

Name _____

Effects of Time-Averaging on Species Richness

Fossil assemblages allow us to reconstruct the species richness or composition of past communities. However, those fossil samples are time-averaged death assemblages, while we are interested in comparing the former living assemblages. There is no way to actually determine the life assemblage, but you can understand general trends in time-averaging and judge whether comparisons between different fossil assemblages are acceptable or not.

As you learned in the video, time-averaging typically increases species richness (the number of species present) in a death assemblage relative to any given life assemblage from that location. Time-averaging also makes death assemblages from different locations look more similar to each other than the life assemblages actually are. The purpose of this exercise is to use simulations to explore possible explanations for those phenomena.

Part 1: The Model (<https://mclapham.shinyapps.io/timeavg/> if you want to try it yourself)

Imagine that you choose a small square of coastline, say 5 m by 5 m, on Monterey Bay and identify the organisms. We can call this the *local community* and it will probably contain some mussels, sea stars, and some less common species. The entirety of Monterey Bay includes many more species than found in your local community, however. We can call the entire group of organisms living in Monterey Bay the *metacommunity* and treat it as an infinitely large (relative to the local community) potential source of species.

For simplicity we will ignore environmental preferences and biological interactions and construct a *neutral model* of the metacommunity and local community. In this model we will populate the local community with organisms drawn randomly from the metacommunity. The probability of drawing an organism from the metacommunity is proportional to that organism's abundance in the metacommunity.

When an organism in the local community dies, that vacancy can be replaced either by a species taken from the metacommunity (immigration) or by an organism "born" from the local community (local "birth"). The model has only one parameter, the *probability of immigration*, which varies between 0 and 1 and determines whether a vacancy is filled by immigration or by local birth. Values close to 1 mean that vacancies are most likely filled by drawing a species from the metacommunity, whereas values close to 0 means that vacancies are most likely filled by drawing a species from the local community.

Part 2: Effects of immigration probability

The goals of this part are 1) to visualize changes in the local community over time and 2) to explore how and why immigration probability influences those changes.

The next command runs a larger version of the neutral model that you already investigated. But first, some background. There are 125 species with a more realistic distribution of abundances (not all equally abundant) and the simulation runs for 18000 time steps. The output will be a graph showing how the species composition of the local community changes through time in the simulation. The difference in species composition is quantified by something called the "Bray-Curtis dissimilarity" – but that isn't important now (we will discuss these measures later). Basically, a value of zero means the community composition is the same as the average and values either higher or lower than zero indicate increasing dissimilarity from the average.

Answer the following questions:

1. How does the variability in species composition differ between the low and high immigration probability simulations? Describe and compare (A) the magnitude of the changes away from zero and (B) the length of trends in community composition.
2. Why does immigration probability have this effect in the simulations? Hint: think about the implications of filling a vacancy from the infinitely-large metacommunity vs. the limited local community.
3. These results are for the life assemblage communities. The death assemblage will be an average of those life assemblages over a few hundred to maybe thousand timesteps. How will a typical death assemblage compare to the metacommunity (zero is average) – will it be more similar to the metacommunity than any single life assemblage chosen at random, less similar, or about the same?
4. Given that result, how and why will time-averaging affect the observed similarity of species composition between death assemblages at different locations?

Part 3: Effects on species richness

The final step is to investigate how immigration probability and the duration of time-averaging affect recorded species richness in the death assemblage. The code runs the same simulation used in part 2, but additionally places the organisms into a death assemblage once they “die” in the local community. At the end, it calculates the ratio of species richness in the death assemblage to species richness in the life assemblage (both are estimated from 100 individuals). It does this many times and plots the results as a box-and-whisker plot, which shows the median (the middle value) with the thick line, the interquartile range (the range between 25% and 75% of the data) with the box, and the total range of data with the whiskers (some outliers are shown as isolated dots). The median is the important value and is reported as the average richness inflation at the top of the plot.

Answer these questions:

5. How does the duration of time-averaging affect inflation of richness in death assemblages? What mechanism causes this effect in the simulation?
6. How does the immigration probability affect inflation of richness? What mechanism is responsible? Hint: think back to the similarity results from part 2.

When you are done, reflect on your answers and write a short paragraph explaining how and why time-averaging affects species richness and similarity among fossil assemblages.

If you finish with those questions, you can consider these additional issues:

- A. How would changes in sediment accumulation rate change the magnitude of diversity inflation between life and death assemblages? Explain why.
- B. What other factors (related to the organisms themselves or the environment) could lead to inflation of species richness in death assemblages?