Where does the time go?: Mixing and the depth-dependent distribution of fossil ages

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ABSTRACT

Knowing how time is distributed within a fossil record is fundamental to paleobiology. Many efforts to quantify temporal resolution have estimated rates of specimen decay from the frequency distribution of specimen ages in near-surface assemblages. The implicit assumption has been that the shape of these distributions is invariant with depth and thus decay-rate estimates reflect the temporal resolution of a fossil record's deeper layers as well. Here we present a new model that predicts how age-frequency distribution shape will change with depth due to the interplay of burial, mixing, and decay. Unlike previous models, this model distinguishes the dimensions of time, specimen age, and depth, and predicts a right-to-left shift in age-frequency distribution skewness, and a decrease in kurtosis, with increasing stratigraphic depth. We find support for these predictions with the accelerator mass spectrometry ^{14}C dating of 80 small mammal specimens spanning the Quaternary fossil record of Homestead Cave, Utah (United States). Our study indicates (1) that previous models overestimate rates of specimen decay, (2) that the acuity of ecological information captured in near-surface assemblages is higher than previously inferred, and (3) how time-averaging can alter the apparent dynamics of biodiversity over time. We thereby offer a new quantitative framework to account for time-averaging, to merge modern and paleontological archives, and to place ecological systems within the context of their past dynamics.

INTRODUCTION

Paleobiological reconstructions of ecological and evolutionary dynamics require robust geochronological frameworks. Time-averaging—the degree to which non-contemporaneous skeletal specimens are combined within the depositional layers of a fossil record—establishes the temporal scales at which questions can be addressed and dictates appropriate sampling and analytical frameworks (Flessa et al., 1993; Olszewski, 2004; Kosnik et al., 2013; Tomašových et al., 2014). The processes that lead to time-averaging can have both positive and negative consequences for the quality of biological information that fossils record (Kowalewski et al., 1998; Olszewski, 1999; Martin et al., 2002; Alin and Cohen, 2004). On the one hand, it blurs information by intermixing noncontemporaneous specimens. On the other, it modulates fine-scale variability, allowing temporal trends to emerge with less sampling effort. This poses both challenges and opportunities for paleobiology, particularly for the growing field of conservation paleobiology (Kidwell, 2013).

Increasing effort has been devoted to characterizing the age-frequency distributions of modern and sub-fossil skeletal assemblages to determine their temporal resolution (Flessa et al., 1993; Meldahl et al., 1997; Kowalewski et al., 1998; Olszewski, 1999; Carroll et al., 2003; Kidwell et al., 2005; Kosnik et al., 2009, 2013, 2014; Krause et al., 2010; Tomašových et al., 2014). In these studies, a regular pattern has emerged: age-frequency distributions are typically right-skewed, dominated by specimens of younger ages (reviewed in Kidwell, 2013). This

has prompted the fitting of exponential survivorship models to quantify rates of specimen decay, with the inference being that high decay rates explain the high concordance that is seen between "live" and "dead" biodiversity surveys of intact modern ecological communities (Olszewski, 1999, 2012; Kidwell, 2002, 2013).

However, two deviations from exponential decay are common in these predominantly surficial marine assemblages: age-frequency distributions show fewer than expected specimens of the very youngest ages and are "L-shaped", characterized by heavier-than-expected tails of older-age specimens (Flessa et al. 1993; Kosnik et al., 2013; Tomašových et al., 2014). Furthermore, an implicit assumption has been that the shape of near-surface age-frequency distributions persists below the depositional surface, such that near-surface decay rates reflect the temporal resolution of a fossil record's deeper layers as well. The degree to which the shapes of age-frequency distributions change in older, deeper assemblages that are cut off from the influx of new skeletal material has remained untested (but see Kosnik et al. [2014]). Yet resolving these issues is key to disentangling the effects of time-averaging on biodiversity dynamics and bridging between neontological and paleontological archives.

Here we present a model to understand how time becomes distributed within the sedimentary layers of a fossil record. By explicitly considering the dimensions of depth, time, and specimen age, our model explains the aforementioned deviations from exponential decay near the depositional surface and offers the following
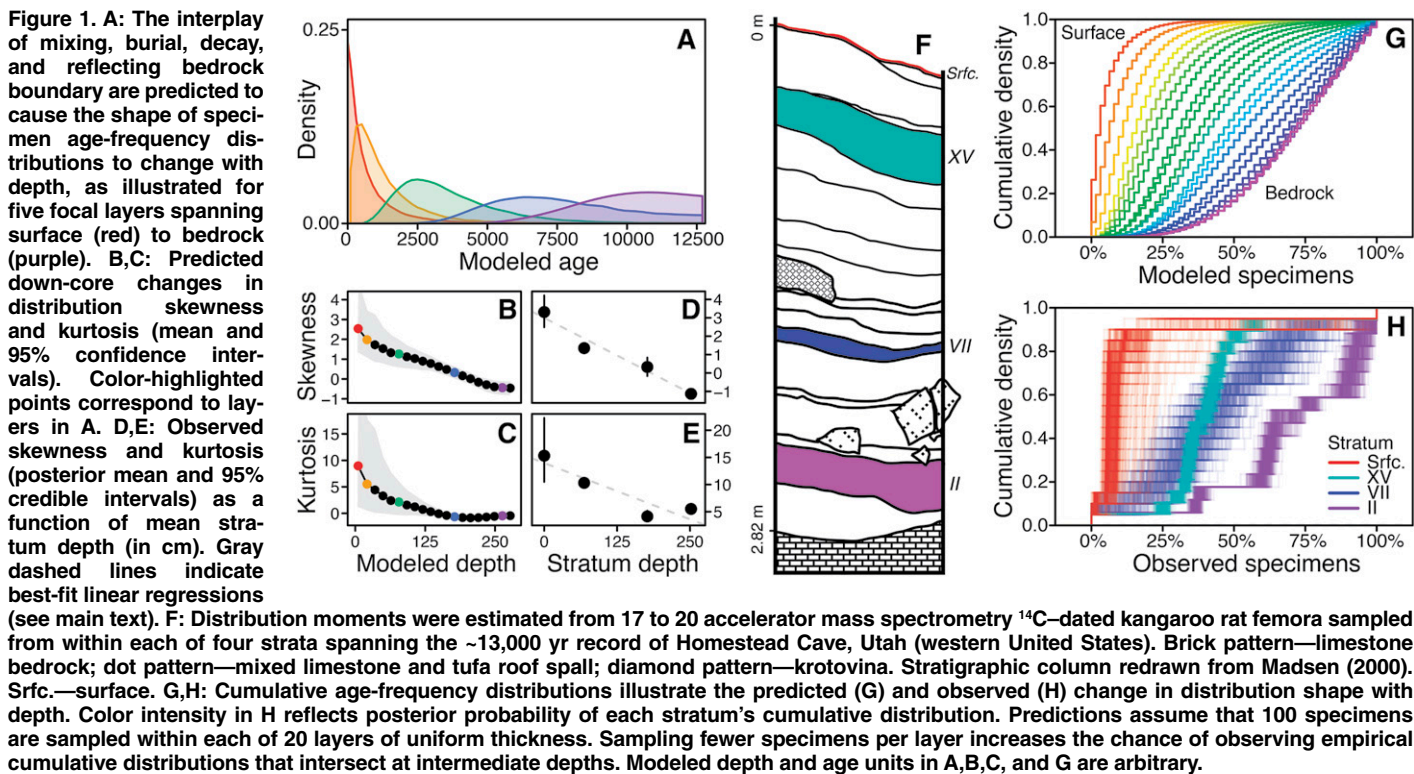
new predictions for age-frequency distributions below the surface: distributions will exhibit a secular trend from right skew to left skew, and a pattern of decreasing kurtosis, with increasing stratigraphic depth. We test and find support for these predictions using empirical age-frequency distributions of 80 kangaroo rat (*Dipodomys* spp.) femora, dated by accelerator mass spectrometry ^{14}C, from the modern to early Holocene small mammal record of Homestead Cave, Utah (western United States).

MODELED AGE-FREQUENCY DISTRIBUTIONS

Our model may be expressed in the form of a partial differential equation,

$$\frac{\partial f}{\partial t} + \frac{\partial f}{\partial a} = m\frac{\partial^2 f}{\partial x^2} - hf, \qquad (1)$$

[where $0 < x < d(t)$, $t > 0$, and $a > 0$], which we approximate with an agent-based formulation. The model describes the frequency of specimens f of age a at depth x and time t as being the result of four processes: surface influx, burial, mixing, and decay. The influx of specimens occurs at the surface [$x = d(t)$]. Both the surface and the bedrock ($x = 0$) are reflecting boundaries. Column depth increases over time from an initial depth d_0 at burial rate b (i.e., $d(t) = d_0 + bt$). Although the parameters that represent the mixing (m), burial (b), and hazard (h) rates are themselves likely to be interdependent functions of depth, time, and specimen age, we consider these to be independent and constant. For example, we consider the hazard rate (the per-individual probability of specimen destruction) to be independent of time, age, and depth [i.e., $h(t,a,x) = \lambda$], corresponding to exponential decay. We similarly consider diffusive mixing as an approximation to more complex processes (Meysman et al., 2010) and specify a constant specimen influx rate at the surface (i.e., that influx is stochastically constant at time scales less than the resolution of the record) because almost any age-frequency distribution may be obtained with a time-varying influx (Kowalewski and Rimstidt, 2003; Krause et al., 2010; Olszewski, 2012). The reflecting bedrock makes the model most applicable to terrestrial Quaternary fossil records such as cave deposits, but the model may be extended to systems with distant or permeable boundaries (e.g., marine deposits) by relaxing this boundary condition. Despite the processes of mixing and burial having long been considered important (Flessa et al., 1993;

Figure 1. A: The interplay of mixing, burial, decay, and reflecting bedrock boundary are predicted to cause the shape of specimen age-frequency distributions to change with depth, as illustrated for five focal layers spanning surface (red) to bedrock (purple). B,C: Predicted down-core changes in distribution skewness and kurtosis (mean and 95% confidence intervals). Color-highlighted points correspond to layers in A. D,E: Observed skewness and kurtosis (posterior mean and 95% credible intervals) as a function of mean stratum depth (in cm). Gray dashed lines indicate best-fit linear regressions (see main text). F: Distribution moments were estimated from 17 to 20 accelerator mass spectrometry ^{14}C–dated kangaroo rat femora sampled from within each of four strata spanning the ~13,000 yr record of Homestead Cave, Utah (western United States). Brick pattern—limestone bedrock; dot pattern—mixed limestone and tufa roof spall; diamond pattern—krotovina. Stratigraphic column redrawn from Madsen (2000). Srfc.—surface. G,H: Cumulative age-frequency distributions illustrate the predicted (G) and observed (H) change in distribution shape with depth. Color intensity in H reflects posterior probability of each stratum's cumulative distribution. Predictions assume that 100 specimens are sampled within each of 20 layers of uniform thickness. Sampling fewer specimens per layer increases the chance of observing empirical cumulative distributions that intersect at intermediate depths. Modeled depth and age units in A,B,C, and G are arbitrary.

Kidwell, 2013), previous efforts to describe age-frequency distributions have considered only the survivorship component of our model and have conflated time and specimen age (see the GSA Data Repository[1]).

The explicit consideration of burial, mixing, and survivorship leads to predictions regarding the down-core shape of age-frequency distributions that differ qualitatively from survivorship-only models (Figs. 1A–1C, 1G; Figs. DR1 and DR2 in the Data Repository). Age-frequency distributions from shallow strata should be strongly right-skewed, appearing exponential-like except for a reduced density of the youngest specimen ages and a heaver-than-exponential tail of older specimens. This occurs because mixing is biased downwards by the declining gradient of specimen densities away from the surface. Mixing will thus move more younger specimens deeper than older specimens shallower. Strata of intermediate depth, less influenced by either boundary, will exhibit increasingly symmetrical age-frequency distributions. In contrast, mixing of the first-deposited, deepest specimens is biased in the direction of the surface by the reflecting bedrock, leading to left-skewed age-frequency distributions near the lower boundary. The longer exposure of deeper strata to mixing also results in a down-

ward decline in their temporal acuity, evidenced by a decrease in excess kurtosis (Fig. 1C) and an increase in the range of specimen ages contained within a given interval of depth (Fig. DR3). In the first-deposited strata, the bedrock's influence counters this overall acuity trend, causing a small increase in kurtosis (Fig. DR2). The magnitude of this reversal depends on the relative rates of mixing and burial.

EMPIRICAL AGE-FREQUENCY DISTRIBUTIONS

We tested our model predictions using empirical age-frequency distributions constructed from 80 kangaroo rat (*Dipodomys* spp.) femora, dated by AMS ^{14}C, selected at random from within each of four strata of the Holocene terrestrial record of Homestead Cave, Utah (Fig. DR4). Homestead Cave is an exceptional faunal sequence that represents a typical depositional setting for Quaternary vertebrate fossils, and whose stratigraphic framework is known in detail from surface to bedrock (Madsen, 2000) (see the Data Repository).

We used OxCal 4.1 (Bronk Ramsey, 2009) and the IntCal 09 calibration curve for the Northern Hemisphere (Reimer et al., 2009) to convert radiocarbon age estimates to calendar yr B.P. (before A.D. 1950). Age estimates for "modern" (post-bomb; after the addition of "artificial" radiocarbon to the atmosphere as a result of nuclear weapons testing) specimens from the surface assemblage were calibrated using the Bomb04NH curve (Hua and Barbetti, 2004).

All dates were expressed as calendar years prior to A.D. 2000 to combine pre- and post-bomb samples. OxCal returns a Bayesian posterior probability distribution that describes the range of possible calibrated dates for each specimen. We used the highest probability peaks of these distributions as point estimates of specimen age for constructing age-frequency distributions, and obtained mean and 95% credible intervals for the first four distribution moments by sampling from each specimen's posterior distribution. Skewness and excess kurtosis were calculated by their population estimators. Because histograms and density plots are sensitive to binning and bandwidth choices, and each estimate of specimen age is associated with an uncertainty, we used empirical cumulative distributions to more robustly visualize age-frequency distribution shape.

RESULTS

Consistent with model predictions, the empirical age-frequency distributions from the four strata from Homestead Cave varied in their shape with increasing stratigraphic depth (Figs. 1D–1F, 1H; Fig. DR3). The modern surface assemblage was highly right skewed, with the youngest ages less frequent than expected by survivorship-only processes. Skewness then declined as distributions became symmetrical and then left-skewed with increasing depth ($F_{1,2}$ = 47.27, $p = 0.02$). Excess kurtosis also declined with increasing depth ($F_{1,2}$ = 10.18, $p = 0.08$) and increased again within the deepest sampled stratum near the bedrock.

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[1]GSA Data Repository item 2015172, details on methods, and AMS ^{14}C data, is available online at www.geosociety.org/pubs/ft2015.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

DISCUSSION

The correspondence between our model predictions and empirical results bears several important implications for the reconstruction of ecological information from sedimentary archives.

Estimating Rates of Specimen Decay

Standard practice has been to fit models of exponential decay (age-independent hazard rates) to the age-frequency distributions of surface or near-surface assemblages (Flessa et al., 1993; Olszewski, 1999; Carroll et al., 2003; Kidwell et al., 2005; Krause et al., 2010; Kosnik et al., 2009, 2013). Tomašových et al. (2014) have recently shown models with age-varying hazard rates to outperform constant hazard rate models in describing shallow age-frequency distributions. Our model confirms that surface distributions will appear to have been generated by age-dependent hazard rates, but suggests a different mechanism for their non-exponential shape. Specifically, our model, which assumes a constant hazard rate, reveals that survivorship-only models will overestimate decay rates when fit to the age-frequency distributions of surface or near-surface layers, and will eventually underestimate them when fit to the deeper layers of a fossil sequence.

The estimation bias inherent to the fitting of survivorship-only models may be seen by rearranging the terms of our model to show how specimen densities change with respect to their age:

$$\frac{\partial f}{\partial a} = -hf + m\frac{\partial^2 f}{\partial x^2} - \frac{\partial f}{\partial t}, \qquad (2)$$

where $\frac{\partial f}{\partial a} = -hf$ corresponds to a survivorship-only model of any functional form (e.g., exponential, Weibull, etc.). For simplicity, assume that the total density of specimens in the record is near steady state ($\frac{\partial f}{\partial t} \approx 0$). Given that the mixing rate m must be positive, our model predicts a more negative $\frac{\partial f}{\partial a}$ compared to survivorship-only models when $\frac{\partial^2 f}{\partial x^2}$ is negative. This will occur when the density of specimens has a concave-down shape with respect to depth x, which for diffusive mixing will be the profile that is found near the surface. Mixing therefore causes shallow age-frequency distributions to be suggestive of larger, more negative decay rates than is true. At greater depths the density of specimens will have a concave-up shape with respect to depth such that $\frac{\partial^2 f}{\partial x^2}$ will be positive. Hence, the down-core increase in the relative rate at which older specimens were mixed toward the surface will cause deeper age-frequency distributions to be suggestive of smaller decay rates than is true when survivorship alone is considered. An unbiased estimation of decay rates depends on a random sampling and age determination of many specimens from across the entire stratigraphic sequence if the mixing rate is unknown.

Temporal Acuity of Near-Surface Assemblages

The observation that surface assemblages show right-skewed age-frequency distributions has been key to explaining why communities recorded in modern time-averaged death assemblages show high agreement with their living counterparts (Kidwell, 2013). The dominance of recently input young specimens causes high live-dead fidelity despite the large total age range of specimens. Live-dead mismatches may therefore signal the occurrence of shifting baselines, with the dead providing robust historical targets on which to focus conservation efforts (Kidwell, 2007, 2013; Terry, 2010).

Our model supports this mechanism and extends the expectation of high temporal acuity, and thus ecological fidelity, below the surface. Because of mixing and burial, younger specimens will be underrepresented within shallow subsurface assemblages that are detached from the direct input of new specimens, shifting the mode of age-frequency distributions toward older specimen ages (Fig. 1A). This offset toward older ages results in a narrowing of the window of time in which the bulk of specimen ages falls, compared to when age-frequency distributions are determined only by survivorship. Thus, shallow subsurface assemblages provide a more crisp ecological snapshot of historical communities than previously appreciated. Because the offset's magnitude is dependent on mixing and burial rates and the thickness at which sedimentary layers are excavated, estimates of these rates and an appropriate scaling of excavation depths should permit increased precision in the detection and dating of ecological baseline shifts.

Apparent Dynamics of Biodiversity

Deeper strata will provide successively lower-resolution snapshots of the living communities from which they were derived due to a decline in age-frequency distribution kurtosis. However, most deeper strata will still retain a temporal acuity that is finer than the maximum age range of specimens would suggest (Fig. DR5). This is because deeper age-frequency distributions remain leptokurtotic for much of the record (Figs. 1C and 1E). Thus the temporal acuity of deeper strata both is higher and persists for longer within successively older buried assemblages than previously expected (Flessa et al., 1993; Kidwell, 2013).

Nevertheless, down-core changes in distribution shape affect changes in the degree to which non-contemporaneous communities are combined, which will alter the apparent diversity across stratigraphic layers. To investigate this, we simulated a community assuming that the identity of specimens was such that only a single species was present in the "live" community at each time step (Fig. DR6). Community richness and evenness of the true "live" community were thus constant.

Results show that even hypothetically simple communities that have experienced constant diversity over time will exhibit trends in apparent diversity (Fig. 2; Fig. DR6). In records extending down to a reflecting bedrock, apparent diversity is expected to peak in layers of intermediate age, followed by a steady decline toward the recent. This perceived decline will be expressed both in richness, as less total time is encompassed per unit depth with increasing proximity to the surface, and in evenness, as age-frequency distributions become more peaked. Depositional systems lacking a reflecting boundary are expected to exhibit monotonic declines in diversity without an intermediate peak. The skewness of age-frequency distributions in such systems will decline with increasing depth but will not become negative, and kurtosis will decline without an increase in the deepest layers. The fact that these trends are not driven by true ecological change stresses the importance of
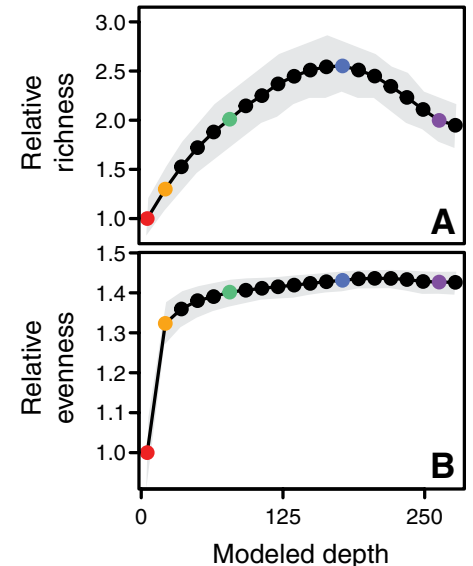

Figure 2. Apparent per-stratum richness (A) and evenness (B) (mean and 95% confidence intervals), relative to modern surface stratum, as perceived by sampling 100 specimens within each of 20 layers of uniform thickness. Down-core changes in age-frequency distribution shape create apparent trends in biodiversity even when richness and evenness are constant over time in the living community from which the fossil record is derived. Color-highlighted layers and arbitrarily chosen parameter values are as in Figures 1A–1C, 1G.

accounting for time-averaging when interpreting biodiversity dynamics.

CONCLUSIONS

By distinguishing the dimensions of time, depth, and specimen age, our model moves beyond survivorship-only processes acting at the depositional surface to make predictions regarding how the interplay of survivorship with burial and mixing shapes age-frequency distributions at varying stratigraphic depths within a fossil record. In doing so, our model also accounts for the persistent deviations from exponential decay documented in previous age-frequency distributions from the depositional surface. We support our model's predictions with empirical data that provide the first evaluation of age-frequency distributions in a terrestrial system. The processes captured by our model warrant tests of their generality and nuances in additional systems and depositional settings, and across larger spatial and temporal scales (e.g., Scarponi et al., 2013; Kosnik et al., 2014). Much remains to be learned about the interdependent effects of depth, specimen age, and time on mixing, burial, and hazard rates, just as there is about the effects of time-varying influx rates on distribution shape. Such information is needed to evaluate the degree to which apparent diversity dynamics of the past are driven by true ecological change or by the confounding effects of time-averaging. Key to future progress will be the continued consideration of age-frequency distributions rather than just the total age range of specimens that an assemblage contains, as well as the development of efficient specimen sampling protocols conducive to fitting models to data. These considerations are especially important as focus continues to grow on the wealth of prehistoric and historic ecological information that archives of skeletal remains can provide to inform today's pressing conservation and management efforts.

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