Remembrance of things past: modelling the relationship between species’ abundances in living communities and death assemblages

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Accumulations of dead skeletal material are a valuable archive of past ecological conditions. However, such assemblages are not equivalent to living communities because they mix the remains of multiple generations and are altered by post-mortem processes. The abundance of a species in a death assemblage can be quantitatively modelled by successively integrating the product of an influx time series and a post-mortem loss function (a decay function with a constant half-life). In such a model, temporal mixing increases expected absolute dead abundance relative to average influx as a linear function of half-life and increases variation in absolute dead abundance values as a square-root function of half-life. Because typical abundance distributions of ecological communities are logarithmically distributed, species’ differences in preservational half-life would have to be very large to substantially alter species’ abundance ranks (i.e. make rare species common or vice-versa). In addition, expected dead abundances increase at a faster rate than their range of variation with increased time averaging, predicting greater consistency in the relative abundance structure of death assemblages than their parent living community.

Keywords: time averaging; death assemblage; fossil assemblage; convolution; moving average process

1. INTRODUCTION
A major objective of community ecology is to understand the processes governing the composition and structure of multi-species assemblages. The death remains of organisms can provide a record of past ecological conditions, and therefore have great potential to shed light on community dynamics and to provide vital information on ecological baselines [1–4]. However, death assemblages differ from living communities because they are typically time-averaged—i.e. they mix the remains of multiple generations [5–8]. In shallow marine settings, shells of dead molluscs and brachiopods can be tens to thousands of years old—long enough to span substantial environmental and ecological change and complicating the interpretation of past conditions. Because death assemblages form over a much longer time than can be investigated through direct experimentation, modelling is an essential tool for understanding their genesis and properties [14–16].

The primary data of community ecology consist of the identities and abundances of species in local assemblages, so the fundamental question regarding the fidelity of death assemblages concerns the factors determining the dead abundance of individual species. The abundance of a single species in a death assemblage can be conceptualized as a balance between influx and loss [7,17,18]. The influx $F(t)$ of skeletal material to an accumulating death assemblage is governed by the standing crop and mortality rate of the living population as well as physical processes influencing the rate and episodicit of sedimentation and reworking (figure 1a; physical processes can influence loss as well as influx). Once dead skeletal elements have been added to an accumulation, they stand some chance per unit time of being destroyed or removed ($G(t)$) [6], resulting in a decaying post-mortem age distribution (figure 1b) [17,18]. Mathematically, the abundance of a species in a death assemblage is the integral of the product of the influx and loss functions: $F(t)G(t)dt$ (figure 1c). Consecutive application of this integral to an influx time series (a mathematical convolution or moving average process) provides a means of modelling changes in the dead abundance of a single species (figure 1d).

2. METHODS
In the model, post-mortem loss is quantified as an exponential function: $G(t) = \exp(-t\ln 2/T_{1/2})$, where $t = \text{time}$ and $T_{1/2} = \text{half-life}$ (the duration in which 50% of initially present material is expected to be lost). The exponential function assumes that every individual has an equal probability of loss at every moment in time [17–20]. Although this is a reasonable first-order approximation in the absence of other information, it should be noted that neither the environmental conditions controlling loss nor the preservational properties of skeletal material need remain constant through time.

Influx is modelled here as a stationary time series derived as the product of an influx time series $F(t)$ and a lognormal distribution $F(t)$ transformed to have a mean of zero and a standard deviation of one; in addition, $k \sigma(t)$ and $\mu$ are independent of one another. The lognormal distribution resembles a boom–bust dynamic: most deviations from the average are small but they are punctuated by occasional high magnitude events, a pattern expected for opportunistic populations in harsh or fluctuating environments [21]. A variety of other symmetrical and skewed distributions were also explored (normal, uniform, logistic, exponential, exponentially transformed logistic and Cauchy), and the outcomes were consistent with the results of the lognormal model. In all simulations, influx parameters $\mu$ and $k$ were set so that all values in the influx series were greater than zero.

3. RESULTS
Integrating the product of $F(t)$ and $G(t)$ results in an expression for the abundance of a species in the death assemblage at time $t$:

$$
\int_0^\infty [\mu + k \sigma(s - t)] \exp \left(-\frac{t \ln 2}{T_{1/2}}\right) dt
= \frac{\mu T_{1/2}}{ln 2} + k \int_0^\infty \sigma(s - t) \exp \left(-\frac{t \ln 2}{T_{1/2}}\right) dt.
$$

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The first term on the right-hand side, \( k_s \sigma(s - t) \exp(-t \ln 2/T_{1/2})dt \), describes the effect of influx variation. The magnitude, \( k_s \), has a linear effect on variation of dead abundance—i.e. doubling influx variation doubles dead abundance variation. As a moving average process, the standard deviation of dead abundances is expected to be \( \sqrt{T_{1/2}/2 \ln 2} \) times the standard deviation of influx [22] (figure 2b,c). This relationship indicates that although dead abundance variation increases with time averaging, it does so at a slower rate than the linear increase in the expected value of dead abundance. In contrast to standard deviation, both skewness and kurtosis of dead abundances decrease as half-life increases (figure 2c)—i.e. temporal mixing leads to dead abundances that are more symmetrical and less prone to extreme values than the influx series [23]. Lastly, temporal mixing induces a degree of autocorrelation in dead abundances equal to \( \exp(-s \ln 2/T_{1/2}) \) at a lag of \( s \) [22] (figure 2d). The degree of autocorrelation is a measure of a dead abundance series’ memory of its own past: autocorrelation is reduced to approximately 0.5 after one half-life and is negligible after five half-lives.

4. DISCUSSION
The model presented here indicates that rather than converging on an expected value [5–7,24,25], variation of absolute dead abundance values increases with increasing time averaging. The reason is that ‘taphonomic inertia’ [26] makes dead abundances hard to push away from their value at any moment. Once they have deviated from their expected value owing to a few above-average or below-average influx events, they have a tendency to stay deviated, and the magnitude and duration of this effect increases with time averaging.

Despite the increase in variance with time averaging, meta-analysis of 85 live–dead comparisons of shallow, marine mollusc communities [27] indicated that an average of 20 per cent of the variation in dead abundance ranks could be explained by living abundance ranks (mean Spearman \( r^2 = 0.203 \)). This degree of rank fidelity appears to be owing to the fact that ecological abundances are typically distributed on a logarithmic scale [16,28], whereas the effects of temporal mixing on expected dead abundances are linear—i.e. substantial shifts in abundance rank from live to dead would require species to have differences in influx or loss much larger than their rank differences. In addition, the model predicts that the range of dead abundance variation relative to expected absolute abundance should decrease with increased time averaging as a function of \( (T_{1/2})^{-1/2} \), consistent with recent multispecies models which have found that time-averaged death assemblages are less variable than sympatric live assemblage [15,16,25].

5. CONCLUSION
The model of time averaging presented here clearly glosses over the full complexities of population dynamics, post-mortem alteration and sedimentary burial. Nevertheless, by stripping a wide array of interacting processes down to simple fundamentals, it refines our
understanding of the effects of time averaging on variation in death assemblages and connects processes of influx, burial and loss to measurable patterns like post-mortem age frequency distributions [20]. By emphasizing that death assemblages are no more static than living communities, it highlights the need to acquire dead abundance series for comparison with corresponding living series over durations relevant to time averaging [29]. Even as data improve, modelling will provide a powerful tool both for understanding deep-time fossil assemblages as well as for using death assemblages as baselines of ecological change in the present day.

This work was supported by NSF grant EAR-0617355. Insightful and constructive reviews were provided by Michal Kowalewski and Adam Tomášovych.

Figure 2. Effect of increasing half-life on the distribution of dead abundances. (a) Dead abundance time series for $T_{1/2} = 1, 4, 16,$ and 64 timesteps from bottom to top (respective mean dead abundance values are 1.4, 5.8, 23.1 and 92.3; based on an influx with $\mu = 1$ and $k = 1$). (b) Solid black line is median deviation from expected average dead abundance; dashed lines denote 95% quantile interval. (c) Effect of time averaging on the properties of the statistical distribution of dead abundances. Influx distribution had standard deviation: (squares) 8.56 and kurtosis (triangles) 241.86. (d) Autocorrelation of dead abundance time series based on different post-mortem half-lives (indicated for each curve). Autocorrelation of influx series and cross-correlation of dead and influx series were not significantly different from zero for all half-lives and lags (dashed line).


