Package: heritable (via r-universe)

June 10, 2026

Title Heritability Estimation from Mixed Models

Version 0.1.0

Description Reporting heritability estimates is an important to quantitative genetics studies and breeding experiments. Here we provide functions to calculate various broad-sense heritabilities from 'asreml' and 'lme4' model objects. All methods we have implemented in this package have extensively discussed in the article by Schmidt et al. (2019) <doi:10.1534/genetics.119.302134>.

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Imports asremlPlus, boot, cli, emmeans, MASS, Matrix, methods, reformulas, stringr, vctrs

Suggests testthat (>= 3.0.0), agridat, knitr, rmarkdown, lme4, pbkrtest, dplyr, ggplot2, tidyr, purrr, here

SystemRequirements asreml (4.2.0)

Config/testthat/edition 3

Encoding UTF-8

Roxygen list(markdown = TRUE)

RoxygenNote 7.3.3

Depends R (>= 4.1.0)

LazyData true

VignetteBuilder knitr

URL `https://anu-aagi.github.io/heritable/`

Language en

Config/pak/sysreqs cmake libfftw3-dev libfontconfig1-dev libfreetype6-dev libfribidi-dev git make libharfbuzz-dev libgit2-dev libicu-dev libjpeg-dev libpng-dev libtiff-dev libuv1-dev libwebp-dev libxml2-dev libssl-dev libx11-dev zlib1g-dev

Repository https://anu-aagi.r-universe.dev

Date/Publication 2026-03-12 02:55:41 UTC

RemoteUrl https://github.com/anu-aagi/heritable

RemoteRef HEAD

RemoteSha 29d7ba58d81a35f34e5cc5f12020406c13f6618e

Contents

`bootstrap_asreml` *Parametric bootstrap for an asreml model.*

Description

Simulate $\hat{y} \sim N(X\hat{\beta}, V)$ according to the current asreml fit and then refit to obtain the targeted statistics.

Usage

```
bootstrap_asreml(model, FUN, nsim = 1, use.u = FALSE, seed = NULL, ...)
```

Arguments

`model`	An `asreml` fitted model. Must be fitted with `model.frame = TRUE`.
`FUN`	A function with signature `function(fit)` returning a scalar (the statistic to bootstrap).
`nsim`	Integer. Number of bootstrap replicates.

`use.u`	A logical indicating whether to resample random effects, or only resample residuals.
`seed`	Optional integer seed for reproducibility.
`...`	Additional arguments passed to `boot::boot()`.

Details

Fits parametric bootstrap replicates for an `asreml` model by:

- Extracting the fixed-effect fit yhat = X * beta.
- Extracting V = Var(y) on the observation scale,
- Simulating new responses y* = yhat + L %*% z where L is a Cholesky factor of V,
- Refitting the same asreml call on each simulated dataset,
- Returning a `boot` object.

Value

A `boot` object.

Examples

```
## Not run:
  lettuce_subset <- lettuce_phenotypes |> subset(loc == ”L2”)
  lettuce_asreml <- asreml(
    fixed = y ~ rep * pseudo_var1,
    random = ~gen,
    sparse = ~pseudo_var2,
    data = lettuce_subset,
    trace = FALSE
  )

  b <- bootstrap_asreml(
    lettuce_asreml,
    R = 200,
    statistic = function(fit) coef(fit)$fixed[”(Intercept)”, ”effect”],
    seed = 1
  )
  boot::boot.ci(b, type = ”perc”)

## End(Not run)
```

`confint.heritable` *Bootstrap confidence interval for heritability*

Description

Computes a confidence interval for a heritability estimate using parametric bootstrap of the underlying mixed model.

Usage

```
## S3 method for class 'heritable'
confint(
  object,
  parm = NULL,
  level = 0.95,
  B = 100,
  random_effect = c("resample", "conditional"),
  type = c("basic", "norm", "perc"),
  return_model = TRUE,
  seed = NULL,
  ...
)
```

Arguments

`object`	A heritability object returned by `H2()` (broad-sense). The object must store the fitted model as an attribute.
`parm`	a specification of which parameters are to be given confidence intervals, either a vector of numbers or a vector of names. If missing, all parameters are considered.
`level`	Confidence level.
`B`	Integer. Number of bootstrap replicates.
`random_effect`	Character. Strategy for handling random effects. `"resample"` Resample random effects to propagate uncertainty. `"conditional"` Condition on estimated random effects.
`type`	Character. Bootstrap interval type; one of `"basic"`, `"norm"`, or `"perc"`.
`return_model`	Logical. Whether to return to the `boot` object.
`seed`	Optional random seed.
`...`	Additional arguments passed to the bootstrap routine.

Value

A matrix of confidence intervals.

Examples

```
## Not run:
  lettuce_subset <- lettuce_phenotypes |> subset(loc == "L2")
  lettuce_asreml <- asreml(
    fixed = y ~ rep * pseudo_var1,
    random = ~gen,
    sparse = ~pseudo_var2,
    data = lettuce_subset,
    trace = FALSE
  )

  my_H2 <- H2(lettuce_asreml, "gen", c("Cullis", "Standard"))

  confint(my_H2)

## End(Not run)
```

`get_fixed_fit_asreml` *Fixed-effects-only fitted values from an asreml model*

Description

Returns the fitted values based on fixed effects only ($\hat{y} = X\hat{\beta}$), excluding all random effects.

Usage

```
get_fixed_fit_asreml(model)
```

Arguments

`model`	An object of class `"asreml"`, fitted with `model.frame = TRUE`.

Details

This function reconstructs the fixed-effect design matrix from the stored model frame and multiplies it by the estimated fixed coefficients. Sparse fixed terms (if any) are included.

Random effects (BLUPs) are not included.

Value

A numeric vector of length N, giving the fixed-effects-only fitted value for each observation.

`H2` *Calculate heritability from mixed model object*

Description

A case-specific wrapper for calculating heritability.

- The upper case prefix `H2_` refers to the wrapper or subfunctions e.g. `H2_Delta()` for calculating broad sense heritability

Usage

```
H2(model,
   target,
   method = c("Cullis", "Oakey", "Delta", "Piepho", "Standard"),
   options = NULL,
   ...
   )
```

Arguments

`model`	Model object of class `lmerMod/merMod` or `asreml`
`target`	The name of the random effect for which heritability is to be calculated.
`method`	Character vector of name of method to calculate heritability. See details.
`options`	NULL by default, for internal checking of model object before calculations.
`...`	Additional arguments that specify heritability calculation when interactions with genotype effects are modelled.

Details

The following methods are currently implemented for broad-sense heritability `H2(method = "XX")`:

- `"Cullis"`:

$$H^2_{Cullis} = 1 - \frac{PEV^{BLUP}_{\overline{\Delta ij}}}{2\sigma^2_g}$$

- `"Oakey"`:

$$H^2_{Oakey} = \frac{\sum_{i=n_z+1}^{n_g} \lambda_i}{\sum_{n_g}^{\lambda_i \neq 0}}$$

- `"Delta"`:

$$H^2_{\Delta ..} = 1 - \frac{PEV^{BLUP}_{\overline{\Delta ..}}}{2\sigma^2_g}$$

- `"Piepho"`:

$$H^2_{Piepho} = \frac{\sigma^2_g}{\sigma^2_g + \overline{PEV_{BLUE_g}}/2}$$

- `"Standard"`:

$$H^2_{Standard} = \frac{\sigma^2_g}{\sigma^2_g + \frac{1}{n_g}\sum_{n_g}^{i=1} \sigma^2_p/n_{gi}}$$

For further details of a specific method - take a look at help file for each subfunctions `?H2_Cullis`

Value

A named numeric vector, length matching number of methods supplied

References

- Cullis, B. R., Smith, A. B., & Coombes, N. E. (2006). On the design of early generation variety trials with correlated data. Journal of Agricultural, Biological, and Environmental Statistics, 11(4), 381–393. https://doi.org/10.1198/108571106X154443
- Oakey, H., Verbyla, A., Pitchford, W., Cullis, B., & Kuchel, H. (2006). Joint modeling of additive and non-additive genetic line effects in single field trials. Theoretical and Applied Genetics, 113(5), 809–819. https://doi.org/10.1007/s00122-006-0333-z
- Schmidt, P., Hartung, J., Rath, J., & Piepho, H.-P. (2019). Estimating Broad-Sense Heritability with Unbalanced Data from Agricultural Cultivar Trials. Crop Science, 59(2), 525–536. https://doi.org/10.2135/cropsci2018.06.0376
- Piepho, H.-P., & Möhring, J. (2007). Computing Heritability and Selection Response From Unbalanced Plant Breeding Trials. Genetics, 177(3), 1881–1888. https://doi.org/10.1534/genetics.107.074229
- Falconer, D. S., & Mackay, T. F. C. (1996). Introduction to quantitative genetics (4th ed.). Longman.

See Also

`H2_Cullis()`, `H2_Oakey()`, `H2_Delta()`, `H2_Piepho()`, `H2_Standard()`

Examples

```
# lme4 model
lettuce_subset <- lettuce_phenotypes |> subset(loc == "L2")
lettuce_lme4 <- lme4::lmer(y ~ rep + (1 | gen), data = lettuce_subset)
H2(lettuce_lme4, target = "gen", method = c("Standard", "Delta"))

# asreml model (Requires license)
## Not run:
lettuce_asreml <- asreml::asreml(fixed = y ~ rep,
                                 random = ~ gen,
                                 data = lettuce_subset,
                                 trace = FALSE
                                 )

H2(lettuce_asreml, target = "gen", method = c("Standard", "Delta"))

## End(Not run)
```

`H2_Cullis` *Calculate Cullis' heritability from model object*

Description

Compute "generalised heritability" for unbalanced experimental designs. See Cullis, Smith and Coombes (2006) for derivation.

Usage

```
H2_Cullis(model, target, options, ...)
```

Arguments

`model`	Model object of class `lmerMod/merMod` or `asreml`
`target`	The name of the random effect for which heritability is to be calculated.
`options`	NULL by default, for internal checking of model object before calculations.
`...`	Additional arguments that specify heritability calculation when interactions with genotype effects are modelled.

Details

The equation for Cullis heritability is as follow

$$H^2_{Cullis} = 1 - \frac{PEV^{BLUP}_{\overline{\Delta}ij}}{2\sigma^2_g}$$

where:

- PEV is the prediction error variance matrix of the pairwise differences among BLUPS
- σ^2 is the variance attributed to differences between genotype

Value

Numeric value

References

Cullis, B. R., Smith, A. B., & Coombes, N. E. (2006). On the design of early generation variety trials with correlated data. Journal of Agricultural, Biological, and Environmental Statistics, 11(4), 381–393. https://doi.org/10.1198/108571106X154443

Examples

```
# lme4 model
lettuce_subset <- lettuce_phenotypes |> subset(loc == "L2")
lettuce_lme4 <- lme4::lmer(y ~ rep + (1 | gen), data = lettuce_subset)
H2_Cullis(lettuce_lme4, target = "gen")

# asreml model (Requires license)
## Not run:
lettuce_asreml <- asreml::asreml(fixed = y ~ rep,
                                 random = ~ gen,
                                 data = lettuce_subset,
                                 trace = FALSE
                                 )

H2_Cullis(lettuce_asreml, target = "gen")

## End(Not run)
```

`H2_Cullis_parameters` *Calculate Cullis heritability using variance parameters*

Description

Compute the Cullis heritability for genotype means using the average variance of pairwise differences of best linear unbiased predictors (BLUPs).

Usage

```
H2_Cullis_parameters(vd_BLUP_avg, vc_g)
```

Arguments

`vd_BLUP_avg`	Numeric. Average variance of pairwise differences among BLUPs
`vc_g`	Numeric. Genotype variance component

Details

The equation for Cullis heritability is as follow

$$H^2_{Cullis} = 1 - \frac{PEV^{BLUP}_{\overline{\Delta}ij}}{2\sigma^2_g}$$

where:

- PEV is the prediction error variance matrix of the pairwise differences among BLUPS
- σ^2 is the variance attributed to differences between genotype

Value

Numeric value

References

Cullis, B. R., Smith, A. B., & Coombes, N. E. (2006). On the design of early generation variety trials with correlated data. Journal of Agricultural, Biological, and Environmental Statistics, 11(4), 381–393. https://doi.org/10.1198/108571106X154443

Examples

```
H2_Cullis_parameters(vd_BLUP_avg = 0.25, vc_g = 0.8)
```

`H2_Delta` *Calculate average heritability of differences between genotypes from model object*

Description

Instead of computing heritability on a "entry-mean" basis, this method calculates heritability using "entry-differences". Entry here is referring to the genotype, line or variety of interest. See reference for origin and interpretation of `H2_Delta` and it’s variants

Usage

```
H2_Delta(model, target,
         type = c("BLUP", "BLUE"),
         aggregate = c("arithmetic", "harmonic"),
         options,
         ...
         )
```

Arguments

`model`	Model object of class `lmerMod/merMod` or `asreml`
`target`	The name of the random effect for which heritability is to be calculated.
`type`	character, whether heritability is calculated using BLUEs or BLUPs
`aggregate`	character, when taking means in the calculation, should harmonic or arithmetic mean be used?
`options`	NULL by default, for internal checking of model object before calculations
`...`	Additional arguments that specify heritability calculation when interactions with genotype effects are modelled.

Details

The heritability of differences between genotypes is given by:

$$H^2_{\Delta..} = 1 - \frac{PEV^{BLUP}_{\overline{\Delta}..}}{2\sigma^2_g}$$

where:

- $PEV^{BLUP}_{\overline{\Delta}..}$ is the mean of the prediction error variance matrix for the pairwise differences among BLUPs (BLUEs if `method = "BLUE"`) across all genotypes
- σ^2 is the variance attributed to differences between genotype

See reference page 995 - 997 for full derivation of this heritability measure and related variants

Value

Numeric

References

Schmidt, P., Hartung, J., Rath, J., & Piepho, H.-P. (2019). Estimating Broad-Sense Heritability with Unbalanced Data from Agricultural Cultivar Trials. Crop Science, 59(2), 525–536. https://doi.org/10.2135/cropsci2018.06.03

See Also

`H2_Delta_by_genotype()`, `H2_Delta_pairwise()`

Examples

```
# lme4 model
lettuce_subset <- lettuce_phenotypes |> subset(loc == "L2")
lettuce_lme4 <- lme4::lmer(y ~ rep + (1 | gen), data = lettuce_subset)
H2_Delta(lettuce_lme4, target = "gen", type = "BLUP")

# asreml model (Requires license)
## Not run:
lettuce_asreml <- asreml::asreml(fixed = y ~ rep,
                                 random = ~ gen,
                                 data = lettuce_subset,
                                 trace = FALSE
                                 )

H2_Delta(lettuce_asreml, target = "gen", type = "BLUP")

## End(Not run)
```

`H2_Delta_by_genotype` *Calculate heritability of differences for a given genotype from model object*

Description

Instead of computing heritability on a "entry-mean" basis, this method calculates heritability using "entry-differences". Entry here is referring to the genotype, line or variety of interest. See reference for origin and interpretation of `h2/H2_Delta_by_genotype` and it's variants

Usage

```
H2_Delta_by_genotype(model, target, type = c("BLUP", "BLUE"), options, ...)
```

Arguments

`model`	Model object of class `lmerMod/merMod` or `asreml`
`target`	The name of the random effect for which heritability is to be calculated.
`type`	character, whether heritability is calculated using BLUEs or BLUPs
`options`	NULL by default, for internal checking of model object before calculations
`...`	Additional arguments that specify heritability calculation when interactions with genotype effects are modelled.

Details

The heritability of differences for a given genotype is given by:

$$H^2_{\Delta i.} = 1 - \frac{PEV^{BLUP}_{\overline{\Delta i.}}}{2\sigma^2_g}$$

where:

- $PEV^{BLUP}_{\overline{\Delta i.}}$ is the arithmetic mean of the prediction error variance matrix for pairwise differences among BLUPs (or BLUEs if `method = "BLUE"`) for a given genotype
- σ^2 is the variance attributed to differences between genotype

See reference page 995 - 997 for full derivation of this heritability measure and related variants

Value

Numeric

Named list, with each element containing a named numeric vector

References

Schmidt, P., Hartung, J., Rath, J., & Piepho, H.-P. (2019). Estimating Broad-Sense Heritability with Unbalanced Data from Agricultural Cultivar Trials. Crop Science, 59(2), 525–536. https://doi.org/10.2135/cropsci2018.06.03

See Also

`H2_Delta()`, `H2_Delta_pairwise()`

Examples

```
# lme4 model
lettuce_subset <- lettuce_phenotypes |> subset(loc == "L2")
lettuce_lme4 <- lme4::lmer(y ~ rep + (1 | gen), data = lettuce_subset)
H2_Delta_by_genotype(lettuce_lme4, target = "gen", type = "BLUP")

# asreml model (Requires license)
## Not run:
lettuce_asreml <- asreml::asreml(fixed = y ~ rep,
                                 random = ~ gen,
                                 data = lettuce_subset,
                                 trace = FALSE
                                 )

H2_Delta_by_genotype(lettuce_asreml, target = "gen", type = "BLUP")

## End(Not run)
```

`H2_Delta_pairwise` *Calculate pairwise heritability of differences between genotypes from model object*

Description

Instead of computing heritability on a "entry-mean" basis, this method calculates heritability using "entry-differences". Entry here is referring to the genotype, line or variety of interest. See reference for origin and interpretation of `h2/H2_Delta_pairwise` and it's variants

Usage

```
H2_Delta_pairwise(model, target, type = c("BLUP", "BLUE"), options, ...)
```

Arguments

`model`	Model object of class `lmerMod/merMod` or `asreml`
`target`	The name of the random effect for which heritability is to be calculated.
`type`	character, whether heritability is calculated using BLUEs or BLUPs
`options`	NULL by default, for internal checking of model object before calculations
`...`	Additional arguments that specify heritability calculation when interactions with genotype effects are modelled.

Value

A `dspMatrix`

References

Schmidt, P., Hartung, J., Rath, J., & Piepho, H.-P. (2019). Estimating Broad-Sense Heritability with Unbalanced Data from Agricultural Cultivar Trials. Crop Science, 59(2), 525–536. https://doi.org/10.2135/cropsci2018.06.03

See Also

`H2_Delta_by_genotype()`, `H2_Delta()`

Examples

```
# lme4 model
lettuce_subset <- lettuce_phenotypes |> subset(loc == "L2")
lettuce_lme4 <- lme4::lmer(y ~ rep + (1 | gen), data = lettuce_subset)
H2_Delta_pairwise(lettuce_lme4, target = "gen", type = "BLUP")

# asreml model (Requires license)
## Not run:
lettuce_asreml <- asreml::asreml(fixed = y ~ rep,
                                 random = ~ gen,
                                 data = lettuce_subset,
                                 trace = FALSE
                                 )

H2_Delta_pairwise(lettuce_asreml, target = "gen", type = "BLUP")

## End(Not run)
```

H2_Delta_parameters *Calculate heritability of pairwise differences using variance parameters*

Description

Compute broad-sense heritability of differences using the variance of differences between two BLUPs/BLUEs

Usage

```
h2_Delta_parameters(G_g, vd_matrix, type)

H2_Delta_parameters(vc_g, vd_matrix, type)
```

Arguments

`vc_g`	Numeric. Genotype variance component
`vd_matrix`	Matrix. Variance of pairwise differences among BLUES or BLUPs
`type`	Character. Either BLUES or BLUPS used to compute the variance of pairwise differences.
`G_g`	Numeric. Genotypic variance-covariance matrix.

Details

See `H2_Delta()` and reference for full derivation and equation for heritability Delta

Value

Matrix of pairwise heritability of differences among BLUES or BLUPs

References

Schmidt, P., Hartung, J., Rath, J., & Piepho, H.-P. (2019). Estimating Broad-Sense Heritability with Unbalanced Data from Agricultural Cultivar Trials. Crop Science, 59(2), 525–536. https://doi.org/10.2135/cropsci2018.06.03

Examples

```
h2_Delta_parameters(G_g = diag(0.15, 2, 2), vd_matrix = matrix(c(NA,0.2,0.2,NA),2,2), type = "BLUP")

H2_Delta_parameters(vc_g = 0.01, vd_matrix = matrix(c(NA,0.2,0.2,NA),2,2), "BLUE")
```

`H2_Oakey` *Calculate Oakey's heritability from model object*

Description

Compute heritability for genotype means using the variance–covariance matrix of the genotype BLUPs as described by Oakey et al. (2006).

Usage

```
H2_Oakey(model, target, options, ...)
```

Arguments

`model`	Model object of class `lmerMod/merMod` or `asreml`
`target`	The name of the random effect for which heritability is to be calculated.
`options`	NULL by default, for internal checking of model object before calculations.
`...`	Additional arguments that specify heritability calculation when interactions with genotype effects are modelled.

Details

$$H^2_{Oakey} = \frac{\sum_{i=n_z+1}^{n_g} \lambda_i}{\sum_{n_g}^{\lambda_i \neq 0}}$$

where:

- n_g is the number of genotypes

- n_z is the number of zero eigenvalues
- λ_i is the ith eigenvalue of the matrix $I_m - G^{-1}C^{gg}$
- σ^2 is the variance attributed to differences between genotype

See pages 813 and 818 of the reference for full derivation and explanation for Oakey's heritability

Value

Numeric

References

Oakey, H., Verbyla, A., Pitchford, W., Cullis, B., & Kuchel, H. (2006). Joint modeling of additive and non-additive genetic line effects in single field trials. Theoretical and Applied Genetics, 113(5), 809–819. https://doi.org/10.1007/s00122-006-0333-z

Examples

```
# lme4 model
lettuce_subset <- lettuce_phenotypes |> subset(loc == "L2")
lettuce_lme4 <- lme4::lmer(y ~ rep + (1 | gen), data = lettuce_subset)
H2_Oakey(lettuce_lme4, target = "gen")

# asreml model (Requires license)
## Not run:
lettuce_asreml <- asreml::asreml(fixed = y ~ rep,
                                 random = ~ gen,
                                 data = lettuce_subset,
                                 trace = FALSE
                                 )

H2_Oakey(lettuce_asreml, target = "gen")

## End(Not run)
```

`H2_Oakey_parameters` *Calculate Oakey's heritability using variance parameters*

Description

Rather than providing a model object, supply the necessary components to compute this heritability measure.

Usage

```
H2_Oakey_parameters(Gg_inv, C22_g)
```

Arguments

`Gg_inv`	The inverse of the genotypic variance-covariance matrix.
`C22_g`	Prediction error variance matrix associated with the genotype effects.

Value

Numeric value

Examples

```
Gg_inv = diag(1/0.15, 3, 3)
C22_g <- matrix(
  c(
    0.08, 0.01, 0.00,
    0.01, 0.07, 0.01,
    0.00, 0.01, 0.09
  ),
  nrow = 3, byrow = TRUE
)
H2_Oakey_parameters(Gg_inv, C22_g)
```

`H2_Piepho` *Calculate Piepho's heritability from model object Compute Piepho's heritability using variance differences between genotype BLUEs*

Description

Calculate Piepho's heritability from model object Compute Piepho's heritability using variance differences between genotype BLUEs

Usage

```
H2_Piepho(model, target, options, ...)
```

Arguments

`model`	Model object of class `lmerMod/merMod` or `asreml`
`target`	The name of the random effect for which heritability is to be calculated.
`options`	NULL by default, for internal checking of model object before calculations.
`...`	Additional arguments that specify heritability calculation when interactions with genotype effects are modelled.

Details

The equation for Piepho's heritability is as follows:

$$H^2_{Piepho} = \frac{\sigma^2_g}{\sigma^2_g + \overline{PEV_{BLUE_g}}/2}$$

where:

- $\overline{PEV_{BLUE_g}}$ is the prediction error variance matrix for genotype BLUEs
- σ^2_g is the variance attributed to differences between genotype

See reference for full derivation and details.

Value

Numeric

References

Piepho, H.-P., & Möhring, J. (2007). Computing Heritability and Selection Response From Unbalanced Plant Breeding Trials. Genetics, 177(3), 1881–1888. https://doi.org/10.1534/genetics.107.074229

Examples

```
# lme4 model
lettuce_subset <- lettuce_phenotypes |> subset(loc == "L2")
lettuce_lme4 <- lme4::lmer(y ~ rep + (1 | gen), data = lettuce_subset)
H2_Piepho(lettuce_lme4, target = "gen")

# asreml model (Requires license)
## Not run:
lettuce_asreml <- asreml::asreml(fixed = y ~ rep,
                                 random = ~ gen,
                                 data = lettuce_subset,
                                 trace = FALSE
                                 )

H2_Piepho(lettuce_asreml, target = "gen")

## End(Not run)
```

`H2_Piepho_parameters` *Calculate Piepho's heritability using variance parameters*

Description

Compute Piepho's heritability using the variance of differences between two BLUES.

Usage

```
H2_Piepho_parameters(vc_g, vd_BLUE_avg)
```

Arguments

`vc_g`	Numeric. Genotype variance component
`vd_BLUE_avg`	Numeric. Mean variance of pairwise differences among BLUES

Details

The equation for Piepho's heritability is as follows:

$$H^2_{Piepho} = \frac{\sigma^2_g}{\sigma^2_g + \overline{PEV_{BLUE_g}}/2}$$

where:

- $\overline{PEV_{BLUE_g}}$ is the prediction error variance matrix for genotype BLUEs
- σ^2_g is the variance attributed to differences between genotype

Value

Numeric value

References

Piepho, H.-P., & Möhring, J. (2007). Computing Heritability and Selection Response From Unbalanced Plant Breeding Trials. Genetics, 177(3), 1881–1888. https://doi.org/10.1534/genetics.107.074229

Examples

```
H2_Piepho_parameters(vc_g = 0.25, vd_BLUE_avg = 0.68)
```

`H2_Standard` *Calculate standard heritability from model object*

Description

Compute standard heritability using the classic ratio method of genotypic and phenotypic variance. See Falconer & Mackay (1996)

Usage

```
H2_Standard(model, target, options, ...)
```

Arguments

`model`	Model object of class `lmerMod/merMod` or `asreml`
`target`	The name of the random effect for which heritability is to be calculated.
`options`	NULL by default, for internal checking of model object before calculations.
`...`	Additional arguments that specify heritability calculation when interactions with genotype effects are modelled.

Details

The equation used to calculate standard heritability is:

$$H^2_{Standard} = \frac{\sigma^2_g}{\sigma^2_g + \frac{1}{n_g} \sum_{n_g}^{i=1} \sigma^2_p / n_{gi}}$$

where:

- n_g is the number of genotypes
- n_{gi} is the number of replicate for a given genotype i
- σ_g is the variance attributed to genotype differences
- σ_p is the variance attributed to phenotypic differences

Value

Numeric value

References

Falconer, D. S., & Mackay, T. F. C. (1996). Introduction to quantitative genetics (4th ed.). Longman.

Examples

```
# lme4 model
lettuce_subset <- lettuce_phenotypes |> subset(loc == "L2")
lettuce_lme4 <- lme4::lmer(y ~ rep + (1 | gen), data = lettuce_subset)
H2_Standard(lettuce_lme4, target = "gen")

# asreml model (Requires license)
## Not run:
lettuce_asreml <- asreml::asreml(fixed = y ~ rep,
                                 random = ~ gen,
                                 data = lettuce_subset,
                                 trace = FALSE
                                 )

H2_Standard(lettuce_asreml, target = "gen")

## End(Not run)
```

`H2_Standard_parameters` *Calculate Standard heritability using variance parameters*

Description

Compute Standard heritability for genotype means using the variance components of genotype and residuals.

Usage

```
H2_Standard_parameters(vc_g, vc_e, n_r = 1)
```

Arguments

`vc_g`	Numeric. Genotype variance component
`vc_e`	Numeric. Residuals variance component
`n_r`	A numeric vector of size n_g, the number of genotype replicates.

Details

The equation for Standard heritability is as follows:

$$H^2_{Standard} = \frac{\sigma^2_g}{\sigma^2_g + \frac{1}{n_g} \sum_{n_g}^{i=1} \sigma^2_p / n_{gi}}$$

where:

- n_g is the number of genotypes

- n_{gi} is the number of replicate for a given genotype i
- σ_g is the variance attributed to genotype differences
- σ_p is the variance attributed to phenotypic differences

Value

Numeric value

References

Falconer, D. S., & Mackay, T. F. C. (1996). Introduction to quantitative genetics (4th ed.). Longman.

Examples

```
H2_Standard_parameters(vc_g = 0.25, vc_e = 0.8)
```

`lettuce_markers` *Molecular marker data and genomic relatedness matrix of 89 lettuce varieties*

Description

Molecular marker data and genomic relatedness matrix of 89 lettuce varieties

Usage

```
lettuce_markers

lettuce_GRM
```

Format

`lettuce_markers`**:**

A data frame with 89 rows and 301 columns:

- gen genotype identifier
- 300 genetic markers scored as -1, 0, 1 (see Details)

`lettuce_GRM`**:**

A matrix array with 89 rows and 89 columns where each row/column represents a genotype

Details

The varieties were genotyped with a total of 300 markers (i.e. 95 single nucleotide polymorphisms and 205 amplified fragment length polymorphism markers, see Hayes et al. (2014) for more details of marker matrix. The biallelic marker M_iw for the ith genotype and the wth marker with alleles A_1 (i.e. the reference allele) and A_2 was coded as:

- 1 for A_1 A_1,
- -1 for A_2 A_2
- 0 for A_1 A_2 and A_2 A_1

Source

`https://figshare.com/articles/dataset/Lettuce_trial_phenotypic_and_marker_data_/8299493`

References

Hadasch, S., Simko, I., Hayes, R.J., Ogutu, J.O. and Piepho, H.-P. (2016), Comparing the Predictive Abilities of Phenotypic and Marker-Assisted Selection Methods in a Biparental Lettuce Population. The Plant Genome, 9: plantgenome2015.03.0014. doi:10.3835/plantgenome2015.03.0014

Hayes, R. J., Galeano, C. H., Luo, Y., Antonise, R., & Simko, I. (2014). Inheritance of Decay of Fresh-cut Lettuce in a Recombinant Inbred Line Population from 'Salinas 88' × 'La Brillante'. Journal of the American Society for Horticultural Science, 139(4), 388–398. doi:10.21273/JASHS.139.4.388

`lettuce_phenotypes` *Phenotypic data of 89 lettuce varieties*

Description

89 lettuce varieties tested at three environments, each laid out as a randomized complete block design. The measured trait was resistance to downy mildew scored on a scale ranging from 0 to 5.

Usage

```
lettuce_phenotypes
```

Format

`lettuce_phenotypes`**:**

A data frame with 703 rows and 4 columns:

- `loc` environment identifier
- `gen` genotype identifier
- `rep` replicate identifier
- y resistance to downy mildew scored on a scale ranging from 0 to 5

Source

`https://figshare.com/articles/dataset/Lettuce_trial_phenotypic_and_marker_data_/8299493`

References

Hadasch, S., Simko, I., Hayes, R.J., Ogutu, J.O. and Piepho, H.-P. (2016), Comparing the Predictive Abilities of Phenotypic and Marker-Assisted Selection Methods in a Biparental Lettuce Population. The Plant Genome, 9: plantgenome2015.03.0014. doi:10.3835/plantgenome2015.03.0014

Hayes, R. J., Galeano, C. H., Luo, Y., Antonise, R., & Simko, I. (2014). Inheritance of Decay of Fresh-cut Lettuce in a Recombinant Inbred Line Population from 'Salinas 88' × 'La Brillante'. Journal of the American Society for Horticultural Science, 139(4), 388–398. doi:10.21273/JASHS.139.4.388

`lizard_markers` *Molecular markers data and genomic relatedness matrix of Australian lizards*

Description

Molecular markers data and genomic relatedness matrix of Australian lizards

Usage

```
lizard_markers

lizard_GRM
```

Format

`lizard_markers`:

A data frame with 261 rows and 8438 columns:

- gen individual identifier, equivalent to `liz_id` in `lizard_phenotypes`
- 8437 genetic markers scored as 0, 2, 1 (see Details)

`lizard_GRM`:

A matrix array with 261 rows and 261 columns where each row/column represents a genotype

Details

See `?snpReady::G.matrix` for how GRM was computed. The biallelic marker $M_i w$ for the ith genotype and the wth marker with alleles A_1 (i.e. the reference allele) and A_2 was coded as:

- 0 for A_1 A_1,
- 1 for A_1 A_2 and A_2 A_1
- 2 for A_2 A_2

Source

https://osf.io/hjkxd/?view_only=12a6b6010567474fac9fecd54472aa3d

References

Kar, F., Nakagawa, S. and Noble, D.W.A. (2024) “Heritability and developmental plasticity of growth in an oviparous lizard,” Heredity, 132(2), pp. 67–76. Available at: https://doi.org/10.1038/s41437-023-00660-3.

`lizard_phenotypes` *Phenotypic data of Australian lizards*

Description

Phenotypic data for Australian lizards (*L. delicata*). Lizard eggs were incubated at two different incubation treatment temperatures. Lizards were weighed to investigate differences in growth between treatments.

Usage

```
lizard_phenotypes
```

Format

`lizard_phenotypes`**:**

A data frame with 3928 rows and 9 columns:

- `liz_id` individual identifier, equivalent to `gen` in `lizard_markers` 261 individuals
- `treatment` temperature (degrees celcius) at which lizard eggs were incubated
- `dam_id` dam identifier
- `sire_id` sire identifer
- `mass` mass of lizard in
- `ln_mass` natural log `mass`
- `days_since_hatch` days since hatching (age)
- `z_days_since_hatch` scaled and centered `days_since_hatch` see ?scale()
- `z_days_since_hatch_i2` squared `z_days_since_hatch` see Kar et al 2024 to see details on their analysis

Source

https://osf.io/hjkxd/?view_only=12a6b6010567474fac9fecd54472aa3d

References

Kar, F., Nakagawa, S. and Noble, D.W.A. (2024) “Heritability and developmental plasticity of growth in an oviparous lizard,” Heredity, 132(2), pp. 67–76. Available at: https://doi.org/10.1038/s41437-023-00660-3.

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