



The consequences of time averaging for measuring temporal species turnover in the fossil record

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Modeling time averaging effects with simple simulations allows us to evaluate the magnitude of change in temporal species turnover that is expected to occur in long (paleoecological) time series with fossil assemblages. Distinguishing different modes of metacommunity dynamics (such as neutral, density-dependent, or trade-off dynamics) with time-averaged fossil assemblages requires scaling-up time-averaging effects because the decrease in temporal resolution and the decrease in temporal inter-sample separation (i.e., the two main effects of time averaging) substantially increase community stability relative to assemblages without or with weak time averaging. Large changes in temporal scale that cover centuries to millennia can lead to unprecedented effects on temporal rate of change in species composition. Temporal variation in species composition monotonically decreases with increasing duration of time-averaging in simulated fossil assemblages. Time averaging is also associated with the reduction of species dominance owing to the temporal switching in the identity of dominant species. High degrees of time averaging can cause that community parameters of local fossil assemblages converge to parameters of metacommunity rather than to parameters of individual local non-averaged communities. We find that the low variation in species composition observed among mollusk and ostracod subfossil assemblages can be explained by time averaging alone, and low temporal resolution and reduced temporal separation among assemblages in time series can thus explain a substantial part of the reduced variation in species composition relative to unscaled predictions of neutral model (i.e., species do not differ in birth, death, and immigration rates on per capita basis). The structure of time-averaged assemblages can thus provide important insights into processes that act over larger temporal scales, such as evolution of niches and dispersal, range-limit dynamics, taxon cycles, and speciation modes.