

Package ‘hwep’

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Title Hardy-Weinberg Equilibrium in Polyploids

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Description Inference concerning equilibrium and random mating in autopolyploids. Methods are available to test for equilibrium and random mating at any even ploidy level (>2) in the presence of double reduction at biallelic loci. For autopolyploid populations in equilibrium, methods are available to estimate the degree of double reduction. We also provide functions to calculate genotype frequencies at equilibrium, or after one or several rounds of random mating, given rates of double reduction. The main function is `hwefit()`. This material is based upon work supported by the National Science Foundation under Grant No. 2132247. The opinions, findings, and conclusions or recommendations expressed are those of the author and do not necessarily reflect the views of the National Science Foundation. For details of these methods, see Gerard (2021) <[doi:10.1101/2021.09.24.461731](https://doi.org/10.1101/2021.09.24.461731)>.

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R topics documented:

hwep-package	2
dgamete	3
drbounds	4
freqnext	5
gsegmat	6
gsegmat_symb	7
hweboot	8
hwefit	9
hwefreq	10
hwelike	12
hwenodr	13
hweustat	14
p_from_alpha	15
rmlike	16
zsegarray	17
zygdist	18
Index	19

hwep-package

Hardy-Weinberg Equilibrium in Polyploids

Description

Inference concerning equilibrium and random mating in autopolyploids. Methods are available to test for equilibrium and random mating at any even ploidy level (>2) in the presence of double reduction. For autopolyploid populations in equilibrium, methods are available to estimate the degree of double reduction. We also provide functions to calculate genotype frequencies at equilibrium, or after one or several rounds of random mating, given rates of double reduction. This material is based upon work supported by the National Science Foundation under Grant No. 2132247. The opinions, findings, and conclusions or recommendations expressed are those of the author and do not necessarily reflect the views of the National Science Foundation. For details of these methods, see Gerard (2021) doi: [10.1101/2021.09.24.461731](https://doi.org/10.1101/2021.09.24.461731).

Main Functions

- `hwefit()` Fit either `hwelike()`, `rmlike()`, `hweustat()`, or `hwenodr()` across many loci. Parallelization is supported through the `future` package.
- `hwelike()` Likelihood inference for equilibrium. This function estimates the rate of double reduction given equilibrium, and tests for at most small deviations from equilibrium.
- `rmlike()` Likelihood inference for random mating in polyploids. This function tests for random mating and estimates gametic frequencies given random mating. This function does not assume a model for meiosis.
- `hweustat()` U-statistic approach for equilibrium and double reduction. This function tests for equilibrium given double reduction rates and estimates these rates given equilibrium.

`hwenodr()` Implements a likelihood ratio test that tests for equilibrium in autopolyploids given no double reduction.

`hweboot()` Implements a bootstrap approach to test for equilibrium which is more appropriate for small samples and uncertain genotypes.

Other Functions

`dgamete()` Gamete dosage probability given parental dosage.

`drbounds()` Upper bounds on the rates of double reduction given the complete equational segregation model.

`freqnext()` Update genotype frequencies after one generation of random mating.

`gsegmat()` Gamete dosage probabilities for all possible parental dosages.

`hwefreq()` Generate equilibrium genotype frequencies.

`p_from_alpha()` Obtain gamete frequencies from the major allele frequency and double reduction rates.

`zsegarray()` All zygote dosage distributions given all possible parental dosages.

`zygdist()` Zygote dosage distribution given one pair of parental dosages.

Citation

If you find the methods in this package useful, please run the following in R for citation information:
`citation("hwep")`

Author(s)

David Gerard

dgamete

Gamete dosage probability

Description

Estimates the probability of a gamete dosage given the parent dosage (G), the parent ploidy (ploidy), and the double reduction parameter (alpha). This is for biallelic loci.

Usage

```
dgamete(x, alpha, G, ploidy, log_p = FALSE)
```

Arguments

x	A vector of numerics in $\text{seq}(0, \text{ploidy}/2)$. The dosage of the gametes.
alpha	A numeric vector containing the double reduction parameter(s). This should be a vector of length $\text{floor}(\text{ploidy}/4)$ where $\text{alpha}[i]$ is the probability of exactly i pairs of IBDR alleles being in the gamete. Note that $\text{sum}(\text{alpha})$ should be less than 1, as $1 - \text{sum}(\text{alpha})$ is the probability of no double reduction.
G	The dosage of the parent. Should be an integer between 0 and ploidy.
ploidy	The ploidy of the species. This should be an even positive integer.
log_p	A logical. Should we return the log-probability (TRUE) or not (FALSE)? Defaults to FALSE.

Value

A vector of length $\text{length}(x)$, containing the (log) probabilities of a gamete carrying a dosage of x from a parent of dosage G who has ploidy ploidy and a double reduction rate alpha .

Author(s)

David Gerard

Examples

```
dgamete(x = 0:2, alpha = 0, G = 2, ploidy = 4)
```

drbounds

Upper bounds on rates of double reduction

Description

Calculates the upper bounds of the double reduction parameters according to the complete equation segregation model. See Huang et. al. (2019) for details.

Usage

```
drbounds(ploidy)
```

Arguments

ploidy	The ploidy of the species. Should be even and at least 4.
--------	---

Value

A vector of length $\text{floor}(\text{ploidy}/4)$. Element i is the upper bound on the probability of i pairs of identical-by-double-reduction alleles being in an individual.

Author(s)

David Gerard

References

- Huang, K., Wang, T., Dunn, D. W., Zhang, P., Cao, X., Liu, R., & Li, B. (2019). Genotypic frequencies at equilibrium for polysomic inheritance under double-reduction. *G3: Genes, Genomes, Genetics*, 9(5), 1693-1706. doi: [10.1534/g3.119.400132](https://doi.org/10.1534/g3.119.400132)

Examples

```
drbounds(4)
drbounds(6)
drbounds(8)
drbounds(10)
drbounds(12)
drbounds(14)
drbounds(16)
```

freqnext

*Update genotype frequencies after one generation***Description**

After one generation of random mating, update the genotype frequencies.

Usage

```
freqnext(freq, alpha, segmat = NULL, more = FALSE, check = TRUE)
```

Arguments

freq	The current genotype frequencies. This should be a vector of length $K+1$, where K is the ploidy of the species. <code>freq[i]</code> could contain the proportion of individuals that have genotype $i-1$.
alpha	A numeric vector containing the double reduction parameter(s). This should be a vector of length $\text{floor}(\text{ploidy}/4)$ where <code>alpha[i]</code> is the probability of exactly i pairs of IBDR alleles being in the gamete. Note that $\text{sum}(\text{alpha})$ should be less than 1, as $1 - \text{sum}(\text{alpha})$ is the probability of no double reduction.
segmat	You can provide your own segregation matrix. <code>segmat[i, j]</code> is the probability that a parent with dosage $i-1$ produces a gamete with dosage $j-1$.
more	A logical. Should we return more output (TRUE) or less (FALSE). See the Value section for details.
check	Should we correct for minor numerical issues? Defaults to TRUE.

Value

If `more = FALSE`, then returns a vector of length `length(freq)` that contains the updated genotype frequencies after one generation of random mating. If `more = TRUE`, then returns a list with these genotype frequencies (q) as well as the parental gamete frequencies (p).

Author(s)

David Gerard

Examples

```
freq <- c(0.5, 0, 0, 0, 0.5)
freqnext(freq = freq, alpha = 0)
```

gsegmat

Segregation probabilities of gametes

Description

Produces the segregation probabilities for gamete dosages given parental dosages and the double reduction rate.

Usage

```
gsegmat(alpha, ploidy)
```

Arguments

alpha	A numeric vector containing the double reduction parameter(s). This should be a vector of length <code>floor(ploidy/4)</code> where <code>alpha[i]</code> is the probability of exactly i pairs of IBDR alleles being in the gamete. Note that <code>sum(alpha)</code> should be less than 1, as <code>1 - sum(alpha)</code> is the probability of no double reduction.
ploidy	The ploidy of the species. This should be an even positive integer.

Value

A matrix of dimension `ploidy + 1` by `ploidy / 2 + 1`. Element (i, j) is the probability that a parent carrying dosage $j - 1$ produces a gamete with dosage $i - 1$.

Author(s)

David Gerard

Examples

```
gsegsym(alpha = NULL, ploidy = 2)
gsegsym(alpha = 1/6, ploidy = 4)
gsegsym(alpha = 0.3, ploidy = 6)
gsegsym(alpha = c(0.35, 0.02), ploidy = 8)
gsegsym(alpha = c(0.4, 0.05), ploidy = 10)
```

gsegsym

Symbolic representation of the segregation probability matrix

Description

Two alleles are identical-by-double-reduction (IBDR) if they originate from the same (by origin) allele in the parent. We let "a" be the probability of zero IBDR alleles, "b" be the probability of one IBDR pair, "c" be the probability of two IBDR pairs, etc...

Usage

```
gsegsym(ploidy, out = c("str", "exp"))
```

Arguments

ploidy	The ploidy of the species
out	Should we return a character matrix ("str") or an expression matrix ("exp")?

Value

A character or expression matrix containing the mathematical form for the segregation matrix. Element (i, j) is the probability a parent with dosage i-1 produces a gamete with dosage j-1.

Author(s)

David Gerard

See Also

[gsegsym\(\)](#) for numerical expressions.

Examples

```
gsegsym(4)
gsegsym(6)
gsegsym(8)
```

hweboot

Bootstrap procedure to test for equilibrium

Description

Iteratively resample individuals/genotypes, calculating the U-statistic for each resample, and use these resamples to test against the null of no equilibrium.

Usage

```
hweboot(n, nboot = 2000, more = FALSE)
```

Arguments

n	One of two forms A vector of length ploidy + 1 Element i is the number of individuals with genotype i. A matrix with nsamp rows and ploidy+1 columns Element (i, j) is the posterior probability that individual i has ploidy j-1.
nboot	The number of bootstrap samples to run.
more	A logical. Should we return the bootstrap replicates (FALSE) or just the p-value, with 95% confidence interval of the p-value (TRUE).

Value

A list with some or all of the following elements

p_hwe The bootstrap p-value against the null of equilibrium.

p_ci The 95% confidence interval of p_hwe.

alpha_boot The bootstrap samples of the double reduction parameter.

u_boot The bootstrap samples of the U-statistic.

Author(s)

David Gerard

Examples

```
set.seed(1)
ploidy <- 6
size <- 100
r <- 0.5
alpha <- 0.1
qvec <- hwefreq(r = r, alpha = alpha, ploidy = ploidy)
nvec <- c(rmultinom(n = 1, size = size, prob = qvec))
bout <- hweboot(n = nvec, more = TRUE, nboot = 1000)
bout$p_hwe
```



```

bout$p_ci
hist(bout$test_boot)
abline(v = bout$test_stat, lty = 2, col = 2)

```

hwefit

Equilibrium and random mating estimation and testing for many loci.

Description

Estimates and tests for either equilibrium or random mating across many loci using [hwelike\(\)](#), [hweustat\(\)](#), [rmlike\(\)](#), [hwenodr\(\)](#), or [hweboot\(\)](#).

Usage

```

hwefit(
  nmat,
  type = c("ustat", "mle", "rm", "nodr", "boot"),
  effdf = TRUE,
  thresh = 1,
  nboot = 2000
)

```

Arguments

nmat	A matrix of counts. The rows index the loci and the columns index the genotypes. So <code>nmat[i, j]</code> is the number of individuals that have genotype <code>j-1</code> at locus <code>i</code> . The ploidy is assumed to be <code>ncol(nmat)-1</code> .
type	The method to use: "ustat" U-statistic approach to test for equilibrium and estimate double reduction rates given equilibrium. The default. See hweustat() . "mle" Maximum likelihood estimation and testing. Only supported for ploidies less than or equal to 10. See hwelike() . "rm" Testing random mating, and estimating gamete frequencies given random mating. See rmlike() . "nodr" Testing equilibrium given no double reduction. See hwenodr() . "boot" Bootstrap approach to test for equilibrium. See hweboot() .
effdf	A logical. Should we use the effective degrees of freedom? Only applicable if <code>type = "mle"</code> or <code>type = "ustat"</code> .
thresh	A non-negative numeric. The threshold for aggregating genotypes. Only applicable if <code>type = "mle"</code> , <code>type = "ustat"</code> , or <code>type = "rm"</code> .
nboot	The number of bootstrap iterations to use if <code>type = "boot"</code> .

Details

We provide parallelization support through the [future](#) package.

Value

A data frame. The columns of which can be described in `hwelike()`, `hweustat()`, `rmlike()`, or `hwenodr()`.

Author(s)

David Gerard

Examples

```
## Generate random data
set.seed(5)
ploidy <- 4
nloc <- 100
size <- 1000
r <- 0.25
alpha <- 1/12
qvec <- hwefreq(r = r, alpha = alpha, ploidy = ploidy)
nmat <- t(rmultinom(n = nloc, size = size, prob = qvec))

## Run the analysis in parallel on the local computer with two workers
future::plan(future::multisession, workers = 2)
hout <- hweufit(nmat = nmat,
               type = "ustat")

## Shut down parallel workers
future::plan("sequential")

## Show that p-values are uniform
obs <- sort(hout$p_hwe)
plot(x = ppoints(n = length(obs)),
     y = obs,
     xlab = "theoretical",
     ylab = "observed",
     main = "qqplot")
abline(0, 1, col = 2, lty = 2)
mean(hout$p_hwe < 0.05, na.rm = TRUE)

## Consistent estimate for alpha
alpha
mean(hout$alpha1)
```

hwefreq

Generate HWE genotype frequencies

Description

Generate genotype frequencies under Hardy-Weinberg equilibrium given the allele frequency of the reference allele (r), the double reduction parameter (α), and the ploidy of the species (p).

Usage

```
hwefreq(
  r,
  alpha,
  ploidy,
  niter = 100,
  tol = sqrt(.Machine$double.eps),
  more = FALSE
)
```

Arguments

<code>r</code>	The allele frequency of the reference allele.
<code>alpha</code>	A numeric vector containing the double reduction parameter(s). This should be a vector of length <code>floor(ploidy/4)</code> where <code>alpha[i]</code> is the probability of exactly <code>i</code> pairs of IBDR alleles being in the gamete. Note that <code>sum(alpha)</code> should be less than 1, as <code>1 - sum(alpha)</code> is the probability of no double reduction.
<code>ploidy</code>	The ploidy of the species. This should be an even positive integer.
<code>niter</code>	The maximum number of iterations to simulate.
<code>tol</code>	The stopping criterion on the Chi-square divergence between old and new genotype frequencies.
<code>more</code>	A logical. Should we return more output (TRUE) or less (FALSE). See the Value section for details.

Details

If `alpha` is not all 0, then this function repeatedly applies `freqnext()` to simulate genotype frequencies under HWE. Otherwise, it uses `dbinom()`.

Value

If `more = FALSE`, then returns just the genotype frequencies after `niter` generations of random mating. If `more = TRUE`, then returns a list with these genotype frequencies, as well as the parental gamete frequencies.

Author(s)

David Gerard

Examples

```
freq1 <- hwefreq(r = 0.5, alpha = 0, ploidy = 4)
freq2 <- hwefreq(r = 0.5, alpha = 1/6, ploidy = 4)

plot(x = 0:4,
     y = freq1,
     type = "h",
     ylim = c(0, 0.4),
```

```

      xlab = "dosage",
      ylab = "Pr(dosage)")
plot(x = 0:4,
     y = freq2,
     type = "h",
     ylim = c(0, 0.4),
     xlab = "dosage",
     ylab = "Pr(dosage)")

```

hwelike

Maximum likelihood approach for equilibrium testing and double reduction estimation.

Description

Genotype frequencies from Huang et al (2019) are used to implement a likelihood procedure to estimate double reduction rates and to test for equilibrium while accounting for double reduction. This approach is only implemented for ploidies 4, 6, 8, and 10.

Usage

```
hwelike(nvec, thresh = 0, effdf = FALSE)
```

Arguments

nvec	A vector containing the observed genotype counts, where <code>nvec[[i]]</code> is the number of individuals with genotype <code>i-1</code> . This should be of length <code>ploidy+1</code> .
thresh	The threshold for ignoring the genotype. We keep genotypes such that <code>nvec >= thresh</code> . Setting this to 0 uses all genotypes.
effdf	A logical. Should we use the ad-hoc "effective degrees of freedom" (TRUE) or not (FALSE)?

Value

A list with some or all of the following elements:

alpha	The estimated double reduction parameter(s). In diploids, this value is NULL.
r	The estimated allele frequency.
chi_sq_hwe	The chi-square test statistic for testing against the null of equilibrium.
df_hwe	The degrees of freedom associated with <code>chi_sq_hwe</code> .
p_hwe	The p-value against the null of equilibrium.

Author(s)

David Gerard

References

- Huang, K., Wang, T., Dunn, D. W., Zhang, P., Cao, X., Liu, R., & Li, B. (2019). Genotypic frequencies at equilibrium for polysomic inheritance under double-reduction. *G3: Genes, Genomes, Genetics*, 9(5), 1693-1706. doi: [10.1534/g3.119.400132](https://doi.org/10.1534/g3.119.400132)

Examples

```
thout <- hwefreq(alpha = 0.1, r = 0.3, ploidy = 6)
nvec <- c(stats::rmultinom(n = 1, size = 100, prob = thout))
hwelike(nvec = nvec)
```

hwenodr	<i>Test for HWE in autopolyploids under the assumption of no double reduction</i>
---------	---

Description

We run a likelihood ratio test against the null of no HWE, assuming that there is no double reduction.

Usage

```
hwenodr(nvec)
```

Arguments

nvec A vector containing the observed genotype counts, where `nvec[[i]]` is the number of individuals with genotype `i-1`. This should be of length `ploidy+1`.

Value

A list with some or all of the following elements

r The estimated allele frequency.

chisq_hwe The chi-square statistic against the null of equilibrium given no double reduction.

df_hwe The degrees of freedom associated with `chisq_hwe`.

p_hwe The p-value against the null of equilibrium given no double reduction.

Author(s)

David Gerard

Examples

```
set.seed(10)
qvec <- c(0.2, 0.3, 0.4, 0.1)
nvec <- c(stats::rmultinom(n = 1, size = 100, prob = qvec))
hwenodr(nvec = nvec)
```

hweustat	<i>U-process minimizer approach to equilibrium testing and double reduction estimation</i>
----------	--

Description

Estimates double reduction and tests for equilibrium while accounting for double reduction. It does this using an approach called "U-process minimization", where we minimize a function of a U-statistic that should be 0 at equilibrium given the true double reduction rate.

Usage

```
hweustat(nvec, thresh = 1, effdf = TRUE)
```

Arguments

nvec	A vector containing the observed genotype counts, where <code>nvec[[i]]</code> is the number of individuals with genotype <code>i-1</code> . This should be of length <code>ploidy+1</code> .
thresh	The threshold for ignoring the genotype. We keep genotypes such that <code>nvec >= thresh</code> . Setting this to 0 uses all genotypes.
effdf	A logical. Should we use the ad-hoc "effective degrees of freedom" (TRUE) or not (FALSE)?

Details

This is a two-step estimator, where we first obtain a consistent estimate of the double reduction parameter, use this to estimate the covariance of estimators, then use this to obtain our final estimate of the double reduction parameter.

Value

A list with some or all of the following elements:

alpha	The estimated double reduction parameter(s). In diploids, this value is NULL.
chisq_hwe	The chi-square test statistic for testing against the null of equilibrium.
df_hwe	The degrees of freedom associated with <code>chisq_hwe</code> .
p_hwe	The p-value against the null of equilibrium.

Author(s)

David Gerard

Examples

```

set.seed(99)
ploidy <- 6
size <- 100
r <- 0.5
alpha <- 0.1
qvec <- hwefreq(r = r, alpha = alpha, ploidy = ploidy)
nvec <- c(rmultinom(n = 1, size = size, prob = qvec))
hweustat(nvec = nvec)

```

p_from_alpha	<i>Obtain gamete frequencies at equilibrium given rates of double reduction.</i>
--------------	--

Description

Given the rate of double reduction and the major allele frequency, this function will calculate the gametic frequencies.

Usage

```
p_from_alpha(alpha, p, ploidy)
```

Arguments

alpha	A numeric vector containing the double reduction parameter(s). This should be a vector of length $\text{floor}(\text{ploidy}/4)$ where $\text{alpha}[i]$ is the probability of exactly i pairs of IBDR alleles being in the gamete. Note that $\text{sum}(\text{alpha})$ should be less than 1, as $1 - \text{sum}(\text{alpha})$ is the probability of no double reduction.
p	The allele frequency of the major allele.
ploidy	The ploidy of the species.

Value

A numeric vector of length $\text{ploidy} / 2 + 1$, where element i is the probability that a gamete carries $i-1$ copies of the major allele.

Author(s)

David Gerard

Examples

```
p_from_alpha(0.2, 0.5, 4)
```

 rmlike

Likelihood inference for random mating

Description

Estimates gamete genotype frequencies using a maximum likelihood approach and runs a likelihood ratio test for random mating.

Usage

```
rmlike(nvec, thresh = 1)
```

Arguments

nvec A vector containing the observed genotype counts, where `nvec[[i]]` is the number of individuals with genotype $i-1$. This should be of length `ploidy+1`.

thresh All groups with counts less than `nvec` will be aggregated together.

Details

Let q be the genotype frequencies. Let p be the gamete frequencies. Then random mating occurs if `q == stats::convolve(p, rev(p), type = "open")`. We test for this hypothesis using likelihood inference, while estimating p .

Value

A list with the following elements:

p The estimated gamete genotype frequencies. `p[[i]]` is the estimated frequency for gamete genotype $i-1$.

chisq_rm The likelihood ratio test statistic for testing against the null of random mating.

df_rm The degrees of freedom associated with `chisq_rm`.

p_rm The p-value against the null of random mating.

Author(s)

David Gerard

Examples

```
## Randomly generate gamete frequencies
set.seed(1)
ploidy <- 10
pvec <- stats::runif(ploidy / 2 + 1)
pvec <- pvec / sum(pvec)

## Genotype frequencies from gamete frequencies under random mating
qvec <- stats::convolve(pvec, rev(pvec), type = "open")
```



```
## Generate data
nvec <- c(stats::rmultinom(n = 1, size = 100, prob = qvec))

## Run rmlike()
rmlike(nvec = nvec)
```

zsegarray *Zygote segregation distributions.*

Description

Obtains offspring genotype probabilities given parental probabilities, the ploidy of the species, and the overdispersion parameter, for all possible parental genotypes.

Usage

```
zsegarray(alpha, ploidy)
```

Arguments

alpha	A numeric vector containing the double reduction parameter(s). This should be a vector of length $\text{floor}(\text{ploidy}/4)$ where $\text{alpha}[i]$ is the probability of exactly i pairs of IBDR alleles being in the gamete. Note that $\text{sum}(\text{alpha})$ should be less than 1, as $1 - \text{sum}(\text{alpha})$ is the probability of no double reduction.
ploidy	The ploidy of the species. This should be an even positive integer.

Value

An array of probabilities. Element (i, j, k) contains the probability of offspring dosage $k-1$ given parental dosages $i-1$ and $j-1$.

Author(s)

David Gerard

Examples

```
ploidy <- 10
alpha <- c(0.5, 0.1)
p1 <- 4
p2 <- 3
segarray <- zsegarray(alpha = alpha, ploidy = ploidy)
graphics::plot(x = 0:10,
               y = segarray[p1 + 1, p2 + 1, ],
               type = "h",
               ylab = "Pr(dosage)",
               xlab = "dosage")
```

```
graphics::mtext(paste0("P1 dosage = ",
                      p1,
                      ", ",
                      "P2 dosage = ",
                      p2))
```

zygdist	<i>Zygote dosage probabilities.</i>
---------	-------------------------------------

Description

Calculates the distribution of an offspring dosages given parental dosages (G1 and G2), the ploidy of the species (ploidy), and the double reduction parameter (alpha).

Usage

```
zygdist(alpha, G1, G2, ploidy)
```

Arguments

alpha	A numeric vector containing the double reduction parameter(s). This should be a vector of length $\text{floor}(\text{ploidy}/4)$ where $\text{alpha}[i]$ is the probability of exactly i pairs of IBDR alleles being in the gamete. Note that $\text{sum}(\text{alpha})$ should be less than 1, as $1 - \text{sum}(\text{alpha})$ is the probability of no double reduction.
G1	The dosage of parent 1. Should be an integer between 0 and ploidy.
G2	The dosage of parent 2. Should be an integer between 0 and ploidy.
ploidy	The ploidy of the species. This should be an even positive integer.

Value

A vector of probabilities. The i th element is the probability that the offspring will have dosage $i-1$.

Author(s)

David Gerard

Examples

```
zygdist(alpha = c(0.5, 0.1), G1 = 4, G2 = 5, ploidy = 8)
```

Index

dbinom, [11](#)
dgamete, [3](#), [3](#)
drbounds, [3](#), [4](#)

freqnext, [3](#), [5](#), [11](#)
future, [2](#), [9](#)

gsegmat, [3](#), [6](#), [7](#)
gsegmat_symb, [7](#)

hweboot, [3](#), [8](#), [9](#)
hwefit, [2](#), [9](#)
hwefreq, [3](#), [10](#)
hwelike, [2](#), [9](#), [10](#), [12](#)
hwenodr, [2](#), [3](#), [9](#), [10](#), [13](#)
hwep (hwep-package), [2](#)
hwep-package, [2](#)
hweustat, [2](#), [9](#), [10](#), [14](#)

p_from_alpha, [3](#), [15](#)

rmlike, [2](#), [9](#), [10](#), [16](#)

zsegarray, [3](#), [17](#)
zygdist, [3](#), [18](#)