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Modeling temporal dynamics of genetic diversity in stage-structured plant populations with reference to demographic genetic structure

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Abstract

Predicting temporal dynamics of genetic diversity is important for assessing long-term population persistence. In stage-structured populations, especially in perennial plant species, genetic diversity is often compared among life history stages, such as seedlings, juveniles, and flowerings, using neutral genetic markers. The comparison among stages is sometimes referred to as demographic genetic structure, which has been regarded as a proxy of potential genetic changes because individuals in mature stages will die and be replaced by those in more immature stages over the course of time. However, due to the lack of theoretical examination, the basic property of the stage-wise genetic diversity remained unclear. We developed a matrix model which was made up of difference equations of the probability of non-identical-by-descent of each life history stage at a neutral locus to describe the dynamics and the inter-stage differences of genetic diversity in stage-structured plant populations. Based on the model, we formulated demographic genetic structure as well as the annual change rate of the probability of non-identical-by-descent (denoted as η). We checked if theoretical expectations on demographic ge-

netic structure and η obtained from our model agreed with computational results of stochastic simulation using randomly generated 3,000 life histories. We then examined the relationships of demographic genetic structure with effective population size N_e , which is the determinants of diversity loss per generation time. Theoretical expectations on η and demographic genetic structure fitted well to the results of stochastic simulation, supporting the validity of our model. Demographic genetic structure varied independently of N_e and η , while having a strong correlation with stable stage distribution: genetic diversity was lower in stages with fewer individuals. Our results indicate that demographic genetic structure strongly reflects stable stage distribution, rather than temporal genetic dynamics, and that inferring future genetic diversity solely from demographic genetic structure would be misleading. Instead of demographic genetic structure, we propose η as an useful tool to predict genetic diversity at the same time scale as population dynamics (i.e., per year), facilitating evaluation on population viability from a genetic point of view.

Keywords: effective population size, expected heterozygosity, life history, matrix model, non-identical-by-descent

1 **1. Introduction**

2 Genetic diversity, or standing genetic variation, is a source of adaptive
3 evolution (Barrett and Schluter, 2008). Populations with high genetic di-
4 versity are more likely to adapt to environmental changes and to persist for
5 a long period (Agashe et al., 2011; Ramsayer et al., 2013). Therefore, it is
6 necessary to examine the temporal dynamics of genetic diversity for assessing

7 long-term population viability (Mimura et al., 2017).

8 The rate of change in genetic diversity per generation time is primarily
9 determined by the effective population size (N_e): the larger N_e , the weaker
10 genetic drift, and the more likely genetic diversity is maintained (Crow and
11 Kimura, 1970). Although N_e was first theoretically proposed for populations
12 without generation overlap, many wild populations including perennial plants
13 have overlapping generations and are made up of individuals differing in
14 age or life history stage. Previous theoretical studies extended the concept
15 of effective population size to populations structured by age (Felsenstein,
16 1971; Hill, 1972, 1979; Johnson, 1977) or by stage (Orive, 1993; Yonezawa
17 et al., 2000) by formulating N_e with demographic rates (age- or stage-specific
18 survival rates and fecundities). These formulations enable us to calculate N_e
19 and to assess the temporal genetic dynamics in species with complex life
20 histories (Waples et al., 2011, 2013).

21 Meanwhile, some empirical genetic studies do not examine N_e to predict
22 future genetic diversity of stage-structured populations. Instead, genetic di-
23 versity is comparatively estimated for each stage class at a single time point
24 with neutral genetic markers (Aldrich et al., 1998; Ally and Ritland, 2006;
25 Kettle et al., 2007; Linhart et al., 1981; Murren, 2003; Schmidt et al., 2018;
26 Vranckx et al., 2014). The resultant stage-wise genetic diversity is sometimes
27 referred to as demographic genetic structure (Aldrich et al., 1998) and is con-
28 sidered to reflect potential genetic changes that accompany the turnover of
29 constituent individuals. For example, if juvenile stage is less diverse than
30 more mature stages, genetic diversity would decrease with the replacement
31 of mature individuals to juveniles. Because species with stage structure are

32 mostly long-lived and long-term genetic monitoring is impractical, demo-
33 graphic genetic structure has been considered as a rough but a convenient
34 empirical approach to infer the temporal genetic dynamics (Mimura et al.,
35 2017; Schmidt et al., 2018).

36 Despite its empirical usage, mathematical and theoretical basis of demo-
37 graphic genetic structure has been in its infancy. Unlike N_e , demographic
38 genetic structure has not been formulated mathematically using demographic
39 rates. Relationships with N_e have also remained unexplored, which raises a
40 question on whether N_e and demographic genetic structure are largely redun-
41 dant or highlight different aspects of temporal genetic dynamics. Moreover,
42 lack of theoretical background draws concerns about the current interpre-
43 tation on demographic genetic structure. While analysis on demographic
44 genetic structure implicitly assumes that individuals sequentially grow and
45 die from juvenile to mature stage classes, this assumption is potentially in-
46 valid in perennial plants. In most perennial plant species, whose life histories
47 are structured by stage, not by age (Silvertown, 1987), aging (or passing of
48 time) does not necessarily promote growth and maturation. Some individ-
49 uals might keep proceeding to more mature stages, while others remain in
50 the same stage for a long period (stasis) or even reverse to more juvenile
51 stages (retrogression), and the probabilities of growth, stasis, and retrogres-
52 sion depend on stage, rather than on age. For example, long-lived woodland
53 perennial herbs of the genus *Trillium* show stasis for more than ten years in
54 juvenile stages as well as go back from a mature reproductive stage to a pre-
55 reproductive one in response to resource exhaustion (Knight, 2004; Ohara
56 et al., 2001; Tomimatsu and Ohara, 2010). The static and bidirectional flows

57 in the life cycle complicate the order of individual turnover in a population.
58 It has not been theoretically confirmed if demographic genetic structure still
59 serves as a proxy for temporal changes despite these challenges. Mathemat-
60 ical formulation that encompasses demographic genetic structure, as well as
61 the temporal change in genetic diversity, will provide integrative understand-
62 ings on all the problems mentioned above in stage-structured populations,
63 but has never been achieved so far.

64 In this study, we develop a matrix model to describe the temporal dy-
65 namics of genetic diversity for a neutral locus of a stage-structured perennial
66 plant species. The model is constructed by deriving difference equations of
67 the probability that two genes randomly sampled from a given life history
68 stage are non-identical-by-descent. Based on the model, we formulate de-
69 mographic genetic structure and N_e . Thus, our model allows integrative
70 analysis on demographic genetic structure, temporal dynamics of genetic di-
71 versity, and their relationships. In the following sections, we describe the
72 derivation procedures of our model (section 2.1), the validation of our model
73 (section 2.2), and the assessment on whether demographic genetic structure
74 serves as a good proxy for the temporal changes in genetic diversity (section
75 2.3).

76 **2. Materials and Methods**

77 *2.1. Model development*

78 *2.1.1. Overview*

79 Felsenstein (1971) derived inbreeding effective population size for age-
80 structured populations by formulating recurrence equations of the probability

81 of non-identical-by-descent, which is also described in Charlesworth (1994).
 82 We partly follow mathematical formulation procedures in Felsenstein (1971)
 83 while adding necessary modifications to extend it to stage-structured popu-
 84 lations. We develop difference equations of the probability of non-identical-
 85 by-descent at a neutral locus for a closed, stage-structured population, sup-
 86 posing a diploid perennial plant species. We do not consider sex differences
 87 because most plants are hermaphrodite (Torices et al., 2011). We assume
 88 that mutations do not newly occur. Besides, as in Felsenstein (1971), we
 89 assume demographic equilibrium, where the census population size and its
 90 allocation to each stage (stage distribution) are constant over time. Cen-
 91 sus population size is set to N , which is divided into n life history stages
 92 (N_1, N_2, \dots, N_n) .

$$N = \sum_{i=1}^n N_i \quad (1)$$

93 The probability of transition (either growth, stasis, or retrogression) from
 94 stage j to stage i is t_{ij} per year. In each year, individuals randomly mate
 95 and f_{ij} newborns join stage i from a parent in stage j . a_{ij} , which denotes
 96 the sum of t_{ij} and f_{ij} , describes the total flow of individuals from stage j to
 97 i between successive years.

$$a_{ij} = t_{ij} + f_{ij}. \quad (2)$$

98 In age-structured life histories, flows of individuals among age classes are
 99 sparse: survival paths connect only adjacent ages in the direction from i to
 100 $i + 1$ (i.e., $t_{ij} = 0$ when $i \neq j + 1$), and reproduction paths join only age
 101 class 1 (i.e., $f_{ij} = 0$ when $i \neq 1$). In plants, however, multiple survival paths
 102 come in and out from each stage by the combination of growth, stasis, and

103 retrogression. Moreover, newborns do not always join the first stage, because
 104 newborn seeds either become dormant to join seed bank stage, or immediately
 105 germinate to join juvenile stages, resulting in multiple destinations (e.g., a
 106 perennial plant *Carduus nutans*, whose life cycle is shown in figure 1 of Shea
 107 and Kelly (1998)). Therefore, stage is not merely a pooling of successive age
 108 classes and stage-structured life histories are essentially different from age-
 109 structured ones. We need to consider all possible transition and reproduction
 110 paths among stages, which is quite a distinct point compared to the age-
 111 structured model in Felsenstein (1971).

112 Population dynamics can be modeled by the following matrix population
 113 model.

$$\begin{pmatrix} N_{1,t} \\ \vdots \\ N_{i,t} \\ \vdots \\ N_{n,t} \end{pmatrix} = \begin{pmatrix} a_{11} & \cdots & a_{1j} & \cdots & a_{1n} \\ \vdots & & \vdots & & \vdots \\ a_{i1} & \cdots & a_{ij} & \cdots & a_{in} \\ \vdots & & \vdots & & \vdots \\ a_{n1} & \cdots & a_{nj} & \cdots & a_{nn} \end{pmatrix} \begin{pmatrix} N_{1,t-1} \\ \vdots \\ N_{i,t-1} \\ \vdots \\ N_{n,t-1} \end{pmatrix}. \quad (3)$$

114 $N_{i,t}$ denotes the number of individuals in stage i in year t , which is always
 115 equal to N_i for any t because we assume demographic equilibrium. Stable
 116 stage distribution, which is the relative number of individuals among stages
 117 in the equilibrium state, is proportional to the leading right eigenvector of
 118 the transition matrix (Caswell, 2001).

119 We define $H_{ij,t}$ as the probability that two genes randomly sampled from
 120 stage i and j with replacement in year t are not identical-by-descent. Each
 121 gene has its own ancestry, and two-gene pairs that are (non-)identical-by-
 122 descent at $t = 0$ will remain the same for any t . Similarly, because we assume

123 no mutations, two-gene pairs that are (non-)identical-by-state at $t = 0$ will
124 also remain the same over time. This means that $H_{ij,t}$ behaves in the same
125 manner as expected heterozygosity, which is the probability of non-identical-
126 by-state and is commonly used as a proxy of genetic diversity. Our goal
127 is to formulate $H_{ij,t}$ for all possible i and j , which enables us to obtain
128 theoretical counterpart of demographic genetic structure, that is, stage-wise
129 genetic diversity at a particular time point.

130 Here, we provide key derivation procedures, highlighting the differences
131 with the preceding age-structured models in Felsenstein (1971). The com-
132 plete derivation procedures are given in Supporting Information 1.

133 *2.1.2. Difference equations of $H_{ij,t}$*

134 We begin with modeling the changes in $H_{ij,t}$ between two successive time
135 points for all i and j , which are the stage-structured version of equations 2
136 to 5 in Felsenstein (1971). We separately consider two mutually exclusive
137 situations: $i \neq j$ (case 1) and $i = j$ (case 2). Both cases can be further
138 split into six situations. Firstly, two genes randomly sampled in year t were
139 either in the same stage (say, stage m , case A) or in different stages (say,
140 stage k and l , case B) in year $t - 1$. Furthermore, genes can move among
141 stages either by survival (grow, stasis, and retrogression) or by reproduction.
142 Survival and reproduction are essentially different because reproduction al-
143 lows one gene to be replicated and to move to multiple stages simultaneously
144 and independently, while survival does not. There are three possibilities in
145 how the two genes sampled were transferred from the previous year: both
146 genes were transferred by survival (case α), one by survival and the other
147 by reproduction (case β), and both by reproduction (case γ). Considering

148 the combinations of where (case A and B) and how (case α , β , and γ) the
 149 two genes sampled came from, there are 6 mutually exclusive situations to
 150 be considered in both case 1 and 2 (Figure 1).

151 This classification scheme is original to our stage-structured model, and is
 152 not adopted in Felsenstein (1971). Compared to age-structured life histories,
 153 classes are more densely interconnected by survival and reproduction in stage-
 154 structured ones. It is necessary to consider as many as 12 situations to handle
 155 the complexity in plant life histories.

156 In case 1 (i.e., $i \neq j$), $H_{ij,t}$ can be decomposed as follows.

$$\begin{aligned}
 H_{ij,t} = & H_{ij,t}|_{1 \cap A \cap \alpha} + H_{ij,t}|_{1 \cap A \cap \beta} + H_{ij,t}|_{1 \cap A \cap \gamma} \\
 & + H_{ij,t}|_{1 \cap B \cap \alpha} + H_{ij,t}|_{1 \cap B \cap \beta} + H_{ij,t}|_{1 \cap B \cap \gamma}, \quad (4)
 \end{aligned}$$

157 where the cap symbol \cap stands for the co-occurrence of multiple cases:
 158 $H_{ij,t}|_{1 \cap Y \cap Z}$ stands for $H_{ij,t}$ that simultaneously satisfies case 1, Y, and Z
 159 ($Y = A, B$; $Z = \alpha, \beta, \gamma$). All six $H_{ij,t}|_{1 \cap Y \cap Z}$ on the right side of equation 4
 160 are formulated as follows (see Supporting Information 1.1 for details).

$$\begin{aligned}
 H_{ij,t}|_{1 \cap A \cap \alpha} &= \sum_{m=1}^n \left\{ \frac{t_{im}t_{jm}N_m^2}{N_iN_j} \times \frac{1}{1 - 1/(2N_m)} H_{mm,t-1} \right\} \\
 H_{ij,t}|_{1 \cap A \cap \beta} &= \sum_{m=1}^n \left\{ \frac{(t_{im}f_{jm} + f_{im}t_{jm})N_m^2}{N_iN_j} \times H_{mm,t-1} \right\} \\
 H_{ij,t}|_{1 \cap A \cap \gamma} &= \sum_{m=1}^n \left(\frac{f_{im}f_{jm}N_m^2}{N_iN_j} \times H_{mm,t-1} \right) \\
 H_{ij,t}|_{1 \cap B \cap \alpha} &= \sum_{k=1}^n \sum_{\substack{l=1 \\ l \neq k}}^n \left\{ \frac{(t_{ik}t_{jl} + t_{il}t_{jk})N_kN_l}{N_iN_j} \times H_{kl,t-1} \right\} \\
 H_{ij,t}|_{1 \cap B \cap \beta} &= \sum_{k=1}^n \sum_{\substack{l=1 \\ l \neq k}}^n \left\{ \frac{(t_{ik}f_{jl} + f_{ik}t_{jl} + t_{il}f_{jk} + f_{il}t_{jk})N_kN_l}{N_iN_j} \times H_{kl,t-1} \right\}
 \end{aligned}$$

$$H_{ij,t}|_{1 \cap B \cap \gamma} = \sum_{k=1}^n \sum_{\substack{l=1 \\ l \neq k}}^n \left\{ \frac{(f_{ik}f_{jl} + f_{il}f_{jk})N_k N_l}{N_i N_j} \times H_{kl,t-1} \right\}. \quad (5)$$

161 Each $H_{ij,t}|_{1 \cap Y \cap Z}$ is shown as a summation of a multiplications of two terms.
 162 The first term is a conditional probability of case $1 \cap Y \cap Z$ given case 1. For
 163 example, the first term of $H_{ij,t}|_{1 \cap A \cap \alpha}$ can be rewritten as $(2t_{im}N_m)/(2N_i) \times$
 164 $(2t_{jm}N_m)/(2N_j)$, which is the number of two-gene pairs that fall into case 1,
 165 A, and α simultaneously under a specific m (i.e., $2t_{im}N_m \times 2t_{jm}N_m$) divided
 166 by the total number of pairs that satisfy case 1 (i.e., $2N_i \times 2N_j$). Here,
 167 the number of genes are twice the number of individuals because we assume
 168 diploid species. Similarly, the first term in the other five equations stand for
 169 the corresponding proportion of two-genes pairs. The second term stands
 170 for the probability of non-identical-by-descent. Considering which stages the
 171 two genes sampled belonged to in year $t - 1$, we replace the probability with
 172 either $H_{mm,t-1}$ or $H_{kl,t-1}$, except $H_{ij,t}|_{1 \cap A \cap \alpha}$. In the case of $1 \cap A \cap \alpha$, genes
 173 sampled from stage i must be mutually exclusive against those from stage
 174 j , because one gene in stage m in year $t - 1$ could not move to both stage
 175 i and j simultaneously without being duplicated through reproduction. In
 176 other words, a gene that were in stage m in the previous year cannot be
 177 sampled twice, which violates the assumption of $H_{mm,t-1}$, that is, “sampling
 178 with replacement.” Therefore, $H_{ij,t}|_{1 \cap A \cap \alpha}$ inherits the probability that two
 179 genes randomly sampled from stage m “without” replacement in year $t - 1$
 180 were not identical-by-descent, which can be obtained by dividing $H_{mm,t-1}$ by
 181 the chance of not sampling the same gene twice ($= 1 - 1/(2N_m)$).

182 Substituting equations 5 to equation 4, $H_{ij,t}$ is formulated as follows.

$$\begin{aligned}
H_{ij,t} = & \sum_{m=1}^n \frac{N_m^2}{N_i N_j} \left\{ \frac{t_{im} t_{jm}}{1 - 1/(2N_m)} + f_{im} t_{jm} + t_{im} f_{jm} + f_{im} f_{jm} \right\} H_{mm,t-1} \\
& + \sum_{k=1}^n \sum_{\substack{l=1 \\ l \neq k}}^n \frac{N_k N_l}{N_i N_j} (a_{ik} a_{jl} + a_{il} a_{jk}) H_{kl,t-1}.
\end{aligned} \tag{6}$$

183 As for case 2 (i.e., $i = j$), we decompose $H_{ii,t}$ into six conditional proba-
184 bilities.

$$\begin{aligned}
H_{ii,t} = & H_{ii,t|2 \cap A \cap \alpha} + H_{ii,t|2 \cap A \cap \beta} + H_{ii,t|2 \cap A \cap \gamma} \\
& + H_{ii,t|2 \cap B \cap \alpha} + H_{ii,t|2 \cap B \cap \beta} + H_{ii,t|2 \cap B \cap \gamma}.
\end{aligned} \tag{7}$$

185 The probabilities of non-identical-by-descent on the right side of equation 7
186 can be formulated with $H_{mm,t-1}$ and $H_{kl,t-1}$, as previously done for $H_{ij,t}$ in
187 case 1 (see Supporting Information 1.2 for details).

$$\begin{aligned}
H_{ii,t|2 \cap A \cap \alpha} &= \sum_{m=1}^n \left\{ \left(\frac{t_{im} N_m}{N_i} \right)^2 \times \frac{1 - 1/(2t_{im} N_m)}{1 - 1/(2N_m)} H_{mm,t-1} \right\} \\
H_{ii,t|2 \cap A \cap \beta} &= \sum_{m=1}^n \left(\frac{2t_{im} f_{im} N_m^2}{N_i^2} \times H_{mm,t-1} \right) \\
H_{ii,t|2 \cap A \cap \gamma} &= \sum_{m=1}^n \left\{ \left(\frac{f_{im} N_m}{N_i} \right)^2 \times \left(1 - \frac{1}{2f_{im} N_m} \right) H_{mm,t-1} \right\} \\
H_{ii,t|2 \cap B \cap \alpha} &= \sum_{k=1}^n \sum_{\substack{l=1 \\ l \neq k}}^n \left(\frac{2t_{ik} t_{il} N_k N_l}{N_i^2} \times H_{kl,t-1} \right) \\
H_{ii,t|2 \cap B \cap \beta} &= \sum_{k=1}^n \sum_{\substack{l=1 \\ l \neq k}}^n \left\{ \frac{2(t_{ik} f_{il} + f_{ik} t_{il}) N_k N_l}{N_i^2} \times H_{kl,t-1} \right\} \\
H_{ii,t|2 \cap B \cap \gamma} &= \sum_{k=1}^n \sum_{\substack{l=1 \\ l \neq k}}^n \left(\frac{2f_{ik} f_{il} N_k N_l}{N_i^2} \times H_{kl,t-1} \right).
\end{aligned} \tag{8}$$

188 Here, as with $H_{ij,t}|_{1 \cap A \cap \alpha}$ in case 1, the second term of $H_{ii,t}|_{2 \cap A \cap \alpha}$ and $H_{ii,t}|_{2 \cap A \cap \gamma}$
189 are not exactly the same as $H_{mm,t-1}$. This is because the sources from which
190 two genes are sampled cannot be replaced with stage m of the previous year.
191 Case $2 \cap A \cap \alpha$ and $2 \cap A \cap \gamma$ are the same situations as the case of " $i = j > 1$ "
192 and " $i = j = 1$ " of the age-structured model in Felsenstein (1971), respec-
193 tively. Therefore, we followed Felsenstein (1971) to adjust $H_{mm,t-1}$ by multi-
194 plying $(1 - 1/(2t_{im}N_m))/(1 - 1/(2N_m))$ and $1 - 1/(2f_{im}N_m)$ in case $2 \cap A \cap \alpha$
195 and $2 \cap A \cap \gamma$. Improving the explanation of Felsenstein (1971) to fit to our
196 stage-structured model, We give detailed procedures on the adjustment of
197 $H_{mm,t-1}$ in Supporting Information 1.2.

198 Substituting equations 8 to equation 7, $H_{ii,t}$ is formulated as follows.

$$\begin{aligned}
H_{ii,t} = & \sum_{m=1}^n \left\{ \left(\frac{t_{im}N_m}{N_i} \right)^2 \frac{1 - 1/(2t_{im}N_m)}{1 - 1/(2N_m)} + \frac{2t_{im}f_{im}N_m^2}{N_i^2} \right. \\
& \left. + \left(\frac{f_{im}N_m}{N_i} \right)^2 \left(1 - \frac{1}{2f_{im}N_m} \right) \right\} H_{mm,t-1} \\
& + \sum_{k=1}^n \sum_{\substack{l=1 \\ l \neq k}}^n \frac{2a_{ik}a_{il}N_kN_l}{N_i^2} H_{kl,t-1}.
\end{aligned} \tag{9}$$

199 Combining case 1 (equation 6) and 2 (equation 9), we construct a matrix
200 equation.

$$\mathbf{h}_t = \mathbf{M}\mathbf{h}_{t-1}. \tag{10}$$

201 \mathbf{h}_t and \mathbf{h}_{t-1} are vectors, each of which consists of $H_{ij,t}$ and $H_{ij,t-1}$ for all
202 possible pairs of i and j ($1 \leq i \leq n$, $1 \leq j \leq n$). As the number of two-stage
203 pairs is $n(n+1)/2$, both \mathbf{h}_t and \mathbf{h}_{t-1} have $n(n+1)/2$ elements. \mathbf{M} is a
204 square matrix whose dimension is $n(n+1)/2$ and whose elements are equal
205 to the corresponding coefficients of $H_{mm,t-1}$ and $H_{kl,t-1}$ in equations 6 and 9

206 (see Supporting Information 2 for the detailed elements of \mathbf{M}). The order of
 207 elements in \mathbf{h}_t is arbitrary as long as it matches with that in \mathbf{h}_{t-1} and \mathbf{M} .

208 In general, multiplying matrix \mathbf{M} is asymptotically the same as multi-
 209 plying the dominant eigenvalue of \mathbf{M} , while \mathbf{h}_t converges to a scalar multi-
 210 plication of the leading right eigenvector, for sufficiently large t .

$$\mathbf{h}_t = \eta \mathbf{h}_{t-1}, \quad (11)$$

$$\mathbf{h}_t \propto \mathbf{w}, \quad (12)$$

211 where η and \mathbf{w} are the leading eigenvalue and its corresponding right eigen-
 212 vector of matrix \mathbf{M} , respectively. We denote w_{ij} as the element of \mathbf{w} that
 213 corresponds to $H_{ij,t}$ of \mathbf{h}_t .

$$H_{ij,t} \propto w_{ij}. \quad (13)$$

214 Equation 11 means that $H_{ij,t}$ changes with a constant rate η over the
 215 course of time for all i and j . Here, we denote H_t as the probability of non-
 216 identical-by-descent of the whole population in time t . H_t can be formulated
 217 as the sum of $H_{ij,t}$ weighted by the number of individuals in stage i and j .

$$H_t = \sum_{i=1}^n \sum_{j=1}^n \frac{N_i N_j}{N^2} H_{ij,t} \propto \sum_{i=1}^n \sum_{j=1}^n \frac{N_i N_j}{N^2} w_{ij}. \quad (14)$$

218 Because we assume that population size (N) and the number of individuals
 219 in a given stage i (N_i) are constant, H_t changes with the same rate as $H_{ij,t}$,
 220 that is, η .

$$H_t = \eta H_{t-1}. \quad (15)$$

221 Felsenstein (1971) also reached an analogous conclusion in his age-structured
 222 model that $H_{ij,t}$ and the probability of non-identical-by-descent of the over-
 223 all population changed at the same rate, which was the largest eigenvalue.

224 However, the proportionality between the array of $H_{ij,t}$ and the leading right
 225 eigenvector \mathbf{w} , which is shown in equations 12 and 13, was not mentioned in
 226 Felsenstein (1971).

227 *2.1.3. Demographic genetic structure*

228 We use the logarithm of the ratio of $H_{ii,t}$ between different stages as
 229 a proxy of demographic genetic structure, that is, comparison of genetic
 230 diversity among stages. With regard to the comparison between stage i and
 231 j , the logarithmic ratio is formulated as follows, based on equation 13.

$$\log\left(\frac{H_{ii,t}}{H_{jj,t}}\right) = \log\left(\frac{w_{ii}}{w_{jj}}\right), \quad (16)$$

232 When $\log(H_{ii,t}/H_{jj,t})$ is positive, $H_{ii,t}$ is larger than $H_{jj,t}$ (genetic diversity is
 233 higher in stage i than in stage j), and when negative vice versa. It should be
 234 noted that $\log(H_{ii,t}/H_{jj,t})$ is time-invariant, although $H_{ii,t}$ and $H_{jj,t}$ them-
 235 selves change with time.

236 We formulate inter-stage genetic differentiation as an extra extension of
 237 our model. While genetic differentiation has not been examined as much as
 238 to the difference in genetic diversity has, it is another aspect of stage-wise
 239 genetic structure. By denoting $\bar{H}_{ii,t}$ and \bar{w}_{ii} as the arithmetic mean of $H_{ii,t}$
 240 for all i and as that of corresponding elements in \mathbf{w} , respectively, we define
 241 inter-stage F_{st} as follows.

$$F_{st} = \frac{H_t - \bar{H}_{ii,t}}{H_t} = 1 - \frac{\bar{w}_{ii}N^2}{\sum_i \sum_j w_{ij}N_iN_j}. \quad (17)$$

242 We use equations 13 and 14 to derive the rightmost-side of equation 17. It
 243 should be noted that F_{st} is also time-invariant, as with $\log(H_{ii,t}/H_{jj,t})$.

244 *2.1.4. Effective population size*

245 As in Felsenstein (1971), we formulate effective population size N_e using
246 the dominant eigenvalue η . The probability of non-identical-by-descent of
247 the overall population decreases with the rate of $1/(2N_e)$ per generation
248 time (Crow and Kimura, 1970).

$$H_{t+T} = \left(1 - \frac{1}{2N_e}\right) H_t, \quad (18)$$

249 where T is generation time and is defined as the mean age of net fecundity
250 in the cohort (Carey & Roach, 2020, see Supporting Information 1.3 for
251 details). Considering that H_t changes with the rate of η per year (equation
252 15), $1 - 1/(2N_e)$ should be equivalent to η^T . Therefore, We formulate N_e as
253 follows.

$$N_e = \frac{1}{2(1 - \eta^T)} \quad (19)$$

254 To sum up, demographic genetic structure and effective population size
255 are derived from the leading right eigenvector and from the dominant eigen-
256 value of matrix \mathbf{M} , respectively. Therefore, our matrix model integrates
257 the two proxies of the temporal genetic dynamics, facilitating comprehensive
258 understandings on demographic genetic structure.

259 *2.2. Validation of the model*

260 To ensure that our model was formulated adequately, we compared the-
261 oretically obtained η and demographic genetic structure with observed ones
262 computed by stochastic simulation. We arranged a set of life histories to
263 be used for the comparison between theory and simulation. We considered
264 perennial plants with two ($n = 2$: juvenile and adult) and three stages ($n = 3$:

265 seed, juvenile, and adult; Figure 2). Equation 10 can be rewritten as follows.

$$\begin{pmatrix} H_{11,t} \\ H_{22,t} \\ H_{12,t} \end{pmatrix} = \mathbf{M}_2 \begin{pmatrix} H_{11,t-1} \\ H_{22,t-1} \\ H_{12,t-1} \end{pmatrix}, \quad (20)$$

266 and

$$\begin{pmatrix} H_{11,t} \\ H_{22,t} \\ H_{33,t} \\ H_{12,t} \\ H_{23,t} \\ H_{13,t} \end{pmatrix} = \mathbf{M}_3 \begin{pmatrix} H_{11,t-1} \\ H_{22,t-1} \\ H_{33,t-1} \\ H_{12,t-1} \\ H_{23,t-1} \\ H_{13,t-1} \end{pmatrix}. \quad (21)$$

267 Equation 20 and 21 correspond to the case of $n = 2$ and $n = 3$, respectively.
 268 The elements of \mathbf{M}_2 and \mathbf{M}_3 are functions of demographic rates (t_{ij} , f_{ij}) and
 269 the number of individuals in each stage (N_i , see Supporting Information 2 for
 270 details). For each of the two- and the three-stage model, we randomly gen-
 271 erated five hundreds life histories which differed in t_{ij} , f_{ij} , and N_j , covering
 272 a wide range of life history strategies (Figure S1). We indirectly determined
 273 parameter values of t_{ij} , f_{ij} , and N_j . Firstly, the total population size N was
 274 set to 100, and then N was randomly divided into all possible survival and
 275 reproduction paths (i.e., $t_{ij}N_j$ and $f_{ij}N_j$). In the case of the two-stage model,
 276 for example, 100 individuals were randomly split into five paths: stasis at
 277 juvenile, growth from juvenile to adult, retrogression from adult to juvenile,
 278 stasis at adult, and reproduction (Figure 2a). Next, N_i was calculated by
 279 $\sum_{i=1}^n (t_{ij}N_j + f_{ij}N_j)$, and finally t_{ij} and f_{ij} were calculated by $t_{ij}N_j/N_j$ and
 280 $f_{ij}N_j/N_j$ respectively (see Supporting Information 3 for details). By deter-

281 mining $t_{ij}N_j$ and $f_{ij}N_j$ first, we could easily search the parameter space while
 282 keeping the number of individuals (i.e., N_i , $t_{ij}N_j$, and $f_{ij}N_j$ for all i and j)
 283 to be always integer. To consider the situation of $N = 500$ and $N = 1,000$,
 284 we multiplied N_1 and N_2 (when $n = 3$, N_3 as well) by 5 and 10 while keeping
 285 demographic rates unchanged. In total, we considered 1,500 sets of parame-
 286 ter values (500 sets of demographic rates \times 3 sets of N) for each of the two-
 287 and the three-stage model.

288 For each parameter set, we simulated 200 years of temporal dynamics
 289 of expected heterozygosity at a neutral biallelic locus 100 times. We calcu-
 290 lated the mean expected heterozygosity over the 100 replicates for the overall
 291 population and for all the two-stage pairs at every t , which were denoted as
 292 \hat{H}_t and $\hat{H}_{ij,t}$, respectively. All simulations were initiated with maximum ex-
 293 pected heterozygosity, in which two alleles share the gene pool half-and-half
 294 in all stages (i.e., $H_0 = H_{ij,0} = 0.5$ for all i and j). It should be noted that the
 295 initial state of equal gene frequencies among classes corresponds to a genetic
 296 equilibrium under no evolutionary forces (i.e., drift, selection, mutation and
 297 gene flow) (Charlesworth, 1994). Therefore, it could be said that our simu-
 298 lation results reflected how genetic drift solely decreased genetic diversity in
 299 stage-structured populations.

300 We calculated the annual change rate of \hat{H}_t by

$$r_t = \frac{\hat{H}_t}{\hat{H}_{t-1}}, \quad (22)$$

301 where $1 \leq t \leq 200$. We took logarithm of r_t and calculated its mean and
 302 standard error, which were subsequently compared to η . η is the theoretical
 303 counterpart r_t and was obtained as the dominant eigenvalue of matrix \mathbf{M}_2
 304 or \mathbf{M}_3 .

305 Using simulation results, we also calculated the mean of demographic
306 genetic structure over the 200 years. As for the two-stage model, we cal-
307 culated $\log(\hat{H}_{11,t}/\hat{H}_{22,t})$. We calculated $\log(\hat{H}_{11,t}/\hat{H}_{22,t})$, $\log(\hat{H}_{22,t}/\hat{H}_{33,t})$ and
308 $\log(\hat{H}_{11,t}/\hat{H}_{33,t})$ in the case of the three-stage model. These four proxies
309 of observed demographic genetic structures were compared to theoretical
310 counterparts, that is, $\log(H_{11,t}/H_{22,t})$ for the two-stage model, as well as
311 $\log(H_{11,t}/H_{22,t})$, $\log(H_{22,t}/H_{33,t})$ and $\log(H_{11,t}/H_{33,t})$ for the three-stage model.
312 These four logarithmic ratios were obtained by solving the leading right eigen-
313 vector of \mathbf{M}_2 and \mathbf{M}_3 and substituting their elements to equation 16.

314 *2.3. Analysis on demographic genetic structure*

315 For the same 3,000 parameter sets as “Validation of the model” section,
316 we analytically obtained η and N_e , which reflect the change rate of all $H_{ij,t}$ per
317 year and per generation, respectively. η was obtained by solving the dominant
318 eigenvalue of \mathbf{M}_2 and \mathbf{M}_3 . Then, using η , we obtained N_e based on equation
319 19. We examined if η and N_e , both of which genuinely represent temporal
320 dynamics of genetic diversity, were correlated with the four logarithmic ratios
321 that stood for demographic genetic structure (i.e., $\log(H_{11,t}/H_{22,t})$ for the
322 two-stage model, and $\log(H_{11,t}/H_{22,t})$, $\log(H_{22,t}/H_{33,t})$ and $\log(H_{11,t}/H_{33,t})$
323 for the three-stage model) to judge if demographic genetic structure could
324 serve as a proxy for temporal dynamics of genetic diversity across a wide
325 range of life history strategies.

326 Moreover, to explore basic behaviors of demographic genetic structure, we
327 analyzed the dependence of demographic genetic structure on total popula-
328 tion size N and stable stage distribution. Stable stage distribution was quan-
329 tified by the logarithm of the ratio among N_1 , N_2 , and N_3 (i.e., $\log(N_1/N_2)$),

330 $\log(N_2/N_3)$, and $\log(N_1/N_3)$.

331 **3. Results**

332 *3.1. Validation of the model*

333 The rate of change in expected heterozygosity of the overall populations
334 (r_t), which was computed by simulation, took almost exactly the same value
335 as the theoretical counterpart η for all 1,500 sets of parameter values in both
336 the two- and the three-stage models (Figure 3, S2).

337 Comparison of demographic genetic structure between simulation and
338 analytical results revealed that our theoretical model yielded almost equiv-
339 alent logarithmic ratio of expected heterozygosity among stages to that of
340 simulation (Figure 4, S3, S4).

341 To further confirm the validity of our model, we checked the temporal
342 dynamics of $\hat{H}_{ij,t}$ and compared it with theoretical expectation, that is, the
343 repeated multiplication of matrix \mathbf{M}_2 or \mathbf{M}_3 to \mathbf{h}_t . We found that theoretical
344 prediction fitted well to simulation results (Figure S5).

345 Thus, our model seems to describe the dynamics and the inter-stage ratio
346 of expected heterozygosity validly across a wide range of parameter space.

347 *3.2. Analysis on demographic genetic structure*

348 All the four proxies of demographic genetic structure, which are theoret-
349 ically obtained based on equation 16, have an apparent correlation neither
350 with N_e nor with η regardless of N (Figure 5, S6-10). On the other hand,
351 demographic genetic structure is clearly associated with total population
352 size N . As N increases, all the four logarithmic ratios gradually converge

353 to zero, which means that expected heterozygosity becomes equal among
354 stages (Figure 6). Moreover, there is a strong positive correlation with sta-
355 ble stage distribution: expected heterozygosity is higher in stages with more
356 individuals (Figure 7). The correlation becomes weaker with increasing N ,
357 as logarithmic ratios converge to zero.

358 4. Discussion

359 *4.1. Comparison with the age-structured model*

360 In this study, we develop the matrix model that describes the dynamics
361 of genetic diversity and demographic genetic structure in stage-structured
362 populations. Although the procedures of model development are similar to
363 the age-structured model in Felsenstein (1971), our model has a much wider
364 applicability. First of all, because age-structured models, in which the proba-
365 bilities of stasis and retrogression are zero, is a special case of stage-structured
366 models, our model is more comprehensive. Besides, many plant species do not
367 show demographic senescence (Jones et al., 2014), showing no age-dependent
368 changes in demographic rates. Using stage-dependent demographic parame-
369 ters would be more appropriate and predictive in plant populations. These
370 points support the novelty of our stage-structured model, especially in terms
371 of expanding the applicability to many plant species.

372 *4.2. Interpreting demographic genetic structure*

373 A common interpretation on demographic genetic structure is that if ju-
374 venile stages are less diverse than mature stages, genetic diversity would
375 decrease with time over the course of generation turnover (Aldrich et al.,

376 1998; Ally and Ritland, 2006; Kettle et al., 2007; Linhart et al., 1981; Mur-
377 ren, 2003; Schmidt et al., 2018; Vranckx et al., 2014). However, our model
378 shows that relative ratio of expected heterozygosity between stage classes
379 does not correlate with either N_e or η : even though N_e and η are small,
380 expected heterozygosity does not necessarily decline from mature to juve-
381 nile stages. Therefore, inferring temporal trends in genetic diversity solely
382 from demographic genetic structure is potentially misleading. This study, to
383 our knowledge, for the first time draws caution on the conventional use of
384 demographic genetic structure.

385 Many previous empirical studies that analyzed demographic genetic struc-
386 ture found that genetic diversity did not decrease from the most mature to
387 the most immature stages and took comparable values among stages (Aldrich
388 et al., 1998; Ally and Ritland, 2006; Kettle et al., 2007; Linhart et al., 1981;
389 Murren, 2003; Schmidt et al., 2018; Vranckx et al., 2014). Our model shows
390 that the logarithmic ratio of expected heterozygosity is distributed around
391 zero, especially under large N , indicating that expected heterozygosity is ba-
392 sically almost equivalent to one another. Therefore, our model might be in
393 line with previous empirical results.

394 While demographic genetic structure is irrelevant to temporal dynamics,
395 it is tightly linked to stable stage distribution: expected heterozygosity is
396 relatively high in stage with more individuals, and low in stage with less
397 individuals (Figure 6). In general, small number of individuals intensifies
398 stochastic genetic drift due to increased sampling bias in gene frequencies,
399 leading to the loss of genetic diversity (Crow and Kimura, 1970). When stage
400 distribution is skewed, the degree of stochasticity will vary among stages.

401 Stage with smaller number of individuals is made up of genes that were
402 sampled fewer times from the gene pool of the previous year, thus suffering
403 random perturbation in gene frequencies to a greater extent. The alleviated
404 stochasticity must have resulted in the lower genetic diversity in stages with
405 fewer individuals.

406 As the total population size N increases, inter-stage difference in genetic
407 diversity disappears even under the skewed stage distribution (Figure 7).
408 This result indicates that the number of individuals of each stage is large
409 enough to reduce stochasticity under large N , leading to comparable level of
410 genetic diversity among stages. Large population size also contributes to the
411 maintenance of genetic diversity, because N_e increases and η approaches to
412 1 with increasing N (Figure S11).

413 To sum up, it can be said that genetic diversity becomes uneven among
414 life history stages under small population size and that the unevenness among
415 stages reflects stable stage distribution rather than the temporal dynamics
416 of genetic diversity.

417 *4.3. Future application of our model*

418 Our model not only provides theoretical background of demographic ge-
419 netic structure, but also has some potential for application. One possible ap-
420 plication is to compare raw demographic genetic structure, which is obtained
421 by any neutral genetic markers, with the theoretical expectation calculated
422 based on the equations we derived. The deviations of observed structure
423 from expectation reflect factors unexplored in our model, such as fluctuating
424 population size, non-random mating, selection, and immigration. Thus, our
425 model can work as a null model of demographic genetic structure. To make

426 the most use of our equations, it is necessary to monitor individuals from year
427 to year to estimate demographic rates of each stage class. If long-term demo-
428 graphic monitoring is unavailable or impractical for some reasons, recording
429 relative number of individuals among stage classes at a single time point
430 would be at least desirable to consider stage distribution, which turned out
431 to be a major determinant of demographic genetic structure in our model.

432 Instead of demographic genetic structure, we want to pay attention to
433 the efficacy of η , which is the annual change rate of the probability of non-
434 identical-by-descent and represents the dynamics of expected heterozygosity
435 well. η can be potentially useful for population viability assessment. Whether
436 population size can be maintained over time (i.e., population growth rate
437 remains high) is considered as a criterion of long-term population persistence
438 (Hens et al., 2017; Knight et al., 2009). Demographic rates have been used to
439 calculate population growth rate per year (usually denoted as λ) by solving
440 the eigenvalue problem of matrix population models (equation 3) (Caswell,
441 2001; Crone et al., 2011). While it is acknowledged that not only population
442 size but also genetic diversity should be maintained for long-term population
443 persistence, there has been no counterpart of population growth rate that
444 can evaluate the change rate of genetic diversity per year (not per generation
445 time). Being a change rate per year, η is directly linked to temporal change
446 in genetic diversity compared to demographic genetic structure and effective
447 population size, and enables us to assess genetic diversity at the same time
448 scale as population dynamics. Therefore, η can serve as the counterpart of
449 λ and can be an useful proxy to evaluate population viability from genetic
450 point of view. It should be noted that we evaluated expected heterozygosity

451 using the probability of non-identical-by-descent in our model. Because this
452 replacement is based on the assumption of no mutation, our results should
453 be applied to a prediction on a time scale, in which *de novo* mutations do not
454 spread throughout the overall population. Evaluating η for a variety types
455 of structured populations will be a future step to make the best use of our
456 model.

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461 **Declaration of Competing Interest**

462 The authors declare no competing interest.

463 **Author Contributions**

464 **Yoichi Tsuzuki:** Conceptualization, Methodology, Investigation, Writ-
465 ing - original draft. **Takenori Takada:** Investigation, Writing - review &
466 editing. **Masashi Ohara:** Writing - review & editing.

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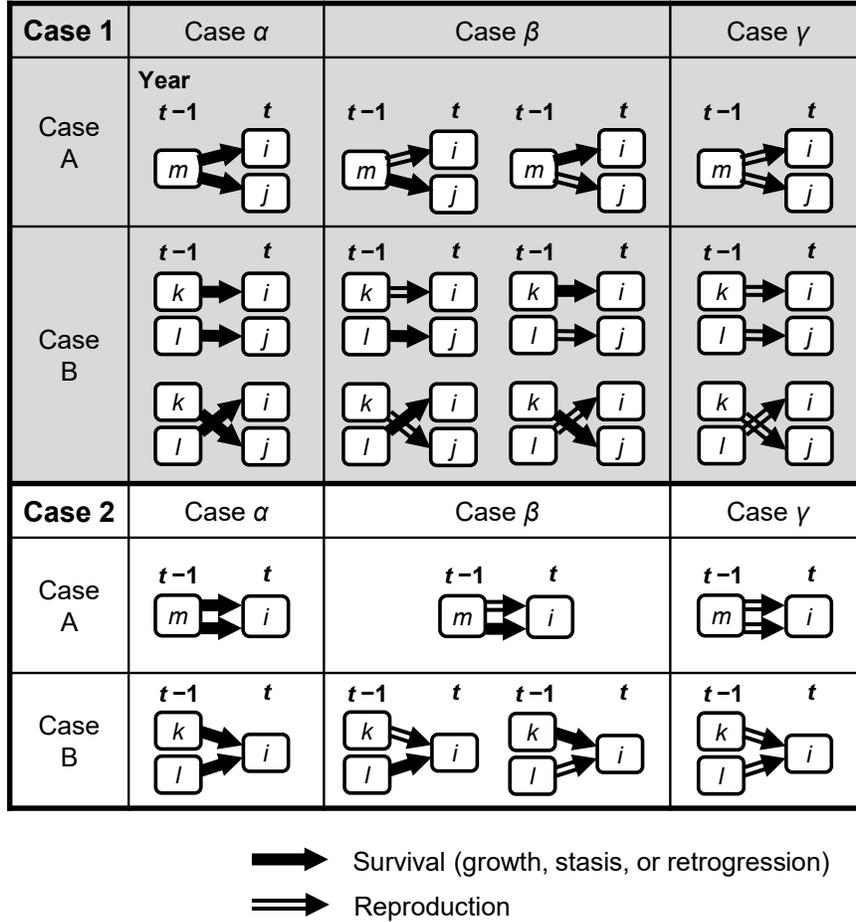


Figure 1: Temporal trajectories from time $t-1$ to t with regard to the two genes sampled in time t . Rounded rectangles stand for life history stages. Arrows stand for the temporal movements of genes either by survival (single line) or reproduction (double line). There are 12 mutually exclusive situations based on three criteria: (1) whether the destinations are different (case 1, shown on gray background) or not (case 2, shown on white); (2) whether the origins are the same (case A) or not (case B); (3) how the two genes were transferred (case α : survival; case β : survival and reproduction; case γ : reproduction)

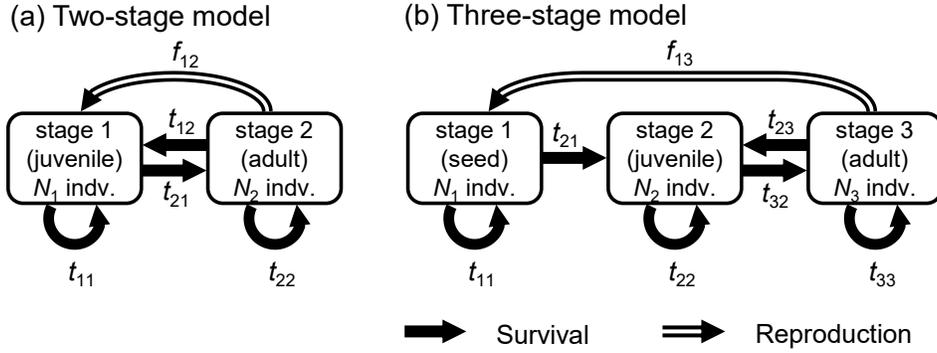


Figure 2: The two model used in analysis: (a) two-stage model and (b) three stage model. Arrows represent flow of individuals, or genes, either by survival (single line) or reproduction (double line)

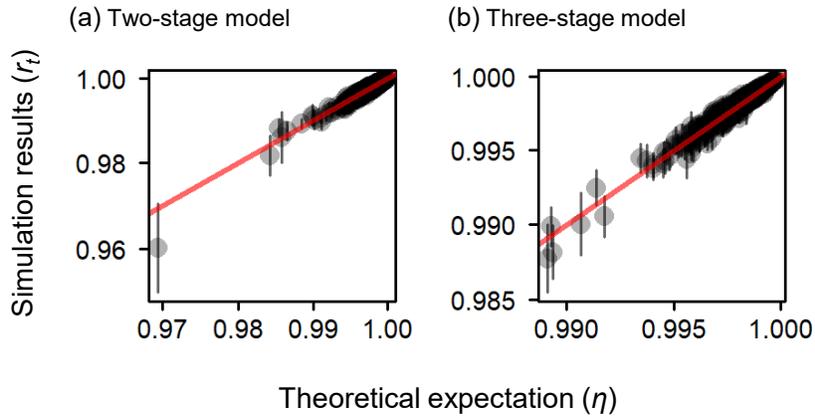


Figure 3: Comparison between the theoretical expectation of the annual change rate of the probability of non-identical-by-descent (η) and the simulation results of that of expected heterozygosity (r_t) for (a) the two-stage and (b) the three-stage model when $N = 100$. Each gray semi-transparent point corresponds to one of the 500 parameter sets. As for r_t , geometric mean over $1 \leq t \leq 200$ is shown with standard error (vertical bar). Red lines represent $\eta = r_t$

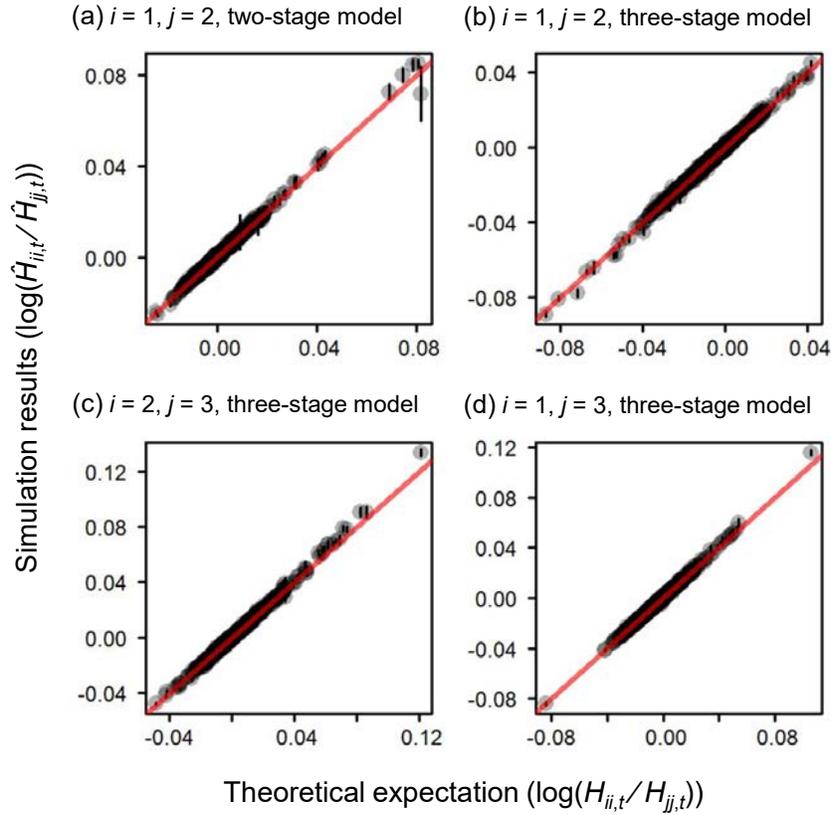


Figure 4: Comparison of demographic genetic structure between the theoretical expectations ($\log(H_{ii,t}/H_{jj,t})$) and the simulation results ($\log(\hat{H}_{ii,t}/\hat{H}_{jj,t})$) when $N = 100$. Each gray semi-transparent point corresponds to one of the 500 parameter sets. As for the simulation results, mean and standard error (vertical bar) over $1 \leq t \leq 200$ are shown. There is one proxy for the two-stage model (a: $i = 1$ and $j = 2$), while there are three proxies for the three-stage model (b: $i = 1$ and $j = 2$; c: $i = 2$ and $j = 3$; d: $i = 1$ and $j = 3$). The theoretical expectations exactly match with the simulation results when plotted on the red lines

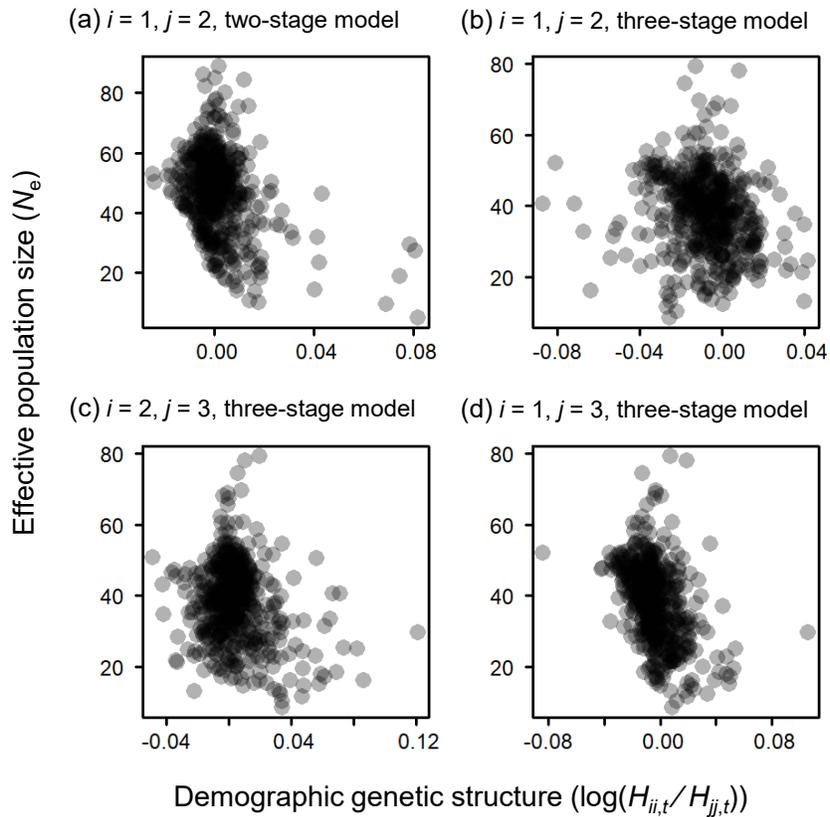


Figure 5: Comparison of demographic genetic structure ($\log(H_{ii,t}/H_{jj,t})$) with effective population size (N_e) when $N = 100$. (a) $i = 1$ and $j = 2$ of the two-stage model, (b) $i = 1$ and $j = 2$, (c) $i = 2$ and $j = 3$, (d) $i = 1$ and $j = 3$ of the three-stage model

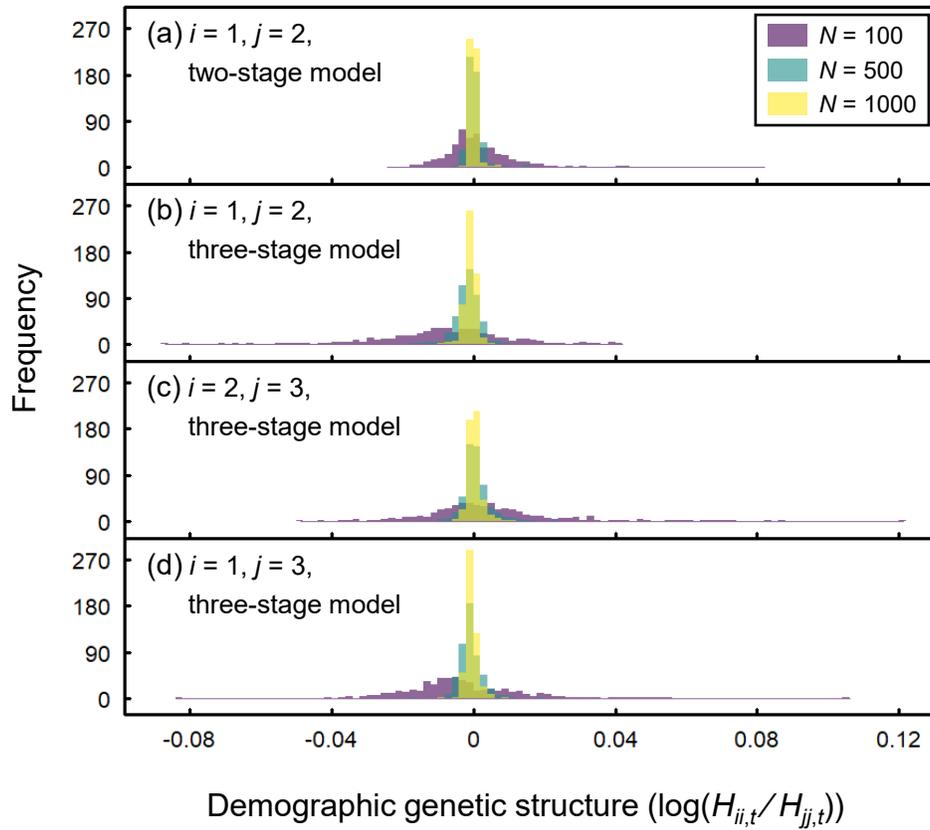


Figure 6: Histogram of demographic genetic structure ($\log(H_{ii,t}/H_{jj,t})$) with varying N . (a) $\log(H_{11,t}/H_{22,t})$ of the two-stage model, (b) $\log(H_{11,t}/H_{22,t})$, (c) $\log(H_{22,t}/H_{33,t})$, (d) $\log(H_{11,t}/H_{33,t})$ of the three-stage model

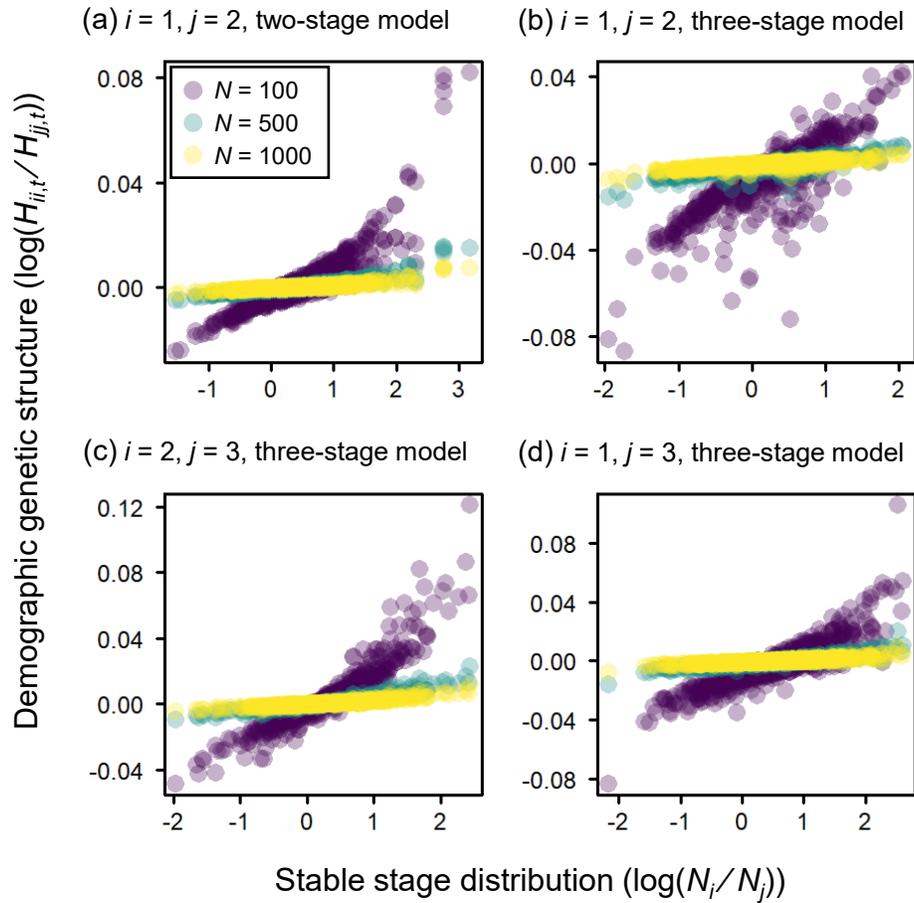


Figure 7: Relationships between stable stage distribution ($\log(N_i/N_j)$) and demographic genetic structure ($\log(H_{ii,t}/H_{jj,t})$) with varying N .

Corrigendum

Corrigendum to ‘Modeling temporal dynamics of genetic diversity in stage-structured plant populations with reference to demographic genetic structure’
[Theoretical Population Biology 148 (2022) 76-85]

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The authors regret that there are typographical errors in the summation operators in Eqs. (5), (6), (8), and (9). In analogous to the age-structured model of Felsenstein (1971), $H_{ij,t}$ (or $H_{kl,t}$) could be also written as $H_{ji,t}$ (or $H_{lk,t}$). Although we consistently used $H_{ij,t}$ ($i \leq j$) when deriving the matrix equation to avoid the redundant notation, as in Eqs. (20) and (21), we mistakenly wrote the range of i and j of the two successive summation operators in the fourth to sixth lines of Eq. (5), the second line of Eq. (6), the fourth to sixth lines of Eq. (8), and the third line of Eq. (9). We corrected these lines to avoid duplicate summations for the same two stages as follows.

$$\begin{aligned}
 H_{ij,t|1 \cap A \cap \alpha} &= \sum_{m=1}^n \left\{ \frac{t_{im}t_{jm}N_m^2}{N_iN_j} \times \frac{1}{1 - 1/(2N_m)} H_{mm,t-1} \right\} \\
 H_{ij,t|1 \cap A \cap \beta} &= \sum_{m=1}^n \left\{ \frac{(t_{im}f_{jm} + f_{im}t_{jm})N_m^2}{N_iN_j} \times H_{mm,t-1} \right\} \\
 H_{ij,t|1 \cap A \cap \gamma} &= \sum_{m=1}^n \left\{ \frac{(f_{im}f_{jm}N_m^2)}{N_iN_j} \times H_{mm,t-1} \right\} \\
 H_{ij,t|1 \cap B \cap \alpha} &= \sum_{k=1}^{n-1} \sum_{l=k+1}^n \left\{ \frac{(t_{ik}t_{jl} + t_{il}t_{jk})N_kN_l}{N_iN_j} \times H_{kl,t-1} \right\} \\
 H_{ij,t|1 \cap B \cap \beta} &= \sum_{k=1}^{n-1} \sum_{l=k+1}^n \left\{ \frac{(t_{ik}f_{jl} + f_{ik}t_{jl} + t_{il}f_{jk} + f_{il}t_{jk})N_kN_l}{N_iN_j} \times H_{kl,t-1} \right\} \\
 H_{ij,t|1 \cap B \cap \gamma} &= \sum_{k=1}^{n-1} \sum_{l=k+1}^n \left\{ \frac{(f_{ik}f_{jl} + f_{il}f_{jk})N_kN_l}{N_iN_j} \times H_{kl,t-1} \right\}.
 \end{aligned} \tag{5}$$

$$\begin{aligned}
 H_{ij,t} &= \sum_{m=1}^n \frac{N_m^2}{N_iN_j} \left\{ \frac{t_{im}t_{jm}}{1 - 1/(2N_m)} + f_{im}t_{jm} + t_{im}f_{jm} + f_{im}f_{jm} \right\} H_{mm,t-1} \\
 &\quad + \sum_{k=1}^{n-1} \sum_{l=k+1}^n \frac{N_kN_l}{N_iN_j} (a_{ik}a_{jl} + a_{il}a_{jk}) H_{kl,t-1}.
 \end{aligned} \tag{6}$$

$$\begin{aligned}
H_{ii,t|2nA\alpha} &= \sum_{m=1}^n \left\{ \left(\frac{t_{im}N_m}{N_i} \right)^2 \times \frac{1 - 1/(2t_{im}N_m)}{1 - 1/(2N_m)} H_{mm,t-1} \right\} \\
H_{ii,t|2nA\beta} &= \sum_{m=1}^n \left(\frac{2t_{im}f_{im}N_m^2}{N_i^2} \times H_{mm,t-1} \right) \\
H_{ii,t|2nA\gamma} &= \sum_{m=1}^n \left\{ \left(\frac{f_{im}N_m}{N_i} \right)^2 \times \left(1 - \frac{1}{2f_{im}N_m} \right) H_{mm,t-1} \right\} \\
H_{ii,t|2nB\alpha} &= \sum_{k=1}^{n-1} \sum_{l=k+1}^n \left(\frac{2t_{ik}t_{il}N_kN_l}{N_i^2} \times H_{kl,t-1} \right) \\
H_{ii,t|2nB\beta} &= \sum_{k=1}^{n-1} \sum_{l=k+1}^n \left\{ \frac{2(t_{ik}f_{il} + f_{ik}t_{il})N_kN_l}{N_i^2} \times H_{kl,t-1} \right\} \\
H_{ii,t|2nB\gamma} &= \sum_{k=1}^{n-1} \sum_{l=k+1}^n \left(\frac{2f_{ik}f_{il}N_kN_l}{N_i^2} \times H_{kl,t-1} \right).
\end{aligned} \tag{8}$$

$$\begin{aligned}
H_{ii,t} &= \sum_{m=1}^n \left\{ \left(\frac{t_{im}N_m}{N_i} \right)^2 \frac{1 - 1/(2t_{im}N_m)}{1 - 1/(2N_m)} + \frac{2t_{im}f_{im}N_m^2}{N_i^2} \right. \\
&\quad \left. + \left(\frac{f_{im}N_m}{N_i} \right)^2 \left(1 - \frac{1}{2f_{im}N_m} \right) \right\} H_{mm,t-1} \\
&\quad + \sum_{k=1}^{n-1} \sum_{l=k+1}^n \frac{2a_{ik}a_{il}N_kN_l}{N_i^2} H_{kl,t-1}.
\end{aligned} \tag{9}$$

The same correction applies to the two successive summation operators in Eqs. S15-S18, S23-S25, and S31-32 in the Supporting Information. The analytical results in the original paper are not impacted by the error because the results were obtained based on the correct equations shown in this corrigendum.

The authors would like to apologise for any inconvenience caused.

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