

THE COALESCENT WITH PARTIAL SELFING AND BALANCING SELECTION: AN APPLICATION OF STRUCTURED COALESCENT PROCESSES

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As a demonstration of a generally applicable technique, a theorem based on separation of time scales in the structured coalescent is used to extend results for the coalescent process with balancing selection to allow partial selfing. The resulting model behaves like the random-mating one, but with different rates of coalescence and recombination. This result has important implications for attempts to locate selectively maintained polymorphisms. Such polymorphisms can in principle be detected through their effect on the pattern of polymorphism in the genomic region surrounding the site under selection, however this is not practically feasible unless the effected region is sufficiently large. An implication of the present results is that the region is expected to be much larger in partially selfing organisms than in outcrossing ones, suggesting that studies attempting to locate selectively maintained polymorphisms should utilize selfing organisms.

1. Introduction. If natural selection has maintained polymorphism at a certain site or locus for a long period of time, the evolutionary dynamics in closely linked regions of the chromosome will be effected. In particular, the expected pattern of neutral polymorphism will be altered in a manner that allows inference about the action of selection directly from molecular polymorphism data, without phenotypic observation [Hudson and Kaplan (1988)]. This phenomenon has been observed in a few cases [Kreitman and Akashi (1995), Hudson (1996)]: MHC (immune system) loci in human; the *S* (self-incompatibility) locus in plants; and *Adh* (alcohol dehydrogenase) in *Drosophila melanogaster*. Although these loci were already known to harbor selectively maintained polymorphisms, the same phenomenon could, in principle, be used to locate such polymorphisms without prior information. For this to be practical, however, the region of the chromosome in which the effects of selection are noticeable must be large enough. One of the aims of this paper is to prove earlier claims [Nordborg et al. (1996), Nordborg (1997), Charlesworth et al. (1997)] that the effected regions will be much wider in partially selfing organisms than in outcrossing

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