanF`) and variance (`varF`) specified by the user (e.g. as in wang2011). This enables the simulation to mimic populations with known inbreeding characteristics, or to simulate hypothetical scenarios of interest. For computational simplicity, allele frequencies are assumed to be constant across all loci and the simulated loci are unlinked. Genotypes (i.e. the heterozygosity/homozygosity status at each locus) are assigned stochastically based on the  $f$  values of the simulated individuals. Specifically, the probability of an individual being heterozygous at any given locus ( $H$ ) is expressed as  $H = H_0(1 - f)$ , where  $H_0$  is the user-specified heterozygosity of a non-inbred individual and  $f$  is an individual's inbreeding coefficient drawn from the beta distribution.

**Value**

`simulate_r2_hf` returns an object of class "inbreed". The functions 'print' and 'plot' are used to print a summary and to plot the  $r^2(h, f)$  values with means and confidence intervals

An 'inbreed' object from `simulate_g2` is a list containing the following components:

call	function call.
estMat	matrix with all $r^2(h, f)$ estimates. Each row contains the values for a given subset of markers
n_ind	specified number of individuals
subsets	vector specifying the marker sets
reps	repetitions per subset
H_nonInb	true genome-wide heterozygosity of a non-inbred individual
meanF	mean realized inbreeding $f$

varF	variance in realized inbreeding f
min_val	minimum g <sup>2</sup> value
max_val	maximum g <sup>2</sup> value
all_CI	confidence intervals for all subsets
all_sd	standard deviations for all subsets

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**Examples**

```
data(mouse_msats)
genotypes <- convert_raw(mouse_msats)
sim_r2 <- simulate_r2_hf(n_ind = 10, H_nonInb = 0.5, meanF = 0.2, varF = 0.03,
                        subsets = c(4,6,8,10), reps = 100,
                        type = "msats")
plot(sim_r2)
```

---

sMLH

*Calculate multilocus heterozygosity (MLH)*

---

**Description**

sMLH is defined as the total number of heterozygous loci in an individual divided by the sum of average observed heterozygosities in the population over the subset of loci successfully typed in the focal individual.

**Usage**

```
sMLH(genotypes)
```

**Arguments**

genotypes      data.frame with individuals in rows and loci in columns, containing genotypes coded as 0 (homozygote), 1 (heterozygote) and NA (missing)

**Value**

Vector of individual standardized multilocus heterozygosities

**Author(s)**

Martin A. Stoffel (martin.adam.stoffel@gmail.com)

**References**

Coltman, D. W., Pilkington, J. G., Smith, J. A., & Pemberton, J. M. (1999). Parasite-mediated selection against inbred Soay sheep in a free-living, island population. *Evolution*, 1259-1267.

**Examples**

```
data(mouse_msats)
genotypes <- convert_raw(mouse_msats)
het <- sMLH(genotypes)
```

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