

Supplemental Material

The coalescent process

If we consider a given pair of alleles in our sample of n and ignore any recombination within the locus, the probability that they both originate from a common ancestral allele in the previous is $1/(2N_e)$; this is a “coalescent event”. If n is $\ll N_e$, there is a negligible chance that two such events occur in the same generation, and the probability of a coalescent event is then $n(n-1)/(4N_e)$. The expected time to such an event is $4N_e/n(n-1)$, which is equal to $2N_e$ for the case of a single pair of alleles; there is an approximately exponential distribution around this mean (with standard deviation equal to the mean). Once this event has occurred, the process repeats itself with a rate parameter $(n-1)(n-2) \dots (n-i)/(4N_e)$, until the number of alleles becomes one, so that the most recent common ancestor (MRCA) of the sample has been reached.

This process generates a gene tree; all variability in the sample arises from mutations that occurred after the MRCA, and the frequency spectrum is determined by the places in the genealogy at which these mutations arose (see Figure 1). The expectation of the pairwise diversity, π , simply reflects the product of the mutation rate and mean time separating a pair of alleles ($4N_e$). The expected number of polymorphic sites in the sample is given by the product of u and the expectation of the sum of the lengths of all the individual branches in the tree (see Figure 1); this sum is equal to $4N_e a_n$, which provides the rationale for the use of θ_w as a measure of variability. Recombination has no effect on these expectations, but greatly reduces the variances of the two estimates of diversity, which reflect the considerable stochasticity of the exponential distributions of coalescent times for each branch.

In many cases it is of interest to know which of the two variants at a site represents the ancestral or derived state, which can be done by comparison with an outgroup species, although this is fraught with technical difficulties (Keightley and Jackson 2018). We can then estimate the “unfolded” SFS, where g_j is the frequency of sites with j copies of the derived variant. The expected unfolded SFS is given by $g_j = (j a_n)^{-1}$, which provides a benchmark against which deviations from the equilibrium model can be tested, as does the comparison of the summary statistics π and θ_w obtained from the data.

Keightley PD, Jackson BC. 2018. Inferring the probability of the derived vs. the ancestral allelic state at a polymorphic site. *Genetics* 209:897–906

Additional references to studies of the effects of selection at linked sites

Notes:

This is not intended as a complete bibliography of the relevant literature. Charlesworth & Campos (2014) provide a list of references to empirical work on the effects of recombination rate on molecular variation and evolution in *Drosophila*. Stephan (2019) provides a list of references to the theoretical and empirical literature on selective sweeps.

Many other relevant references that are not provided in the list below can be found in these papers, and in: Charlesworth B, Charlesworth D, Barton NH. 2003 *Ann. Rev. Ecol. Evol. Syst.* 34:99-125; Neher R. 2013. *Ann. Rev. Ecol. Evol. Syst.* 44:195-215.

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