How to compute the effective size of spatiotemporally structured populations using separation of time scales

Yutaka Kobayashi*, Norio Yamamura

Center for Ecological Research, Kyoto University, Otsu, Shiga 520-2113, Japan

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Abstract

Calculations to derive effective population size become highly complicated when complex population structure is considered. We provide an easy method of computing the effective size of a subdivided population with overlapping generations (a spatiotemporally structured population) using an approximation based on separation of time scales. We also numerically compute the effective size to verify the accuracy of the derived formula. Various interesting quantities, including moments of coalescent time, are readily derived using this approach.

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1. Introduction

One of the key concepts in population genetics is the notion of effective population size (N_e). Among the several definitions of N_e, "inbreeding effective size" in particular is defined as the size of the Wright-Fisher idealized population that experiences the same rate of change in the degree of inbreeding (Crow and Kimura, 1970). In contrast to this classic "forward" view of inbreeding effective size (hereafter, we omit "inbreeding" for simplicity), the recent development of coalescent theory (Kingman, 1982a–c; Hudson, 1983; Tajima, 1983; for reviews, see Donnelly and Tavare, 1995; Nordborg, 2001; Wakeley, 2004) has provided a "backward" interpretation, which may be viewed as the reciprocal of the rate of coalescence of two sample lineages per generation (e.g., Rousset, 2004; Hein et al., 2005). Regardless of the viewpoint, the concept of effective size enables us to apply studies of an idealized population to the investigation of non-ideal populations with various complex structures. Since the pioneering work of Wright (1931), population geneticists have derived many formulae

to calculate effective size under a variety of assumptions, such as separate sexes, non-random contribution of gametes from parents to offspring, or temporally fluctuating population size (for a review, see Caballero, 1994).

In particular, the effective sizes of subdivided populations have interested population geneticists (Chesser et al., 1993; Sugg and Chesser, 1994; Wang, 1997a, b; Whitlock and Barton, 1997; Nunney, 1999; Wang, 1999; Wang and Caballero, 1999). Researchers have also explored the effect of within-subpopulation structure, such as overlapping generations (Felsenstein, 1971; Hill, 1972, 1979; Johnson, 1977; Choy and Weir, 1978; Pollak, 1980, 1990, 2000). Both of these factors significantly affect effective population size. Because many populations in the natural world have simultaneous spatial and age structures, an understanding of their joint effects is important. Rousset (1999) first calculated genetic differentiation and effective size in spatially structured populations (both island-like and stepping-stone populations) with general within-subpopulation class structure. However, the simultaneous consideration of both within-subpopulation and spatial structures entails large and highly complicated calculations.

Here, we present an easy method of calculating the effective size of a spatiotemporally structured population

*Corresponding author. Fax: +81 77 549 8201.
E-mail address: yutaka@ecology.kyoto-u.ac.jp (Y. Kobayashi).

using an approximation based on "separation of time scales" (Nordborg, 1997, 2001; Wakeley and Aliacar, 2001; Nordborg and Krone, 2002). Separation of time scales assumes that the rates of some processes ("fast" processes) are much quicker than those of others ("slow" processes); this method has been successful in reducing a structured coalescent process to (1) an unstructured process (e.g., Nordborg, 1997; see also Nagylaki, 1980), (2) a process very similar to unstructured coalescent (Nordborg and Donnelly, 1997; Möhle, 1998; Wakeley and Aliacar, 2001), or (3) a structured coalescent process with reduced complexity (Nordborg, 1997; Nordborg and Krone, 2002). Our model corresponds to the third case.

2. Theory

We consider a structured coalescent process in a diploid hermaphrodite population subdivided into s subpopulations with overlapping generations. Except for spatial subdivision and migration, this population is essentially the same as that considered in some previous studies (e.g., Felsenstein, 1971; Hill, 1972; Johnson, 1977). The life cycle of the organism is as follows: At any given year, individuals born i years ago are referred to as "age-i individuals," where the lowest age is one. Every subpopulation has N_i individuals of age i. We assume that the demographic structure is in equilibrium, so that N_i does not change over time. Because the size of a cohort does not increase with age, $N_i \geqslant N_j$ when $i < j$. Thus, N_i/N_j gives the survival rate from age j to age i. Every year, reproduction and aging occur, followed by migration.

In the reproductive process, mating occurs within each subpopulation. We assume that a gene of a newborn comes from an age-i individual with probability p_i. This means that an age-i individual is invited to a single mating event with probability p_i/N_i. Therefore, an age-i individual mates with itself with probability p_i/N_i. Note that $\sum_{i=1}^n p_i = 1$, where n is the maximum reproductive age. This setting gives the following transition probability matrix for age transition:

$$\begin{pmatrix} p_1 & p_2 & p_3 & \cdots & p_i & \cdots & p_n \\ 1 & & & & & & \\ & 1 & & & & & \\ & & 1 & & & & \\ & & & 1 & & & \\ & & & & \ddots & & \\ & & & & & 1 & 0 \end{pmatrix}, \tag{1}$$

where the (i,j)th element gives the probability that a gene in age i came from age j in the previous year. Note that the subdiagonal elements are all unity and elements in white space are all zero. This is because a gene of an age-i individual comes from an age-$(i-1)$ individual, i.e., the same individual, with probability one, unless the individual is a newborn ($i=1$). There may be non-

reproductive age classes for which $p_i = 0$. We just suppose that the above matrix is irreducible and aperiodic, which is usually the case, and ensures ergodicity (Nagylaki, 1980). After reproduction, the ages of all individuals increase by one.

Migration then occurs. $N_i m_i$ individuals of age i in each subpopulation are randomly dispersed to the other $s-1$ subpopulations; thus, m_i is the migration rate of age-i individuals. We assume that at least some m_i's are non-zero, so that subpopulations are not entirely isolated. Moreover, we assume "conservative migration," which means the number of immigrants is exactly the same as that of emigrants for each age (Nagylaki, 1980). After the migration phase, the next year begins.

To calculate the effective size, we consider the backward fate of a sample of two genes drawn from the population. For this purpose, we consider the probability that the lineages of the sample genes do not coalesce at least within a given number of years, which we refer to as the "non-coalescence probability." From the definition, the non-coalescence probability is equivalent to the distribution function of the coalescent time. We decompose the non-coalescence probability into two components. First, $H(t)$ is the probability that the two lineages are still separated and in the same subpopulation in year t (we count years backward, so that, for example, $t=0$ and ∞ mean the current year and the infinitely distant past, respectively). Second, $A(t)$ is the probability that the two lineages are still separated and in different subpopulations. Thus, the total non-coalescence probability is given by $H(t) + A(t)$. We further decompose the above two probabilities, although we use this sub-decomposition only for numerical calculation. We define $I_i(t)$ as the probability that the lineages are separated in the same individual of age i. We define $H_{ij}(t)$ as the probability that the lineages are separated in two individuals of ages i and j in the same subpopulation. We define $A_{ij}(t)$ in a similar manner. From the definitions, $H(t) = \sum_i I_i(t) + \sum_{ij} H_{ij}(t)$ and $A(t) = \sum_{ij} A_{ij}(t)$. Note that we did not specify the initial sample configuration, but instead, focused on the ancestral configuration. In this point, our method differs from some prior works, which focused on the initial sample configuration (Slatkin, 1991; Wilkinson-Herbots, 1998). In our setting, the initial sample configuration is specified by the initial condition of the non-coalescence probabilities; that is, for example, $H_{ij}(0) = 1$ means that the two genes were sampled from two individuals of age i and age j in the same subpopulation.

Because we do not assume mutation, the non-coalescence probability $H(t) + A(t)$ decreases with t because of year-to-year coalescence. Once the decreasing rate $[H(t+1) + A(t+1)]/[H(t) + A(t)]$ asymptotically converges on a value, denoted by λ, N_e is calculated from the following relationship (Felsenstein, 1971):

$$N_e = \frac{1}{2T(1-\lambda)}, \tag{2}$$

where T is the "generation time." Roughly speaking, T represents the length of one generation cycle (for a precise definition of T, see Felsenstein, 1971; Johnson, 1977; see also Eq. (7)). From the "forward" viewpoint, λ is equal to the largest non-unit eigenvalue of the transition matrix that gives the change in probabilities of identity by descent between genes of various ages (e.g., Johnson, 1977; Rousset, 2004). We may refer to the effective size given by the above equation as the "asymptotic" effective size to distinguish it from the "instantaneous" effective size, which we define as

$$N_{e,t} = \frac{1}{2T(1 - (H(t+1) + A(t+1))/(H(t) + A(t)))}. \quad (3)$$

Obviously, when t approaches infinity, $N_{e,t}$ must converge on N_e. $N_{e,t}$ is as important as N_e because it can measure the rate of recent coalescence. When there is no confusion, we use "effective size" to mean the asymptotic effective size. Hereafter, we mainly consider a continuous-time approximation, assuming t is a continuous variable. In this case, we may replace $H(t+1)$–$H(t)$ by $dH(t)/dt$ (and treat $A(t)$ similarly), so that the instantaneous effective size is given as

$$N_{e,t} = \frac{H(t) + A(t)}{-2T((dH(t)/dt) + (dA(t)/dt))} \quad (4)$$

and the asymptotic effective size is given as the limit of the above expression where t approaches infinity. From Eq. (4), we have $(d/dt)[H(t)+A(t)] = -(1/2N_{e,t}T)[H(t)+A(t)]$, meaning that the per-year rate of coalescence in year t is given by $1/2N_{e,t}T$, which converges on $1/2N_eT$ under $t \to \infty$.

Now, we show how to calculate the instantaneous and asymptotic effective size using an approximation based on separation of time scales (Nordborg, 1997, 2001; Wakeley and Aliacar, 2001; Nordborg and Krone, 2002). We assume that all migration rates are very low ($m_i \ll 1$) and all age classes are very large in size ($N_i \gg 1$). In the original Wright's island model, if migration occurs on a faster time scale than within-island coalescence, the entire process fully collapses to Kingman's coalescent with appropriate rescaling of the time unit (Wakeley, 2004; Sjödin et al., 2005); this means that sample lineages are exchangeable and that the "coalescent effective size" exists (Nordborg and Krone, 2002; Sjödin et al., 2005). On the other hand, if migration occurs on a slower time scale than within-island coalescence, the process again reduces to Kingman's process, except for the initial short phase, whose span is negligible for the entire process (Wakeley, 2004). We are interested in a situation lying between these two, where the process does not collapse to Kingman's coalescent (Notohara, 1990; Nordborg, 1997; Wilkinson-Herbots, 1998; Nordborg and Krone, 2002). We assume that the following limits exist for all $i \leqslant n$:

$$0 < \lim_{N_s \to \infty} \frac{N_i}{N_s} = a_i < 1 \quad (5a)$$

and for all non-zero m_i:

$$0 < \lim_{N_s \to \infty} m_i N_s = \mu_i < +\infty, \quad (5b)$$

where $N_s = \sum_{n=1}^{n} N_i$, i.e., the total size of a subpopulation. The existence of these limits ensures that migration and coalescence occur on the same time scales (Nordborg, 1997; see also Sjödin et al., 2005). On the other hand, we assume that age transitions occur on a separate, faster time scale than migration and coalescence, which is ensured by

$$\lim_{N_s \to \infty} (1 - P_{ii})N_s = +\infty, \quad (5c)$$

where P_{ij} is the (i,j)th element of matrix (1). Because all diagonal elements of the matrix are 0 except for $P_{11} = p_1$, Eq. (5c) is equivalent to $\lim_{N_s \to \infty}(1 - p_1)N_s = +\infty$. Eq. (5c) means that we assume a "strong-migration limit" for age transitions (Nagylaki, 1980); that is, we consider the limit in which any slow events, i.e., migration and coalescence, do not occur before age transition reaches equilibrium. In terms of Nordborg and Krone (2002), each age group within each subpopulation is a "deme" and each subpopulation is a "cluster" of demes; migration of lineages occurs quickly within each cluster, but slowly between clusters.

We are interested in the rate of coalescence, which occurs on the slower time scale. Therefore, we can assume that the event on the faster time scale, i.e., age transition, is always in equilibrium on the slower time scale, which is the essence of separation-of-time-scales approximation. The equilibrium probability that a lineage is in an age is known as the "class reproductive value" of the age (e.g., Taylor, 1990). We denote the class reproductive value of age i as c_i. Mathematically, c_i is given by the ith component of the dominant left eigenvector of transition probability matrix (1), where the vector is normalized to satisfy $\sum_i c_i = 1$ (e.g., Taylor, 1990; Rousset, 2004). Obviously, for matrix (1), c_i is given as

$$c_i = \sum_{k=i}^{n} \frac{p_k}{T}, \quad (6)$$

where T is the "generation time," and is given as

$$T = \sum_{i=1}^{n} \sum_{k=i}^{n} p_k = \sum_{i=1}^{n} ip_i \quad (7)$$

as shown by Felsenstein (1971) and Johnson (1977). The intuitive meaning of the generation time is the expected age of a parent of a newborn, as is clear from the rightmost expression in Eq. (7). Below, we consider the slow-time-scale events, assuming that each lineage is in age i with probability c_i.

Let us consider how to calculate $H(t+dt)$ and $A(t+dt)$ from $H(t)$ and $A(t)$, where dt is a infinitesimal positive. We first show the results:

$$H(t + dt) = \{1 - 2m_e\,dt - (1/2N_{es}T)\,dt\}H(t) + (2m_e/(s-1))\,dt A(t), \quad (8a)$$

$$A(t + dt) = 2m_e\,dt H(t) + \{1 - 2m_e\,dt/(s-1)\}A(t), \quad (8b)$$

where

$$m_e = \sum_i c_i m_i \tag{8c}$$

and

$$N_{es} = \frac{T}{(1/N_1) + T^2 \sum_{i=2}^{n} c_i^2((1/N_i) - (1/N_{i-1}))}. \tag{8d}$$

We only explain Eq. (8a), since Eq. (8b) is derived analogously. The first term on the right-hand side of Eq. (8a) is the probability that the sample lineages are separated in the same subpopulation in year t and continue to be so until year $t+dt$. On the other hand, the second term is the probability that the sample lineages are separated in different subpopulations in year t and enter a single subpopulation by year $t+dt$. The first term is derived as follows. Suppose that the two lineages are in the same population in year t, which occurs with probability $H(t)$. In this case, two kinds of events can occur: migration or coalescence. Let us first consider migration. Because a lineage is in age i with probability c_i, the per-year probability that a lineage migrates is given by (8c). The quantity m_e, given by Eq. (8c), is known as the "effective migration rate" (Rousset, 1999, 2004). We can ignore the possibility that both lineages migrate during period dt because it occurs with a probability on the order of m_e^2. Therefore, the probability that the two lineages go to different subpopulations is $2(1-m_e dt)$-$m_e dt \approx 2m_e dt$. Next, to consider coalescence, let N_{es} denote the asymptotic effective size of a subpopulation. The formula for N_{es} was derived by Johnson (1977) and given by Eq. (8d). Remember that separation of time scales ensures that the within-subpopulation age transition of sample lineages is in equilibrium. Therefore, the probability that the two lineages coalesce is $(1/2N_{es}T) dt$. In summary, the probability that the two lineages continue to be separated in the same subpopulation is $1-2m_e dt-(1/2N_{es}T) dt$, from which we obtain the first term of Eq. (8a). To derive the second term, suppose that the two lineages are in different subpopulations in year t, which occurs with probability $A(t)$. In this case, coalescence never occurs. The probability that migration pushes the two lineages into the same subpopulation is $2m_e dt/(s-1)$, with small terms neglected; thus, we obtain the second term.

From Eq. (8), we readily obtain the following differential equation describing a continuous Markov chain:

$$\frac{dH(t)}{dt} = -\{2m_e + (1/2N_{es}T)\}H(t) + 2m_e(s-1)^{-1}A(t), \tag{9a}$$

$$\frac{dA(t)}{dt} = 2m_e H(t) - 2m_e(s-1)^{-1}A(t). \tag{9b}$$

Combining Eqs. (9a) and (9b) and rescaling the time unit, we have

$$\frac{d}{du}\begin{pmatrix} H(u) \\ A(u) \end{pmatrix} = \begin{pmatrix} -4Ms - s & 4Ms/(s-1) \\ 4Ms & -4Ms/(s-1) \end{pmatrix}\begin{pmatrix} H(u) \\ A(u) \end{pmatrix}, \tag{10}$$

where $u = t/2sN_{es}T$, and $M = m_e N_{es}T$ is the "effective number of migrants per generation." From Eq. (10), $d(H+A)/du = -sH$, meaning that the non-coalescence probability decreases at a rate of $-(1/2N_{es}T)H$ per year. This is reasonable because coalescence occurs only when the two lineages are in the same subpopulation, and the coalescent probability within the subpopulation is $1/2N_{es}T$. Although Eq. (10) can be readily solved, it is much more interesting to calculate the Laplace transforms of $H(u)$ and $A(u)$, given in Appendix A, because the Laplace transforms include more information about the coalescent process than the effective size (for interesting applications of Laplace transforms to a case with mutation, see Wilkinson-Herbots, 1998).

From the inverse Laplace transformation of Eq. (A.3), we obtain

$$H(u) + A(u) = \frac{1}{\alpha_2 - \alpha_1}\sum_{i=1,2}(-1)^i(\alpha_i + sA(0)$$
$$+ 4s^2 M/(s-1))\exp(\alpha_i u), \tag{11a}$$

where

$$\alpha_i = \frac{-s(4Ms/(s-1) + 1)(1 \mp \gamma)}{2} \tag{11b}$$

and α_1 and α_2 correspond to $-$ and $+$, respectively, and

$$\gamma = \sqrt{1 - \frac{16M(s-1)}{(4Ms + s - 1)^2}}. \tag{11c}$$

From Eqs. (4) and (11a), we obtain

$$N_{e,t} = -\frac{sN_{es}\sum_i(-1)^i(\alpha_i + sA(0) + 4s^2 M/(s-1))\exp(\alpha_i u)}{\sum_i(-1)^i\alpha_i(\alpha_i + sA(0) + 4s^2 M/(s-1))\exp(\alpha_i u)}. \tag{12}$$

In Appendix B, we give the exact dynamics of $I_i(t)$, $H_{ij}(t)$, and $A_{ij}(t)$ without approximation. Fig. 1 shows the comparison between the approximation by Eq. (12) and the numerical results from Eqs. (B.1) and (B.2). Demographic parameters used for the numerical calculations in Figs. 1A–C are given in Tables 1A–C, respectively. Open squares and circles show the numerical results with the initial conditions $H_{11}(0) = 1$ and $A_{11}(0) = 1$, respectively, while the smooth lines show the approximations by Eq. (12). Thus, the approximation fits the real value of $N_{e,t}$ very well (Fig. 1). The asymptotic effective size is readily given as $\lim_{t\to\infty}N_{e,t}$:

$$N_e = -\frac{sN_{es}}{\alpha_1} = \frac{2N_{es}}{(4Ms/(s-1) + 1)(1 - \gamma)}. \tag{13}$$
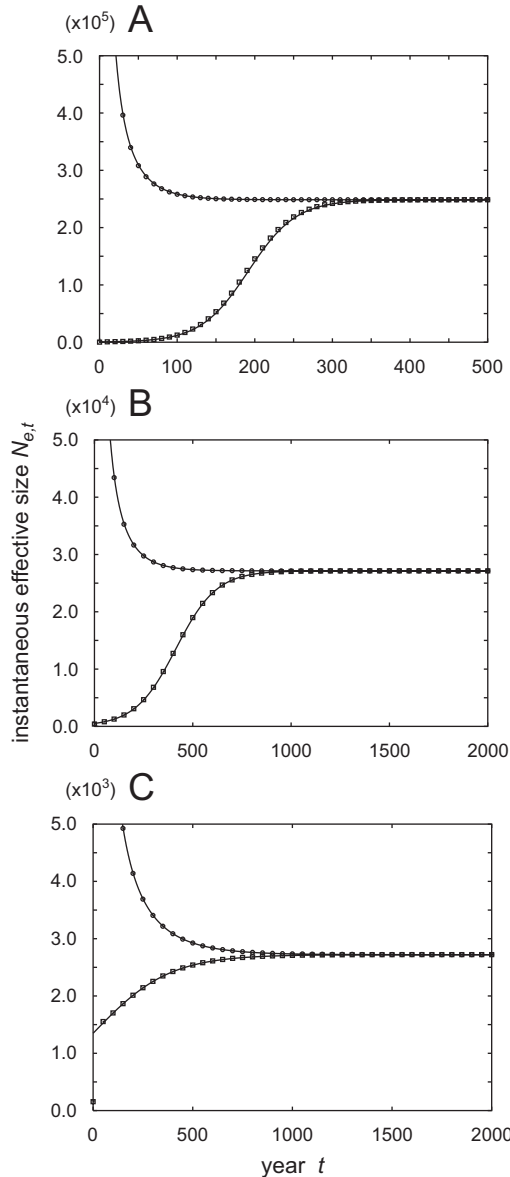
Fig. 1. The dynamics of instantaneous effective size $N_{e,t}$ numerically computed from Eqs. (B.1) and (B.2). The open squares and circles show the results for initial conditions $H_{11}(0) = 1$ and $A_{11}(0) = 1$, respectively. The smooth lines show approximations obtained from the separation-of-time-scale analysis (Eq. (12)). Parameter values for (A)–(C) are given in Tables 1A–C, respectively.

From Eq. (13), it is confirmed that $N_e = N_{es}$ under $s \to 1$, as expected. In contrast, when s is large, we can use the approximations $s/(s-1) \approx 1$ and $\gamma \approx 1 - 8M/s(4M+1)^2$. Thus, Eq. (13) becomes further simplified:

$$N_e = sN_{es}\left(1 + \frac{1}{4M}\right). \tag{14}$$

The above expression of the asymptotic effective size is consistent with the results obtained in prior studies of subdivided populations (see Section 3).

3. Discussion

Above, we show how to derive the instantaneous and asymptotic effective size in a spatiotemporally structured population using an approximation based on separation of time scales. The main result is that we can construct simple recurrence equations to describe the dynamics of non-coalescence probabilities from the local effective size N_{es} and the effective migration rate m_e. Thus, if N_{es} and m_e are known, we do not have to consider within-population details, such as the age-specific non-coalescence probabilities $I_i(t)$, $H_{ij}(t)$, and $A_{ij}(t)$ or size of each age N_i. This allows us to reuse already known formulae for N_{es} to derive the formula for the global N_e. Our approach is also very intuitive if the meaning of reproductive values or the effective migration rate is known. Obviously, this method is not limited to a specific age structure, but is widely applicable to many types of class structure.

As mentioned in Section 2, the coalescent process treated here does not reduce to Kingman's standard coalescent because we assume that migration and within-subpopulation coalescence occur on the same time scale, as is assumed implicitly or explicitly in some models (e.g., Wright, 1931; Notohara, 1990; Wilkinson-Herbots, 1998). Despite this irreducibility, separation-of-time-scale approximation transforms the original complex structured coalescent to a much simpler structured coalescent because it collapses the structure concerning the fast process, i.e., age transition (Nordborg and Krone, 2002).

In the original island model without age structure, the effective size of the entire population is given by $N_e = sN/(1-F_{ST})$ (Wright, 1943), where N is subpopulation size and F_{ST} is Wright's coefficient of inter-subpopulation genetic differentiation (Wright, 1951). As is known well, F_{ST} in this model is approximately given by $F_{ST} = 1/(4Nm+1)$ for sufficiently large s, where m is the migration rate (Takahata, 1983; Crow and Aoki, 1984; Slatkin, 1991; Nei and Takahata, 1993); therefore, we have $N_e = sN(1+1/4Nm)$. Note that Eq. (14) reduces to this formula, when there is only one age class. Moreover, a number of formulae similar to Eq. (14) were derived by prior authors for models with discrete generations (for a review, see Wang and Caballero, 1999). For example, suppose a subdivided population with separate sexes and discrete generations, and let N_m (N_f) and m_m (m_f) denote the number of males (females) per subpopulation and the migration rate of males (females), respectively. Substituting $T = 1$, $N_{es} = 4N_mN_f/(N_m+N_f)$, and $m_e = (m_m+m_f)/2$ for Eq. (14), we obtain the formula of the effective size for diploid organisms (Wang, 1997b; Berg et al., 1998). Likewise, substituting $T = 1$, $N_{es} = 9N_mN_f/(4N_m+2N_f)$, and $m_e = (m_m+2m_f)/3$ for Eq. (14), we obtain the formula for haplodiploid organisms, where males are haploid (Berg et al., 1998; Wang, 1999).

In coalescent theory, the expected or mean coalescent time is a main concern because it is related to various interesting statistical parameters, such as F_{ST} (Slatkin,

Table 1
Demographic parameters used in the numerical computation of the instantaneous effective size $N_{e,t}$

Age (i)	1	2	3	4	5
(A) *Number of subpopulations (s) = 500, number of age classes (n) = 5*					
N_i	250	200	150	100	50
p_i	0.0	0.2	0.4	0.3	0.1
m_i	0.00	0.02	0.03	0.02	0.01
(B) *Number of subpopulations (s) = 50, number of age classes (n) = 3*					
N_i	400	200	100		
p_i	0.5	0.3	0.2		
m_i	0.005	0.004	0.003		
(C) *Number of subpopulations (s) = 2, number of age classes (n) = 5*					
N_i	1000	700	500	300	250
p_i	0.0	0.0	0.1	0.5	0.4
m_i	0.000	0.000	0.001	0.003	0.005

1991). Here, instead, we focus on non-coalescence probabilities to consider instantaneous and asymptotic effective size. We can learn many interesting things from Laplace transforms of non-coalescence probabilities (see also Wilkinson-Herbots, 1998). For example, expected coalescent time for a given sample, ET, is readily derived: As shown by Slatkin (1991), $ET = \int_0^{+\infty}(H(u) + A(u))\,du = L_{H+A}(0)$. Therefore, from Eq. (A.3), we have

$$ET = L_{H+A}(0) = 1 + \frac{A(0)(s-1)}{4Ms}. \tag{15}$$

Thus, the (scaled) expected coalescent time is equal to 1 for two genes from the same subpopulation [$A(0) = 0$] and equal to $1 + (s-1)/4Ms$ for those from different subpopulations [$A(0) = 1$], fully consistent with results of prior works (e.g., Slatkin, 1991; Wilkinson-Herbots, 1998). A more interesting quantity may be expected time spent in the same subpopulation by the sample lineages, which we denote by ET_H:

$$ET_H = L_H(0) = \frac{1}{s}. \tag{16}$$

Therefore, ET_H does not depend on the initial sample configuration. However, the expected time spent in different subpopulations, ET_A, is given by

$$ET_A = L_A(0) = \left(1 - \frac{1}{s}\right)\left(1 + \frac{A(0)}{4M}\right). \tag{17}$$

Hence, if the sample is from the same subpopulation [$A(0) = 0$], then ET_A is $1-1/s$. Whereas ET_H ($= 1/s$) for two lineages from the same subpopulation decreases with increasing the number of subpopulations s, it is counterbalanced by increases in ET_A ($= 1-1/s$); as a result, ET for the two lineages from the same subpopulation does not depend on population subdivision (Hein et al., 2005). Higher moments of these quantities are also readily derived from Laplace transforms of non-coalescence probabilities, although we do not show them here.

Appendix A. Laplace transforms of the solution to Eq. (10)

$L_H(z)$, $L_A(z)$, and $L_{H+A}(z)$, below, are the Laplace transforms of $H(u)$, $A(u)$, and $H(u) + A(u)$, respectively; e.g., $L_H(z) = \int_0^{+\infty} e^{-zu}H(u)\,du$:

$$L_H(z) = \frac{H(0)z + 4Ms/(s-1)}{z^2 + s(4Ms/(s-1) + 1)z + 4s^2M/(s-1)}, \tag{A.1}$$

$$L_A(z) = \frac{A(0)z + 4Ms + sA(0)}{z^2 + s(4Ms/(s-1) + 1)z + 4s^2M/(s-1)}, \tag{A.2}$$

$$L_{H+A}(z) = \frac{z + 4s^2M/(s-1) + sA(0)}{z^2 + s(4Ms/(s-1) + 1)z + 4s^2M/(s-1)}, \tag{A.3}$$

where we used the fact that $H(0) + A(0) = 1$.

Appendix B. Numerical computation of effective size

Here, we give the recurrence equations describing the exact dynamics of non-coalescence probabilities $I_i(t)$, $H_{ij}(t)$, and $A_{ij}(t)$ without derivation. These quantities change with two steps: migration and reproduction. Therefore, we need two sets of corresponding recurrence equations. The following (B.1) equations are recurrence equations for the migration process. Asterisks (*) denote non-coalescence probabilities after one backward migration:

$$I_i^*(t) = I_i(t), \tag{B.1a}$$

$$H_{ij}^*(t) = \left\{ (1-m_i)(1-m_j) + m_i m_j \frac{1}{s-1} \right\} H_{ij}(t)$$
$$+ \left[\{ m_i(1-m_j) + (1-m_i)m_j \} \right.$$
$$\left. + m_i m_j \frac{s-2}{s-1} \right] \frac{1}{s-1} A_{ij}(t), \tag{B.1b}$$

$$H_{ii}^*(t) = \left\{ (1-m_i)\left(\frac{N_i(1-m_i)-1}{N_i-1} \right) + m_i \left(\frac{N_i m_i -1}{N_i-1} \right) \varphi_i \right\} H_{ii}(t)$$
$$+ \left[2m_i(1-m_i)\frac{1}{s-1} + m_i^2 \frac{s-2}{s-1} \varphi_i \right] A_{ii}(t), \tag{B.1c}$$

$$A_{ij}^*(t) = \left\{ (1-m_i)m_j + m_i(1-m_j) + m_i m_j \frac{s-2}{s-1} \right\} H_{ij}(t)$$
$$+ \left[(1-m_i)(1-m_j) + \{ m_i(1-m_j) + (1-m_i)m_j \} \frac{s-2}{s-1} \right.$$
$$\left. + m_i m_j \left(1 - \frac{s-2}{(s-1)^2} \right) \right] A_{ij}(t), \tag{B.1d}$$

$$A_{ii}^*(t) = \left\{ 2m_i \left(\frac{N_i(1-m_i)}{N_i-1} \right) + m_i \frac{N_i m_i -1}{N_i-1}(1-\varphi_i) \right\} H_{ii}(t)$$
$$+ \left[(1-m_i)^2 + 2m_i(1-m_i)\frac{s-2}{s-1} \right.$$
$$\left. + m_i^2 \left\{ 1 - \left(\frac{s-2}{s-1} \right) \varphi_i \right\} \right] A_{ii}, \tag{B.1e}$$

where $i \neq j$ and

$$\varphi_i = \frac{N_i m_i -1}{(s-1)N_i m_i -1}. \tag{B.1f}$$

From Eq. (B.1), it is easily shown that $H_{ij}^*(t) + A_{ij}^*(t) = H_{ij}(t) + A_{ij}(t)$ for any i and j; this is expected because no coalescence occurs during the migration process. The following (B.2) equations are recurrence equations for the reproduction process:

$$I_i(t+1) = I_{i+1}^*(t) + \frac{1}{N_i} p_i H_{1i+1}^*(t) + \frac{1}{2N_i} p_i^2 (H_{11}^*(t) + I_1^*(t)), \tag{B.2a}$$

$$H_{ij}(t+1) = H_{i+1j+1}^*(t) + p_i H_{1j+1}^*(t) + p_j H_{i+11}^*(t) + p_i p_j (H_{11}^*(t) + I_1^*(t)), \tag{B.2b}$$

$$H_{ii}(t+1) = H_{i+1i+1}^*(t) + 2\left(1 - \frac{1}{N_i} \right) p_i H_{1i+1}^*(t) + \left(1 - \frac{1}{N_i} \right) p_i^2 (H_{11}^*(t) + I_1^*(t)), \tag{B.2c}$$

$$A_{ij}(t+1) = A_{i+1j+1}^*(t) + p_i A_{1j+1}^*(t) + p_j A_{i+11}^*(t) + p_i p_j A_{11}^*(t), \tag{B.2d}$$

where $i \neq j$ in Eq. (B.2b).

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