

Package ‘NeStage’

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Type Package

Title Effective Population Size from Stage-Structured Populations

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Description Computes effective population size (N_e) and the N_e/N ratio for stage-structured populations using the matrix population model framework of Yonezawa (2000) <[doi:10.1111/j.0014-3820.2000.tb01244.x](https://doi.org/10.1111/j.0014-3820.2000.tb01244.x)>. Functions are provided for sexually reproducing, clonally reproducing, and mixed (sexual + clonal) populations. Includes sensitivity and elasticity analyses for N_e/N with respect to vital rates.

License GPL-3

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popdemo, rmarkdown, testthat (>= 3.0.0)

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URL <https://github.com/RaymondLTremblay/NeStage>

BugReports <https://github.com/RaymondLTremblay/NeStage/issues>

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Ne_clonal_Y2000	<i>Variance effective population size for 100% clonal stage-structured populations</i>
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Description

Implements Equations 10 and 11 of Yonezawa et al. (2000) for populations that reproduce exclusively through clonal means ($d_i = 1$ for all stages) with Poisson-distributed clonal output ($V_c / c_{\text{bar}} = 1$).

Usage

```
Ne_clonal_Y2000(
  T_mat,
  F_vec = NULL,
  D,
  L = NULL,
  x_max = 500L,
  Ne_target = 50,
  census_N = NULL,
  population = NULL
)
```

Arguments

T_mat	Numeric matrix ($s \times s$). The survival/transition matrix. Row j , column i gives the probability that an individual in stage i at year t is in stage j at year $t+1$. Row/column order: stages 1, 2, ..., s (stage 1 = juvenile/smallest). Column sums must be ≤ 1 (total annual survival per stage).
F_vec	Numeric vector of length s . Fecundity of each stage: the mean number of clonal propagules produced per individual per year. Used only to compute L (generation time) via the stable stage distribution of $A = T_{\text{mat}} + F_{\text{mat}}$. Set $F_{\text{vec}} = \text{NULL}$ if supplying L directly.

D	Numeric vector of length s . The stage frequency distribution: the proportion of the population in each stage. Must sum to 1. Use observed field counts or the stable-stage distribution from eigen analysis (they should be close at equilibrium).
L	Numeric scalar (optional). Generation time in years. If NULL (default), L is computed internally from T_mat and F_vec using the Yonezawa (2000) definition ($x_{\max} = 500$ yr). Supply L directly to replicate a specific published value (e.g., $L = 13.399$ for <i>Fritillaria Miz</i> population).
x_max	Integer. Maximum age (years) for the L iteration (default 500). Ignored if L is supplied directly. Increase for very long-lived species (> 100 yr lifespan).
Ne_target	Numeric. Ne conservation threshold. Common choices: 50 (Franklin 1980, avoid inbreeding depression), 500 (long-term quantitative variation), or 5000 (Lande 1995, long-term evolutionary potential). Default 50.
census_N	Numeric or NULL. Actual or expected census population size. If supplied, $Ne_{at_census} = NeN * census_N$ is added to the output. Default NULL.
population	Character string. Optional label for the population, used in printed output and the returned list.

Value

A named list with the following elements:

population Character label (from population argument)

model "clonal_Y2000" – identifies the model used

NyN Ny/N – annual effective size ratio (Eq. 11)

NeN Ne/N – generation-time effective size ratio (Eq. 10)

L Generation time used in the calculation (years)

L_source "user" if L was supplied; "computed" if derived internally

u_dot Named vector of total annual survival per stage (colSums of T_mat)

u2_bar Stage-weighted mean of squared survivals (key intermediate)

Min_N Minimum census size N for $Ne \geq Ne_target$ (Lande 1995)

Ne_target The Ne threshold used for Min_N (default 5000)

References

Yonezawa K., Kinoshita E., Watano Y., and Zentoh H. (2000). Formulation and estimation of the effective size of stage-structured populations in *Fritillaria camtschatcensis*, a perennial herb with a complex life history. *Evolution* **54**(6): 2007-2013. doi:10.1111/j.00143820.2000.tb01244.x

Lande R. (1995). Mutation and conservation. *Conservation Biology* **9**: 728-791.

Examples

```

# -----
# Example 1: Replicate Yonezawa Table 4 for population Miz
# -----
# Transition matrix from Table 2 of Yonezawa et al. (2000)
T_Miz <- matrix(c(
  0.789, 0.121, 0.054,
  0.007, 0.621, 0.335,
  0.001, 0.258, 0.611
), nrow = 3, byrow = TRUE)

# Observed stage fractions (Table 2)
D_Miz <- c(0.935, 0.038, 0.027)

# Fecundity vector (Table 2) -- clonal propagules per plant per year
F_Miz <- c(0.055, 1.328, 2.398)

# Using L from Table 4 directly (recommended for exact replication)
result <- Ne_clonal_Y2000(
  T_mat      = T_Miz,
  F_vec      = F_Miz,
  D          = D_Miz,
  L          = 13.399,
  population = "Miz"
)
print(result)
# Expected: Ny/N = 2.932, Ne/N = 0.219, Min_N = 22,831

# -----
# Example 2: Let the function compute L internally
# -----
result2 <- Ne_clonal_Y2000(
  T_mat      = T_Miz,
  F_vec      = F_Miz,
  D          = D_Miz,
  population = "Miz (computed L)"
)
print(result2)

# -----
# Example 3: Replicate Table 4 for population Nan
# -----
T_Nan <- matrix(c(
  0.748, 0.137, 0.138,
  0.006, 0.669, 0.374,
  0.001, 0.194, 0.488
), nrow = 3, byrow = TRUE)

D_Nan <- c(0.958, 0.027, 0.015)
F_Nan <- c(0.138, 2.773, 5.016)

result3 <- Ne_clonal_Y2000(

```

```

T_mat      = T_Nan,
F_vec      = F_Nan,
D          = D_Nan,
L          = 8.353,
population = "Nan"
)
print(result3)
# Expected: Ny/N = 2.428, Ne/N = 0.291, Min_N = 17,183

```

Ne_clonal_Y2000_both *Run Ne_clonal_Y2000 with both observed and expected stage fractions*

Description

Run Ne_clonal_Y2000 with both observed and expected stage fractions

Usage

```

Ne_clonal_Y2000_both(
  T_mat,
  F_vec,
  D_obs,
  D_exp = NULL,
  L = NULL,
  Ne_target = 50,
  census_N = NULL,
  population = NULL
)

```

Arguments

T_mat	Survival/transition matrix (s x s).
F_vec	Fecundity vector (length s). Used for L and D_exp.
D_obs	Observed stage fractions from field counts.
D_exp	Expected (equilibrium) stage fractions. If NULL, derived from the dominant eigenvector of $A = T_mat + F_mat$.
L	Generation time (years). If NULL, computed internally.
Ne_target	Numeric. Ne conservation threshold. Common choices: 50 (Franklin 1980, avoid inbreeding depression), 500 (long-term quantitative variation), or 5000 (Lande 1995, long-term evolutionary potential). Default 50.
census_N	Numeric or NULL. Actual or expected census population size. If supplied, $Ne_at_census = NeN * census_N$ is added to the output. Default NULL.
population	Character label for the population.

Value

A list with two Ne_clonal_Y2000 result objects:

observed Results using D_obs

expected Results using D_exp

Examples

```
T_Miz <- matrix(c(
  0.789, 0.121, 0.054,
  0.007, 0.621, 0.335,
  0.001, 0.258, 0.611
), nrow = 3, byrow = TRUE)

both <- Ne_clonal_Y2000_both(
  T_mat      = T_Miz,
  F_vec      = c(0.055, 1.328, 2.398),
  D_obs      = c(0.935, 0.038, 0.027),
  D_exp      = c(0.921, 0.046, 0.033),
  L          = 13.399,
  population = "Miz"
)
print(both$observed) # main values in Table 4
print(both$expected) # parenthetical values in Table 4
```

Ne_mixed_Y2000	<i>Variance effective population size for mixed sexual/clonal stage-structured populations</i>
----------------	--

Description

Implements the full general Equation 6 of Yonezawa et al. (2000) for populations with both sexual and clonal reproduction. Each stage can have a different mix of the two reproductive modes via the per-stage clonal fraction vector d .

Usage

```
Ne_mixed_Y2000(
  T_mat,
  F_vec,
  D,
  d,
  Vk_over_k = NULL,
  Vc_over_c = NULL,
  a = 0,
  L = NULL,
  x_max = 500L,
```

```

    Ne_target = 50,
    census_N = NULL,
    show_Ny = FALSE,
    population = NULL
)

```

Arguments

T_mat	Numeric matrix (s x s). Survival/transition matrix. Row j, column i gives the probability that an individual in stage i
F_vec	Numeric vector (length s). Total fecundity per stage per year: mean number of propagules (sexual + clonal combined) produced per individual. Used for L and $r_i = F_i * D_i$.
D	Numeric vector (length s). Stage frequency distribution. Must sum to 1.
d	Numeric vector (length s). Per-stage clonal reproduction fraction. MUST be supplied – there is no default. $d_i = 0$: stage i reproduces entirely sexually. $d_i = 1$: stage i reproduces entirely clonally. $d_i = 0.7$: 70% of stage i reproduction is clonal. Example: $d = c(0, 0, 0.8)$ for a 3-stage population where stages 1 and 2 are sexual only and stage 3 is mostly clonal.
Vk_over_k	Numeric vector (length s). Variance-to-mean ratio of SEXUAL reproductive output per stage $(V_k/k_bar)_i$. Default $rep(1, s) = \text{Poisson}$: reproductive success is equally distributed among individuals within each stage. Values > 1 reduce Ne (unequal sexual reproductive success).
Vc_over_c	Numeric vector (length s). Variance-to-mean ratio of CLONAL reproductive output per stage $(V_c/c_bar)_i$. Default $rep(1, s) = \text{Poisson}$: clonal output is equally distributed among individuals within each stage. Values > 1 reduce Ne (some individuals produce many more clonal propagules than others).
a	Numeric scalar. Hardy-Weinberg deviation. Default 0 = random mating. Supply a positive value for inbreeding. Must be between -1 and 1.
L	Numeric scalar (optional). Generation time in years. If NULL, computed internally via T^x iteration ($x_max = 500$).
x_max	Integer. Maximum age for L iteration (default 500). Ignored if L is supplied directly.
Ne_target	Numeric. Ne conservation threshold. Common choices: 50 (Franklin 1980, avoid inbreeding depression), 500 (long-term quantitative variation), or 5000 (Lande 1995, long-term evolutionary potential). Default 50.
census_N	Numeric or NULL. Actual or expected census population size. If supplied, $Ne_at_census = NeN * census_N$ is added to the output. Default NULL.
show_Ny	Logical. Whether to compute and return Ny/N (annual effective size, Eq. 11). Default FALSE. Note that Ny/N is defined here using the clonal component of the model and is most meaningful when clonal reproduction dominates.
population	Character string. Optional population label.

Details

Note on relationship to the other two functions: When $d = \text{rep}(0, s)$, `Ne_mixed_Y2000()` reproduces `Ne_sexual_Y2000()` exactly, because $\text{Avr}(Ad)$ vanishes. However, `Ne_mixed_Y2000()` with $d = \text{rep}(1, s)$ does NOT reproduce `Ne_clonal_Y2000()`, because `Ne_clonal_Y2000()` implements the simplified Equations 10-11 via a different algebraic path ($V = 2(1-u_{\text{bar}})$) that is not the same as the general Eq. 6 with $d=1$. For purely clonal populations always use `Ne_clonal_Y2000()` directly.

Value

A named list with elements:

population Character label

model "mixed_Y2000"

NeN N_e/N – generation-time effective size ratio (Eq. 6)

NyN N_y/N – annual effective size ratio (Eq. 11), or NA if `show_Ny = FALSE`

L Generation time used (years)

L_source "user" or "computed"

d Per-stage clonal fractions supplied

u_dot Total annual survival per stage

u_bar Population mean annual survival

u2_bar Stage-weighted mean of squared survivals

r_i Newborn contributions per stage

S_i Per-stage S values

A_i Per-stage A values

Avr_S Recruitment-weighted mean of S_i

Avr_Ad Recruitment-weighted mean of $A_i * d_i$

V Full variance term

V_term1 Between-stage survival variance component

V_term2 Sexual reproductive variance component

V_term3 Clonal reproductive variance component

Vk_over_k Sexual variance ratio used

Vc_over_c Clonal variance ratio used

a Hardy-Weinberg deviation used

Min_N Minimum census N for $N_e \geq N_{\text{target}}$

Ne_target N_e threshold used

References

Yonezawa K., Kinoshita E., Watano Y., and Zentoh H. (2000). Formulation and estimation of the effective size of stage-structured populations in *Fritillaria camtschatcensis*, a perennial herb with a complex life history. *Evolution* **54**(6): 2007-2013. doi:10.1111/j.00143820.2000.tb01243.x

Lande R. (1995). Mutation and conservation. *Conservation Biology* **9**: 728-791.

Examples

```

# -----
# Example 1: 3-stage perennial herb, stage 3 reproduces both
# sexually (seeds) and clonally (rhizomes). Stages 1 and 2
# reproduce sexually only.
# -----
T_herb <- matrix(c(
  0.30, 0.05, 0.00,
  0.40, 0.65, 0.10,
  0.00, 0.20, 0.80
), nrow = 3, byrow = TRUE)

result <- Ne_mixed_Y2000(
  T_mat      = T_herb,
  F_vec      = c(0.0, 0.5, 3.0),
  D          = c(0.60, 0.25, 0.15),
  d          = c(0.0, 0.0, 0.7), # stage 3 is 70% clonal
  population = "mixed herb"
)
print(result)

# -----
# Example 2: Show Ny/N for a predominantly clonal population
# -----
result_Ny <- Ne_mixed_Y2000(
  T_mat      = T_herb,
  F_vec      = c(0.0, 0.5, 3.0),
  D          = c(0.60, 0.25, 0.15),
  d          = c(0.5, 0.8, 0.9),
  show_Ny    = TRUE,
  population = "predominantly clonal herb"
)
print(result_Ny)

```

Ne_mixed_Y2000_both *Run Ne_mixed_Y2000 with both observed and expected stage fractions*

Description

Run Ne_mixed_Y2000 with both observed and expected stage fractions

Usage

```

Ne_mixed_Y2000_both(
  T_mat,
  F_vec,
  D_obs,

```

```

d,
D_exp = NULL,
Vk_over_k = NULL,
Vc_over_c = NULL,
a = 0,
L = NULL,
Ne_target = 50,
census_N = NULL,
show_Ny = FALSE,
population = NULL
)

```

Arguments

T_mat	Survival/transition matrix (s x s).
F_vec	Fecundity vector (length s).
D_obs	Observed stage fractions from field counts.
d	Per-stage clonal fraction vector (length s).
D_exp	Expected (equilibrium) stage fractions. If NULL, derived from stable stage distribution of A.
Vk_over_k	Sexual variance ratio (default Poisson).
Vc_over_c	Clonal variance ratio (default Poisson).
a	Hardy-Weinberg deviation (default 0).
L	Generation time. If NULL, computed internally.
Ne_target	Numeric. Ne conservation threshold. Common choices: 50 (Franklin 1980, avoid inbreeding depression), 500 (long-term quantitative variation), or 5000 (Lande 1995, long-term evolutionary potential). Default 50.
census_N	Numeric or NULL. Actual or expected census population size. If supplied, Ne_at_census = NeN * census_N is added to the output. Default NULL.
show_Ny	Logical. Compute Ny/N? (default FALSE).
population	Character label for the population.

Value

A list with two Ne_mixed_Y2000 result objects:

observed Results using D_obs

expected Results using D_exp

Ne_sensitivity_d *Sensitivity of Ne/N to clonal fraction d_i in one stage*

Description

Sweeps d_i from 0 to 1 for a single focal stage, holding all other inputs constant. Under Poisson defaults ($Vc/c_{\text{bar}} = Vk/k_{\text{bar}} = 1$), Ne/N is constant across all d values. Supply $Vc_{\text{over}_c} \neq 1$ to see a meaningful sensitivity curve.

Usage

```
Ne_sensitivity_d(
  T_mat,
  F_vec,
  D,
  d_fixed,
  stage_index = NULL,
  stage_name = NULL,
  d_range = seq(0, 1, by = 0.1),
  Vk_over_k = NULL,
  Vc_over_c = NULL,
  a = 0,
  L = NULL,
  Ne_target = 5000,
  population = NULL
)
```

Arguments

T_mat	Survival/transition matrix (s x s).
F_vec	Fecundity vector (length s).
D	Stage frequency distribution (length s, sums to 1).
d_fixed	Numeric vector (length s). Clonal fractions for ALL stages. The focal stage value will be overwritten by the sweep. Must be length s.
stage_index	Integer. Which stage to vary. Takes priority over stage_name if both are supplied.
stage_name	Character. Column name of the focal stage in T_mat.
d_range	Numeric vector of d values to test for focal stage. Default seq(0, 1, by = 0.1).
Vk_over_k	Sexual variance vector. Default rep(1, s).
Vc_over_c	Clonal variance vector. Default rep(1, s). Supply values > 1 to see a non-flat sensitivity curve.
a	Hardy-Weinberg deviation. Default 0.
L	Generation time. If NULL, computed internally.
Ne_target	Ne conservation threshold. Default 5000.
population	Character label.

Value

A list with:

data Data frame: d_focal, NeN, Min_N, L, V, V_term1, V_term2, V_term3

plot ggplot2 object showing Ne/N vs d_i

call Matched call

Examples

```
T_herb <- matrix(c(
  0.30, 0.05, 0.00,
  0.40, 0.65, 0.10,
  0.00, 0.20, 0.80
), nrow = 3, byrow = TRUE)

# Under Poisson defaults: flat curve (d_i has no effect)
sens_poisson <- Ne_sensitivity_d(
  T_mat      = T_herb,
  F_vec      = c(0.0, 0.5, 3.0),
  D          = c(0.60, 0.25, 0.15),
  d_fixed    = c(0.0, 0.0, 0.5),
  stage_index = 3,
  population = "mixed herb (Poisson)"
)
sens_poisson$plot

# With non-Poisson clonal variance: d_i matters
sens_nonpoisson <- Ne_sensitivity_d(
  T_mat      = T_herb,
  F_vec      = c(0.0, 0.5, 3.0),
  D          = c(0.60, 0.25, 0.15),
  d_fixed    = c(0.0, 0.0, 0.5),
  stage_index = 3,
  Vc_over_c  = c(1, 1, 3),
  population = "mixed herb (Vc/c_bar = 3 in stage 3)"
)
sens_nonpoisson$plot
```

Ne_sensitivity_L

Sensitivity of Ne/N to generation time L

Description

Sweeps generation time L across a user-defined range for any of the three NeStage model functions. All other inputs are held constant.

Usage

```
Ne_sensitivity_L(
  model_fn,
  T_mat,
  F_vec,
  D,
  d = NULL,
  L_range = seq(2, 30, by = 2),
  L_ref = NULL,
  Vk_over_k = NULL,
  Vc_over_c = NULL,
  a = 0,
  Ne_target = 5000,
  population = NULL
)
```

Arguments

model_fn	The model function: Ne_clonal_Y2000, Ne_sexual_Y2000, or Ne_mixed_Y2000.
T_mat	Survival/transition matrix (s x s).
F_vec	Fecundity vector (length s).
D	Stage frequency distribution (length s, sums to 1).
d	Per-stage clonal fraction vector. Required for Ne_mixed_Y2000; ignored otherwise.
L_range	Numeric vector of L values (years) to test. Default seq(2, 30, by = 2).
L_ref	Numeric. Reference L value to mark on the plot (e.g., the computed or published L). If NULL, computed internally from T_mat and F_vec.
Vk_over_k	Sexual variance vector. Default rep(1, s).
Vc_over_c	Clonal variance vector (mixed model only).
a	Hardy-Weinberg deviation. Default 0.
Ne_target	Ne conservation threshold. Default 5000.
population	Character label.

Value

A list with:

data Data frame: L, NeN, Min_N, V, V_term1, V_term2, and V_term3 (for mixed model)

plot ggplot2 object showing Ne/N vs L

call Matched call

Examples

```
# Clonal model -- how sensitive is Ne/N to L for Fritillaria Miz?
T_Miz <- matrix(c(
  0.789, 0.121, 0.054,
  0.007, 0.621, 0.335,
  0.001, 0.258, 0.611
), nrow = 3, byrow = TRUE)

sens <- Ne_sensitivity_L(
  model_fn = Ne_clonal_Y2000,
  T_mat    = T_Miz,
  F_vec    = c(0.055, 1.328, 2.398),
  D        = c(0.935, 0.038, 0.027),
  L_range  = seq(5, 25, by = 1),
  L_ref    = 13.399,
  population = "Fritillaria Miz"
)
print(sens$data)
sens$plot
```

Ne_sensitivity_Vc

Sensitivity of Ne/N to clonal reproductive variance in one stage

Description

Sweeps (Vc/c_{bar}_i) across a range for a single focal stage. Mixed model only. Under Poisson defaults ($Vc/c_{\text{bar}} = 1 = Vk/k_{\text{bar}}$), clonal fraction d_i has no effect on Ne . Non-Poisson clonal variance ($Vc/c_{\text{bar}} > 1$) is required for d_i to influence Ne .

Usage

```
Ne_sensitivity_Vc(
  T_mat,
  F_vec,
  D,
  d,
  stage_index = NULL,
  stage_name = NULL,
  Vc_range = seq(0.5, 5, by = 0.5),
  Vc_fixed = 1,
  Vk_over_k = NULL,
  a = 0,
  L = NULL,
  Ne_target = 5000,
  population = NULL
)
```

Arguments

T_mat	Survival/transition matrix (s x s).
F_vec	Fecundity vector (length s).
D	Stage frequency distribution (length s, sums to 1).
d	Per-stage clonal fraction vector (length s). Required.
stage_index	Integer. Which stage to vary. Takes priority over stage_name if both are supplied.
stage_name	Character. Column name of the focal stage in T_mat.
Vc_range	Numeric vector of (Vc/c_bar) values to test. Default seq(0.5, 5, by = 0.5).
Vc_fixed	Numeric. (Vc/c_bar) for all OTHER stages. Default 1.
Vk_over_k	Sexual variance vector. Default rep(1, s).
a	Hardy-Weinberg deviation. Default 0.
L	Generation time. If NULL, computed internally.
Ne_target	Ne conservation threshold. Default 5000.
population	Character label.

Value

A list with:

data Data frame: Vc_over_c, NeN, Min_N, L, V, V_term1, V_term2, V_term3

plot ggplot2 object showing Ne/N vs Vc/c_bar

call Matched call

Examples

```
T_herb <- matrix(c(
  0.30, 0.05, 0.00,
  0.40, 0.65, 0.10,
  0.00, 0.20, 0.80
), nrow = 3, byrow = TRUE)

sens <- Ne_sensitivity_Vc(
  T_mat      = T_herb,
  F_vec      = c(0.0, 0.5, 3.0),
  D          = c(0.60, 0.25, 0.15),
  d          = c(0.0, 0.0, 0.7),
  stage_index = 3,
  Vc_range   = seq(0.5, 6, by = 0.5),
  population = "mixed herb"
)
print(sens$data)
sens$plot
```

Ne_sensitivity_Vk *Sensitivity of Ne/N to sexual reproductive variance in one stage*

Description

Sweeps (Vk/k_{bar})_i across a range for a single focal stage, holding all other inputs constant. Works with Ne_sexual_Y2000 and Ne_mixed_Y2000.

Usage

```
Ne_sensitivity_Vk(
  model_fn,
  T_mat,
  F_vec,
  D,
  d = NULL,
  stage_index = NULL,
  stage_name = NULL,
  Vk_range = seq(0.5, 5, by = 0.5),
  Vk_fixed = 1,
  Vc_over_c = NULL,
  a = 0,
  L = NULL,
  Ne_target = 5000,
  population = NULL
)
```

Arguments

model_fn	The model function to use: Ne_sexual_Y2000 or Ne_mixed_Y2000. Do NOT supply Ne_clonal_Y2000 – sexual reproductive variance does not enter that model.
T_mat	Survival/transition matrix (s x s).
F_vec	Fecundity vector (length s).
D	Stage frequency distribution (length s, sums to 1).
d	Per-stage clonal fraction vector. Required if model_fn = Ne_mixed_Y2000; ignored otherwise.
stage_index	Integer. Which stage to vary. Takes priority over stage_name if both are supplied.
stage_name	Character. Column name of the focal stage in T_mat. Used only if stage_index is NULL.
Vk_range	Numeric vector of (Vk/k_{bar}) values to test. Default seq(0.5, 5, by = 0.5).
Vk_fixed	Numeric. (Vk/k_{bar}) for all OTHER stages. Default 1.
Vc_over_c	Clonal variance vector (for Ne_mixed_Y2000 only). Default rep(1, s).

a	Hardy-Weinberg deviation. Default 0.
L	Generation time. If NULL, computed internally.
Ne_target	Ne conservation threshold. Default 5000.
population	Character label.

Value

A list with:

data Data frame: Vk_over_k, NeN, Min_N, L, V, V_term1, V_term2, and V_term3 (for mixed model)

plot ggplot2 object showing Ne/N vs Vk/k_bar

call Matched call

Examples

```
T_herb <- matrix(c(
  0.30, 0.05, 0.00,
  0.40, 0.65, 0.10,
  0.00, 0.20, 0.80
), nrow = 3, byrow = TRUE)

sens <- Ne_sensitivity_Vk(
  model_fn    = Ne_sexual_Y2000,
  T_mat       = T_herb,
  F_vec       = c(0.0, 0.5, 3.0),
  D           = c(0.60, 0.25, 0.15),
  stage_index = 3,
  Vk_range    = seq(0.5, 6, by = 0.5),
  population  = "hypothetical herb"
)
print(sens$data)
sens$plot
```

Ne_sexual_Y2000	<i>Variance effective population size for 100% sexual stage-structured populations</i>
-----------------	--

Description

Implements Equation 6 of Yonezawa et al. (2000) with $d_i = 0$ (no clonal reproduction) for populations that reproduce exclusively through sexual means. The annual effective size N_y is not computed as it applies only to clonal populations (Eq. 11).

Usage

```
Ne_sexual_Y2000(
  T_mat,
  F_vec,
  D,
  Vk_over_k = NULL,
  a = 0,
  L = NULL,
  x_max = 500L,
  Ne_target = 50,
  census_N = NULL,
  population = NULL
)
```

Arguments

T_mat	Numeric matrix (s x s). The survival/transition matrix. Row j, column i gives the probability that an individual in stage i Column sums must be ≤ 1 (total annual survival per stage).
F_vec	Numeric vector of length s. Fecundity of each stage: the mean number of offspring (seeds, juveniles) produced per individual per year through sexual reproduction. Used to compute L and $r_i = F_i * D_i$. Set F_vec = NULL only if supplying L directly AND the function does not need r_i (not recommended).
D	Numeric vector of length s. Stage frequency distribution: the proportion of the population in each stage. Must sum to 1.
Vk_over_k	Numeric vector of length s. The variance-to-mean ratio of sexual reproductive output per stage: $(V_k / \bar{k})_i$. Default is $\text{rep}(1, s)$ – Poisson reproductive variance, meaning reproductive success is equally distributed among individuals within each stage. Values > 1 indicate that some individuals reproduce much more than others (common when pollinators show strong preferences, or when resources are limiting), which reduces Ne. Values < 1 indicate more equal than random reproductive success, which increases Ne.
a	Numeric scalar. Deviation from Hardy-Weinberg proportions. Default 0 = random mating (appropriate for most outcrossing species with no selfing). Supply a positive value if the population has known inbreeding (e.g., from FIS estimates). Must be between -1 and 1.
L	Numeric scalar (optional). Generation time in years. If NULL (default), L is computed internally from T_mat and F_vec using the Yonezawa (2000) definition ($x_{\text{max}} = 500$ yr). Supply L directly to match a specific published value.
x_max	Integer. Maximum age for the L iteration (default 500). Ignored if L is supplied directly.
Ne_target	Numeric. Ne conservation threshold for computing the minimum census size N needed to achieve $Ne \geq Ne_{\text{target}}$. Common choices: 50 (Franklin 1980, avoid inbreeding), 500 (Franklin 1980, maintain quantitative variation), 5000 (Lande 1995, long-term evolutionary potential). Set to the threshold most relevant for your study system. Default 50.

census_N	Numeric or NULL. The actual (or expected) census population size. If supplied, $Ne_{at_census} = NeN * census_N$ is reported in the output, showing the Ne your population is likely achieving right now. Default NULL (not reported).
population	Character string. Optional label for the population.

Value

A named list with the following elements:

population Character label

model "sexual_Y2000"

NeN Ne/N – generation-time effective size ratio (Eq. 6)

L Generation time used (years)

L_source "user" or "computed"

u_dot Total annual survival per stage (colSums of T_mat)

u_bar Population mean annual survival

u2_bar Stage-weighted mean of squared survivals

r_i Newborn contributions per stage ($F_vec * D$)

S_i Per-stage S values used in $Avr(S)$

Avr_S Recruitment-weighted mean of S_i

V Full variance term from Eq. 6

V_component1 Between-stage survival variance component

V_component2 Reproductive variance component

Vk_over_k Variance-to-mean ratio of sexual output used

a Hardy-Weinberg deviation used

Min_N Minimum census N for $Ne \geq Ne_target$

Ne_target Ne threshold used

Ne_at_census Ne at the supplied census_N (NULL if not supplied)

census_N Census size supplied by user (NULL if not supplied)

References

Yonezawa K., Kinoshita E., Watano Y., and Zentoh H. (2000). Formulation and estimation of the effective size of stage-structured populations in *Fritillaria camtschatcensis*, a perennial herb with a complex life history. *Evolution* **54**(6): 2007-2013. doi:10.1111/j.00143820.2000.tb01243.x

Lande R. (1995). Mutation and conservation. *Conservation Biology* **9**: 728-791.

Examples

```

# -----
# Example 1: Simple 3-stage plant, Poisson defaults
# A hypothetical outcrossing perennial herb with three stages:
# Stage 1: seedling/juvenile (high mortality, no reproduction)
# Stage 2: vegetative adult (moderate survival, low reproduction)
# Stage 3: reproductive adult (high survival, high reproduction)
# -----
T_plant <- matrix(c(
  0.30, 0.05, 0.00,
  0.40, 0.65, 0.10,
  0.00, 0.20, 0.80
), nrow = 3, byrow = TRUE)

F_plant <- c(0.0, 0.5, 3.0) # seeds per individual per stage per year
D_plant <- c(0.60, 0.25, 0.15) # observed stage fractions

result <- Ne_sexual_Y2000(
  T_mat      = T_plant,
  F_vec      = F_plant,
  D          = D_plant,
  population = "hypothetical herb"
)
print(result)

# -----
# Example 2: Same population, high reproductive variance in stage 3
#  $V_k/k_{\text{bar}} = 3$  for reproductive adults -- pollinator-limited, so only
# a few adults contribute most of the seeds in any given year.
# This should reduce Ne relative to Example 1.
# -----
result_highvar <- Ne_sexual_Y2000(
  T_mat      = T_plant,
  F_vec      = F_plant,
  D          = D_plant,
  Vk_over_k  = c(1, 1, 3),
  population = "hypothetical herb (high repro variance stage 3)"
)
print(result_highvar)
# Ne/N should be lower than Example 1.

# -----
# Example 3: Supply L directly from a published source
# -----
result_Luser <- Ne_sexual_Y2000(
  T_mat      = T_plant,
  F_vec      = F_plant,
  D          = D_plant,
  L          = 8.5,
  population = "hypothetical herb (published L)"
)
print(result_Luser)

```


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