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Ecological fidelity of functional traits based on species presence-absence in a modern mammalian bone assemblage (Amboseli, Kenya)

Joshua H. Miller, Anna K. Behrensmeyer, Andrew Du, S. Kathleen Lyons, David Patterson, Anikó Tóth, Amelia Villaseñor, Erustus Kanga, and Denné Reed

Abstract.—Comparisons between modern death assemblages and their source communities have demonstrated fidelity to species diversity across a variety of environments and taxonomic groups. However, differential species preservation and collection (including body-size bias) in both modern and fossil death assemblages may still skew the representation of other important ecological characteristics. Here, we move beyond live-dead taxonomic fidelity and focus on the recovery of functional ecology (how species interact with their ecosystem) at the community level for a diverse non-volant mammal community (87 species; Amboseli, Kenya). We use published literature to characterize species, using four functional traits and their associated categorical attributes (i) dietary mode (11 attributes; e.g., browser, grazer), (ii) preferred feeding habitat (16 attributes; e.g., grassland, woodland), (iii) preferred sheltering habitat (17 attributes; e.g., grassland, underground cavity), and (iv) activity time (7 attributes; e.g., diurnal, nocturnal, nocturnally dominated crepuscular). For each functional ecological trait we compare the death assemblage's recovered richness and abundance structure of constituent functional attributes with those of the source community, using Jaccard similarity, Spearman's rho, and the Probability of Interspecific Encounter (evenness). We use Monte Carlo simulations to evaluate whether these empirical comparisons are significantly different from expectations calculated from randomized sampling of species from the source community. Results indicate that although the Amboseli death assemblage is significantly overrepresented by large-bodied species relative to the Amboseli source community, it captures many functional dimensions of the ecosystem within expectations of a randomized collection of species. Additional resampling simulations and logistic regressions further illustrate that the size bias inherent to the Amboseli death assemblage is not a major driver of deviations between the functional ecological properties of the death assemblage and its source community. Finally, the Amboseli death assemblage also enhances our understanding of the mammal community by adding nine species and two functional attributes previously unknown from the ecosystem.

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Introduction

The incomplete nature of the fossil record offers a universal challenge to paleobiology and demands that we understand the variety and quality of biological data retrievable from preserved remains. These concerns have led to a wave of inquiries into the ecological data recorded in modern death assemblages (accumulations of bones, shells, or other durable biological remains), revealing that many characteristics of contemporary faunal communities are captured in their death assemblages with high levels of fidelity to taxonomic composition and relative abundance distribu-

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tions (Kidwell 2001, 2002, 2007; Lockwood and Chastant 2006; Olszewski and Kidwell 2007; Tomašových and Kidwell 2009a,b; Western and Behrensmeyer 2009; Terry 2010a,b; Miller 2011; for reviews, see Kidwell 2013 and Kidwell and Tomašových 2013). There are also indications that death assemblages have high spatial fidelity to species landscape use and diversity gradients (Tomašových and Kidwell 2009b; Miller 1988; Miller 2012; Miller et al. 2013). However, the capacity of death assemblages to record community ecology data beyond various patterns of taxonomic richness and abundance, such as a community's diversity of functional ecological roles, remains largely unknown.

Both paleobiologists and neontologists are increasingly concerned with understanding the functional aspects of species and their ecosystems. For biologists working in modern settings, "functional ecology" explores how species' phenotypes interact with their ecosystem (McGill et al. 2006; Petchey and Gaston 2006; Shipley et al. 2006; Westoby and Wright 2006). It is a process-based approach that focuses on species' ecological roles, ecosystem services, and responses to environmental conditions (Cummins 1974; Calow 1987; Hooper and Vitousek 1997; Tilman et al. 1997; Blondel 2003; Blaum et al. 2011). At its core, functional ecology focuses on life-history traits (e.g., how species move, feed, and breed) and on characterizing their diversity within communities. In studies of modern systems there is a growing interest in quantifying species' functional ecology within an ecosystem, including the diversity of categorical or continuous attributes characterizing each trait, as an additional measure of biodiversity (Stevens et al. 2003; McGill et al. 2006; Petchey and Gaston 2006; Shipley et al. 2006; Westoby and Wright 2006; Cadotte et al. 2011). Such studies reveal that unique information is obtained from separately quantifying ecosystems' taxonomic and functional aspects and that changes in functional diversity and disparity do not necessarily track changes in a community's taxonomic richness and composition (Tilman et al. 1997; Stevens et al. 2003; Fukami et al. 2005; Villéger et al. 2010; Villéger 2012). Analyses incorporating both functional and taxonomic diversity provide a fuller appreciation for how ecological communities are structured as well as how they respond to anthropogenic and environmental perturbations (McGill et al. 2006; Petchey and Gaston 2006; Shipley et al. 2006; Westoby and Wright 2006; Cadotte et al. 2011). In fact, establishing functional responses of species and their communities to environmental and ecological changes over the last few decades is helping to clarify the depth and breadth of current biodiversity crises (Loreau et al. 2001; Stevens et al. 2003; Villéger et al. 2010; Villéger 2012). Similarly, time-averaged fossil records offer paleobiologists a unique and valuable opportunity to test (1) how ecosystem functioning responds to centennial- or millennial-scale (or longer) environmental changes, and (2) how the character of those functional responses (including the development of novel functional types) changes through deep time (Novack-Gottshall 2007; Villéger et al. 2011). This aspect of paleoecology may be especially informative when analyses include species across a wide range of body sizes and trophic guilds, particularly for examining the evolution of functional diversity through time. However, the skeletal remains of species of different body sizes can be differentially affected by preservation and collection biases, which could dramatically skew representation of functional ecological traits and ecological interpretations of the source community.

Paleobiologists have long used functional interpretations of fossil species or the disparity of species morphologies to examine macroecological and macroevolutionary changes in lineages and biotas through time (Andrews et al. 1979; Damuth et al. 1992; Foote 1993, 1994, 1995, 1999; Harris 1993; Lupia 1999; Lofgren et al. 2003; Friedman 2010; Anderson et al. 2011). Comparisons between the functional data available from fossil deposits and expectations derived from modern ecosystems have also been used to evaluate sampling bias and reliability of available paleoecological data (Robb 2002; Soligo and Andrews 2005; Andrews 2006; Le Fur et al. 2011). Morphological data, isotopic proxies, and other methods provide information on functional aspects of species leading to detailed hypotheses about the ecological settings represented by fossil deposits and their evolutionary significance (Andrews et al. 1979; Van Valkenburgh 1987; Spencer 1995; Jernvall et al. 1996; Reed 1998; Cerling and Harris 1999; Fortelius and Solounias 2000; Novack-Gottshall 2007; Badgley et al. 2008; Uno et al. 2011; Villéger et al. 2011; Cerling et al. 2013). Although functional aspects of an ecosystem offer important contributions to our understanding of extinct communities and their ecological and evolutionary changes through time, no previous study has tested the capacity of death assemblages to accurately record a community's functional diversity. Here, we evaluate how faithfully skeletal remains in a modern death assemblage (Amboseli National Park, Kenya) record the cumulative functional ecology (i.e., the diversity of functional characteristics) of the mammalian source community.

Using the Amboseli ecosystem, where the living mammal community and its death assemblage are well-known, we compare the functional ecological diversity of the entire non-volant mammal community (e.g., all rodents, carnivores, primates, ungulates, etc.) to that recovered from the dead. This goes beyond testing live-dead concordance of species composition and abundance; previous work has demonstrated a high level of taxonomic and relative abundance fidelity for the 15 most common Amboseli herbivores and proportional abundances for some herbivore dietary types (Western and Behrensmeyer 2009). Our goal is to test how well a death assemblage captures ecological features of its source community (the collection of known species that could have contributed to the death assemblage at some point during its formation) when using the kinds of functional ecological attributes often employed by paleoecologists and neoecologists (e.g., browser, grazer, carnivore). As a result, we evaluate species across six orders of body-size magnitude, making this the largest range of body sizes examined for a fidelity study of a mammalian death assemblage on a landscape surface (see Hadly 1999 for species recovery across body sizes in a cave setting). Because data on fossil assemblages are often restricted to presence-absence, we confine our knowledge of the Amboseli ecosystem (whether living or dead) to species lists and their associated functional ecological attributes. As part of this work, we also evaluate the relationships between body size and functional ecology and test how body size affects the biological data recorded by death assemblages.

The Amboseli Mammal Community.—Amboseli National Park, Kenya is part of a savanna ecosystem in southern Kenya near the Tanzania border (Fig. 1A). The mammals and plants of Amboseli have been extensively studied for the last 40+ years (e.g., Western 1973, 2006; Western and von Praet 1973; Altmann et al. 2002). Amboseli lies just south of the equator (2°S), within the latitudinal zone that is home to the richest mammalian communities on earth (Willig et al. 2003; Ceballos and Ehrlich 2006). Based on traditional ecological monitoring (~1960–2010), the living non-volant mammal community consists of 78 species spanning six orders of magnitude in body size. The first research on the Amboseli death assemblage was initiated in 1975 (Behrensmeyer 1978; Behrensmeyer et al. 1979) and has continued intermittently since then, with the latest bone surveys in 2010 (Behrensmeyer et al. 2012). Because of burial, weathering, and other bone-recycling processes, most identifiable skeletal remains disappear from the surface within 10–15 years, but bones of larger animals (e.g., rhino, elephant, giraffe) can survive 30+ years (Behrensmeyer 1978; Western and Behrensmeyer 2009). The documented death assemblage thus provides a record of the Amboseli mammal community that extends roughly from 1965 to 2010, the same time span represented by available surveys of the living community (Williams 1967; Western 1973; Kanga et al. 2004; Western and Behrensmeyer 2009).

Unique species (with unique functional ecological attributes) were recovered from surveys of both the living community and death assemblage. Thus, we present data on three different categorizations of the Amboseli mammal community: species known from surveys of living animals ("live" or $\mathrm{AMB}_{\mathrm{Live}}$), species known from the death assemblage ("dead" or $\mathrm{AMB}_{\mathrm{Dead}}$), and the best current

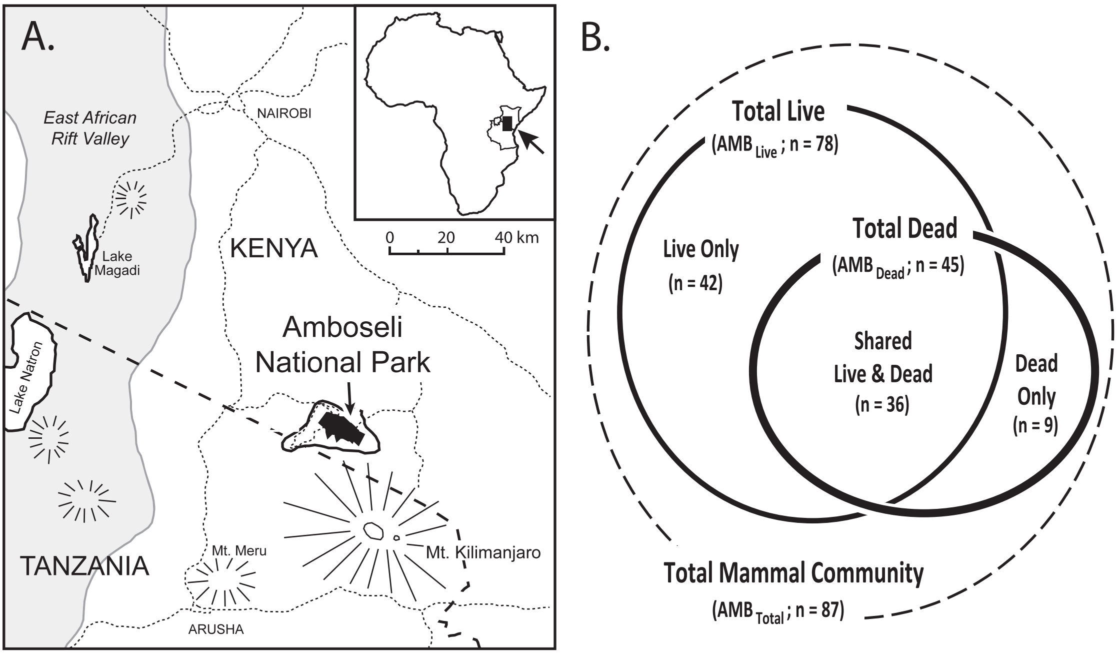

FIGURE 1. A, Map of Kenya showing the location of Amboseli National Park (black polygon) and surrounding basin (solid line). B, Schematic diagram showing the relationships of the different samples of the Amboseli non-volant mammal community used in this study. Data from surveys of the living community (AMB_{Live}) and surveys of the death assemblage (AMB_{Dead}) are known from a similar temporal window (i.e., the first bone surveys [1975] documented some skeletal materials from individuals contemporaneous to the first living surveys [~1960s]). Thus, the composite total of all unique species (AMB_{Total}) represents a decadally averaged estimate of all species in the Amboseli ecosystem over the past ~50 years (Supplementary Appendix A). Dashed line is a reminder that the Amboseli mammal community likely includes additional unsampled species.

estimate of the total source community ("total" or AMB_{Total}, based on a composite of the live and dead) (Fig. 1B). Vertebrate death assemblages are known to exhibit high spatial fidelity (Terry 2010a; Miller 2012; Miller et al. 2013); thus we can reasonably assume that all species known from AMB_{Dead} are members of the Amboseli community (or were at one point during the sampling duration). Combining unique species from AMB_{Dead} and AMB_{Live} offers an enhanced census of the overall mammal community. Because knowledge of the dead and the live extends across a similar ~50 year window, we treat AMB_{Live}, AMB_{Dead}, and AMB_{Total} as time-averaged and temporally equivalent species lists. We note that where living faunas are known across significantly shorter durations than the time period represented by local death assemblages (e.g., centennial- to millennial-scale time-averaging observed in many marine molluscan death assemblages: Meldahl et al. 1997; Kidwell et al. 2005; Kosnik et al. 2009; Kidwell 2013) careful consideration of such temporal incongruities is warranted before similarly aggregating data sets. Finally, while we offer live-dead (AMB_{Live}–AMB_{Dead}) and live-total (AMB_{Live}–AMB_{Total}) comparisons throughout this study, we are primarily concerned with the question of how faithfully the dead record functional ecological data of the source community (AMB_{Dead}–AMB_{Total} comparisons).

Methods

To determine the functional ecological diversity of AMB_{Total} and quantify the fidelity with which AMB_{Dead} captures that diversity, we assembled the following data sets: (1) species lists for wild (i.e., non-domesticated), non-volant mammals found in the living Amboseli community and in the death assemblage, and (2) a set of descriptive traits characterizing the functional ecological properties of the species in the community. To assess the fidelity between AMB_{Dead} and AMB_{Total} (and assess specific biasing factors, such as body size), we used similarity metrics, multivariate ordination (i.e., nonmetric multidimensional scaling), and logistic models (Gotelli and Ellison 2004; Kidwell 2007; Terry 2010a; Miller 2011; Legendre and Legendre 2012; Sokal and Rohlf 2012). Species' body sizes, which are an important factor in the destruction and loss rates of skeletal elements (Behrensmeyer et al. 1979), are considered separately from the targeted functional ecological traits to permit tests of how trait attributes are distributed across body sizes. Sample size is a critical issue for all paleoecological analyses; thus we used Monte Carlo simulations (Gotelli and Ellison 2004; Kowalewski and Novack-Gottshall 2010) to test how recovery of different proportions of available species diversity (i.e., differing sample completeness of AMB_{Dead} with respect to AMB_{Total}) affects inferences about the community-wide functional ecology of Amboseli.

Species Data on the Live and the Dead.—To compile a list of mammals living in the Amboseli community, literature accounts of all known species observed in Amboseli were tabulated (Williams 1967; Western 1973). To supplement our understanding of mammals less than 1 kg (small mammals), we used live-trapping surveys conducted in 2002–2003 (Kanga et al. 2004). Occurrences of species in the death assemblage were compiled from 40 years of bone surveys (Behrensmeyer et al. 1979; Western and Behrensmeyer 2009) and supplemented by analysis of small-mammal remains found in owl pellets (Reed et al. 2006). Because bats are very rare in most of the mammalian fossil record, we have limited our analyses to non-volant species.

Ecological Traits and their Character Attributes.—Four functional ecological traits were used to characterize the ecology of the Amboseli mammal community: preferred diet ("Diet"), preferred sheltering habitat ("Sheltering Habitat"), preferred feeding habitat ("Feeding Habitat"), and period of greatest activity during a 24-hour period ("Activity Time"). For each of these traits, multiple categorical attributes (Violle et al. 2007) were developed organically by searching out known ecological characteristics of species from the literature (Kingdon 1971, 1984a,b,c, 1989a,b,c,d, 1997; Estes 1991; Haltenorth and Diller 1995; Reed 2007) and web-based databases and information sources (MOM v. 3.3, ARKive; IUCN Red List; University of Michigan Animal Diversity Web [http://animaldiversity.ummz.umich.edu/]). The definitions of species' functional attributes were also based, in part, on the ETE Database of Species Characters (Damuth et al. 1997; http://www.mnh.si.edu/ete/ETE_Database_Manual.html). In some cases, especially for small mammals, consistent descriptions of species' functional ecological attributes were difficult to obtain. When sources differed, we relied upon the primary literature of researchers with established field programs in the region (Kingdon 1971, 1984a,b,c, 1989a,b,c,d, 1997; Reed 2007). Body-mass estimates come from an updated version of the MOM database (Smith et al. 2003). For species that range outside Africa and for which separate mass estimates are available from different regions, we used African-based body masses. Diet was characterized as the primary food resource consumed by the species. Feeding Habitat is the environment where animals spend most of their foraging time. Sheltering Habitat is defined by where species spend most of their non-feeding hours. Activity Time is the part of the daily cycle of greatest activity. Functional attributes could be appended with secondary and tertiary modifiers denoting decreasing importance of those respective attributes. For example, a species that primarily feeds in grasslands, occasionally in bushlands, and less frequently in woodland habitats is summarized as: "grassland-bushland-woodland." If functional attributes were not explicitly available from the literature, they were inferred from behavioral descriptions. For example, although knowledge of the sheltering ecology is limited for Kaiser's rock rat (*Aethomys kaiseri*), they are known to utilize cracks in soils as well as fallen timber or boulders (Kingdon 1984c). Thus, we classified their sheltering habitat as cavity-dwelling, including above-ground cavities (abbreviated: cav.ag, Supplementary Appendix A). Species' ecological traits were applied to both living and dead representatives.

Testing for Body-size Bias and Examining the Role of Body Size in Functional Ecology.—To test for body-size bias in $\mathrm{AMB_{Dead}}$ and $\mathrm{AMB_{Live}}$ (i.e., differences in $\log_{10}$ body sizes of species recovered versus species not recovered), we used Wilcoxon two-sample tests (Sokal and Rohlf 2012). To test for differences among body-size distributions we used Komolgorov-Smirnov two-sample tests (Sokal and Rohlf 2012). We used logistic regression of species recovery and non-recovery in $\mathrm{AMB_{Dead}}$ and $\mathrm{AMB_{Live}}$ to provide a supporting measure of the strength and significance of size bias (Sokal and Rohlf 2012). Logistic models also provided predicted probabilities that individual species would be recovered, given their $\log_{10}$-transformed body mass. All analyses and simulations (see below) were scripted in the open-source language, R (v. 3.0.2; R Development Core Team 2013).

To examine the relationships between body size and functional ecology we calculated the overall ranges of $\log_{10}$-transformed body size and associated body-size frequency distributions for species sharing each functional attribute within each of the four functional traits. One way for size bias to obscure or delete information on a community's functional traits is if particular functional attributes are found only in species whose body sizes are not sampled by $\mathrm{AMB_{Dead}}$ (e.g., perhaps cavity-dwelling species include only a narrow range of small-bodied species). Thus, it is important to establish whether functional attributes within each of the four traits are composed of nonrandom collections of available body sizes. To test whether functional attributes are composed of biased body-size subsets of the Amboseli mammal community ($\mathrm{AMB_{Total}}$) we used bootstrap simulations. These simulations tested whether the observed ranges of body sizes within each functional attribute are different from expectations based on randomized sorting of species (sampling with replacement). Body-size ranges of functional attributes were calculated after species were randomly assigned (holding species richness of attributes to that observed in $\mathrm{AMB_{Total}}$). Randomizations were repeated 10,000 times to produce null mean expectations and 95% confidence intervals of body-size ranges for each functional attribute.

Testing the Dead's Fidelity to Whole-Community Functional Ecology.—To compare how the functional ecological data in $\mathrm{AMB_{Dead}}$ compare with $\mathrm{AMB_{Total}}$, we first counted the number of species sharing each attribute within the four functional traits. We then used standard ecological metrics to investigate specific aspects of how $\mathrm{AMB_{Dead}}$ records functional ecological data from $\mathrm{AMB_{Total}}$, including the recovery of available trait attributes (Jaccard similarity), and whether $\mathrm{AMB_{Dead}}$ records more nuanced aspects of functional ecological structure, including the rank order (Spearman rank-order correlation) and evenness (Probability of Interspecific Encounter: PIE; Hurlbert 1971) of attribute abundance profiles within traits. For evenness, we were interested in both raw PIE and the difference in PIE (**Δ**PIE; Olszewski and Kidwell 2007) between $\mathrm{AMB_{Dead}}$ and $\mathrm{AMB_{Total}}$. **Δ**PIE is a useful metric for comparing evenness of two samples, because if $\mathrm{AMB_{Dead}}$ is a perfect representation of $\mathrm{AMB_{Total}}$, **Δ**PIE will equal zero. Finally, we explored the multidimensional functional ecospace of the total Amboseli mammal community using nonmetric multidimensional scaling (NMDS). NMDS results were calculated by using a Gower's distance matrix derived from species similarities based on all four functional traits. Results from a principal coordinates analysis (also done on a Gower's distance matrix) were used as the initial configuration from which to start iterative searches in NMDS. Within the NMDS, we then highlighted the species recovered by $\mathrm{AMB_{Dead}}$ to identify portions of ecospace both recorded and not recorded by the dead.

We used simulations to evaluate whether offsets observed between centroids of $\mathrm{AMB_{Live}}$ and $\mathrm{AMB_{Dead}}$ (the two subsamples of the total community) and the global centroid (located at [0,0]) were significantly larger than offsets expected on the basis of randomized groupings of species. We calculated the null expectations by randomly assigning species (sampling with replacement) to "live" and "dead" groups (using sample sizes consistent with the species richness observed in $\mathrm{AMB_{Live}}$

and AMB_{Dead}) and calculating the Euclidean distances between group and global centroids. In this way, the simulations provided expectations of offset between group and global centroids that control for sample-size differences between AMB_{Dead} and AMB_{Live}. To establish how AMB_{Dead} and AMB_{Live} sample the overall multivariate functional ecospace of AMB_{Total}, we compared the dispersion (multivariate spread) of species in AMB_{Live} with that of AMB_{Dead}, using a modified test of homogeneity of multivariate dispersion (HMD; Anderson 2006; Tomašových and Kidwell 2011). To incorporate the full multidimensionality of the data (as opposed to limiting the analysis to two NMDS axes), we calculated dispersion in full principal coordinate space. Following Tomašových and Kidwell (2011), dispersion of AMB_{Live} was calculated as the mean multivariate Euclidean distance between all AMB_{Live} species and the multivariate centroid of AMB_{Live}. Addressing the autocorrelative nature of AMB_{Live} and AMB_{Dead}, the dispersion of the AMB_{Dead} was calculated as the mean distance between all AMB_{Dead} species and the centroid of AMB_{Live} (Tomašových and Kidwell 2011). We calculated confidence intervals for all simulations as well as HMD tests of significance using the results of 10,000 permutations.

Establishing Null Expectations for Death Assemblage Fidelity.—Does the functional ecological data provided by AMB_{Dead} approximate a random sample of the whole community? If the answer is yes, this has positive implications for the recovery of functional data from fossil records. Our empirical data (e.g., our data on AMB_{Dead} and AMB_{Total}) provide a single set of comparisons (e.g., one Jaccard similarity value for each functional trait). However, even if that comparison shows "high" or "low" fidelity, it is necessary to establish a null framework for understanding that comparison and assessing whether AMB_{Dead} is within or deviates from expectations of a randomized collection of species from AMB_{Total}. We used Monte Carlo simulations to examine our single AMB_{Dead}–AMB_{Total} comparison in the context of a null distribution of bias-free samples of AMB_{Total} (i.e., iteratively comparing the total Amboseli source community with a random subsample of itself using the aforementioned ecological metrics; AMB_{Total}–AMB_{Random}). To model the sampling mode of the death assemblage, species were sampled in our simulations without replacement (once a species is sampled, it cannot be resampled; however, replacement mode has no bearing on our results). As before, comparisons were made separately for each of the four functional ecological traits (Diet, Feeding Habitat, Sheltering Habitat, Activity Time). Using these simulations, we then calculated 95% confidence intervals to summarize similarities of the complete AMB_{Total} versus a randomized sample of itself and to offer a quantitative framework against which to judge whether similarities between AMB_{Dead} and AMB_{Total} are within null expectations.

Because samples of species from fossil assemblages are often limited, we also determined how the confidence interval changes with different sampling intensities. Thus, simulations were run iteratively from five species (an arbitrary low sample size corresponding to ~5% of AMB_{Total}) to the total number of species available in AMB_{Total}. Simulations were repeated 10,000 times at each richness/sample size.

To characterize deviations from random with which AMB_{Dead} records functional ecological data with increased sampling, we reran the simulations (using the same ecological metrics as before), comparing only the diversity of functional attributes found in AMB_{Dead} to those of AMB_{Total}. Simulations ranged from five species to the total number of species recovered by AMB_{Dead} (45). We then compared this subsampling envelope for randomized AMB_{Dead}–AMB_{Total} similarities with the null sampling distribution for the total community (AMB_{Total}–AMB_{Random}).

How Does Size Bias Affect Ecological Characteristics in a Simulated Death Assemblage?—To establish how size bias in AMB_{Dead} affects sampling of the functional ecology from AMB_{Total}, we calculated null expectations for the dead's accumulation of functional ecological data under the effects of its empirically sampled size bias. We accomplished this by calculating the probabilities that species of any given body size will be successfully sampled by $\mathrm{AMB_{Dead}}$ (based on our logistic regression of species presence-absence in $\mathrm{AMB_{Dead}}$ on logged body size) and then weighting the retrieval of species from $\mathrm{AMB_{Total}}$ in the Monte Carlo simulations by that probability. We then compared the size-biased collection of functional ecological data to that generated under purely random sampling without a size bias (discussed above: $\mathrm{AMB_{Total}}$–$\mathrm{AMB_{Random}}$). In this way, we can assess how a common paleobiological concern (i.e., size bias) affects the recovery of ecological data and compare that result with both idealized (random) data recovery and data from the actual death assemblage.

Results

Species Recovery for the Live and the Dead.—Ecological research and surveys of Amboseli's living mammal populations over the past ~50 years have yielded a total of 78 species known to currently or previously occur in the non-volant community ($\mathrm{AMB_{Live}}$; $S = 78$; Fig. 1B). Bone surveys recovered 45 mammal species ($\mathrm{AMB_{Dead}}$; $S = 45$). In total, 36 species are shared between the live ($\mathrm{AMB_{Live}}$) and the dead ($\mathrm{AMB_{Dead}}$; Fig. 1B); 41% of $\mathrm{AMB_{Live}}$ were recovered by $\mathrm{AMB_{Dead}}$, while 80% of $\mathrm{AMB_{Dead}}$ species were represented by $\mathrm{AMB_{Live}}$. $\mathrm{AMB_{Live}}$ includes 42 species only known from traditional ecological methods (Fig. 1B: "Live Only"), whereas $\mathrm{AMB_{Dead}}$ includes nine species not observed in $\mathrm{AMB_{Live}}$ (i.e., not previously recorded in the Amboseli ecosystem). Combining unique species from both samples ($\mathrm{AMB_{Live}}$ and $\mathrm{AMB_{Dead}}$) gives a total estimated richness for the time-averaged Amboseli non-volant mammal community of 87 species ($\mathrm{AMB_{Total}}$; $S = 87$), which is higher than observed in either $\mathrm{AMB_{Live}}$ or $\mathrm{AMB_{Dead}}$.

As recovered from studies of other African mammal communities (Kelt and Meyer 2009), the body-size frequency distribution of $\mathrm{AMB_{Total}}$ is bimodal (Fig. 2). Species larger than 100 kg are recovered equally in $\mathrm{AMB_{Live}}$ and $\mathrm{AMB_{Dead}}$ (as previously recognized: Behrensmeyer et al. 1979; Western and Behrensmeyer 2009). The 42 species found only in $\mathrm{AMB_{Live}}$ (Fig. 2: "Live-Only Species") encompass the full range of body sizes less than 100 kg, while the nine species recovered solely from $\mathrm{AMB_{Dead}}$ (Fig. 2: "Dead-Only Species") are limited to body sizes less than 1 kg. Median $\log_{10}$-body sizes for $\mathrm{AMB_{Dead}}$ (1.31) and $\mathrm{AMB_{Live}}$ (0.92) are both larger than $\mathrm{AMB_{Total}}$ (0.62), and Wilcoxon tests of $\log_{10}$-body size between species recovered in $\mathrm{AMB_{Dead}}$ (or $\mathrm{AMB_{Live}}$) and species not recovered reveal that these differences are significant (p-values < 0.01; Supplementary Table S1). $\mathrm{Log_{10}}$-body sizes of $\mathrm{AMB_{Dead}}$ and $\mathrm{AMB_{Live}}$ are not significantly different ($p > 0.05$; Supplementary Table S1). Separate logistic regressions also reveal strong size biases in both $\mathrm{AMB_{Live}}$ ($p < 0.01$) and $\mathrm{AMB_{Dead}}$ ($p < 0.05$), with larger-bodied species significantly more likely to be sampled than smaller-bodied species (Supplementary Table S2). Predicted probabilities that species in $\mathrm{AMB_{Total}}$ are recovered in $\mathrm{AMB_{Dead}}$ are generally high, with all species larger than 2 kg showing greater than 50% probability of recovery based on body size alone (Supplementary Table S3). Recovery probabilities for species larger than 10^2 kg are greater than 65%, with species larger than 10^3 kg having recovery probabilities of ~75% or higher (Supplementary Table S3).

Functional Ecological Attributes and Body Size.—In Amboseli, functional ecological attributes are generally shared by species across wide ranges of body size (see Supplementary Appendix A for tabulation of species, body size, and functional ecological traits). In total, there are 51 functional attributes, 39 of which are shared by multiple species (i.e., 12 are represented only by single species). Thirty-eight of these 39 (97%) range across more than one order of magnitude in body size and 28 (72%) include species that are both below and above 1 kg (i.e., include both "small" and "large" species; Supplementary Appendix A, Fig. 3). Such broad overlap of functional attributes across body sizes indicates that even size-biased collections of species can incorporate large proportions of available functional attributes (i.e., high Jaccard similarity).

There is little indication of a consistent body-size frequency distribution among individual functional attributes, or that any of them are uniformly distributed across body sizes (which, if true, would improve recovery of functional ecological data even in size-

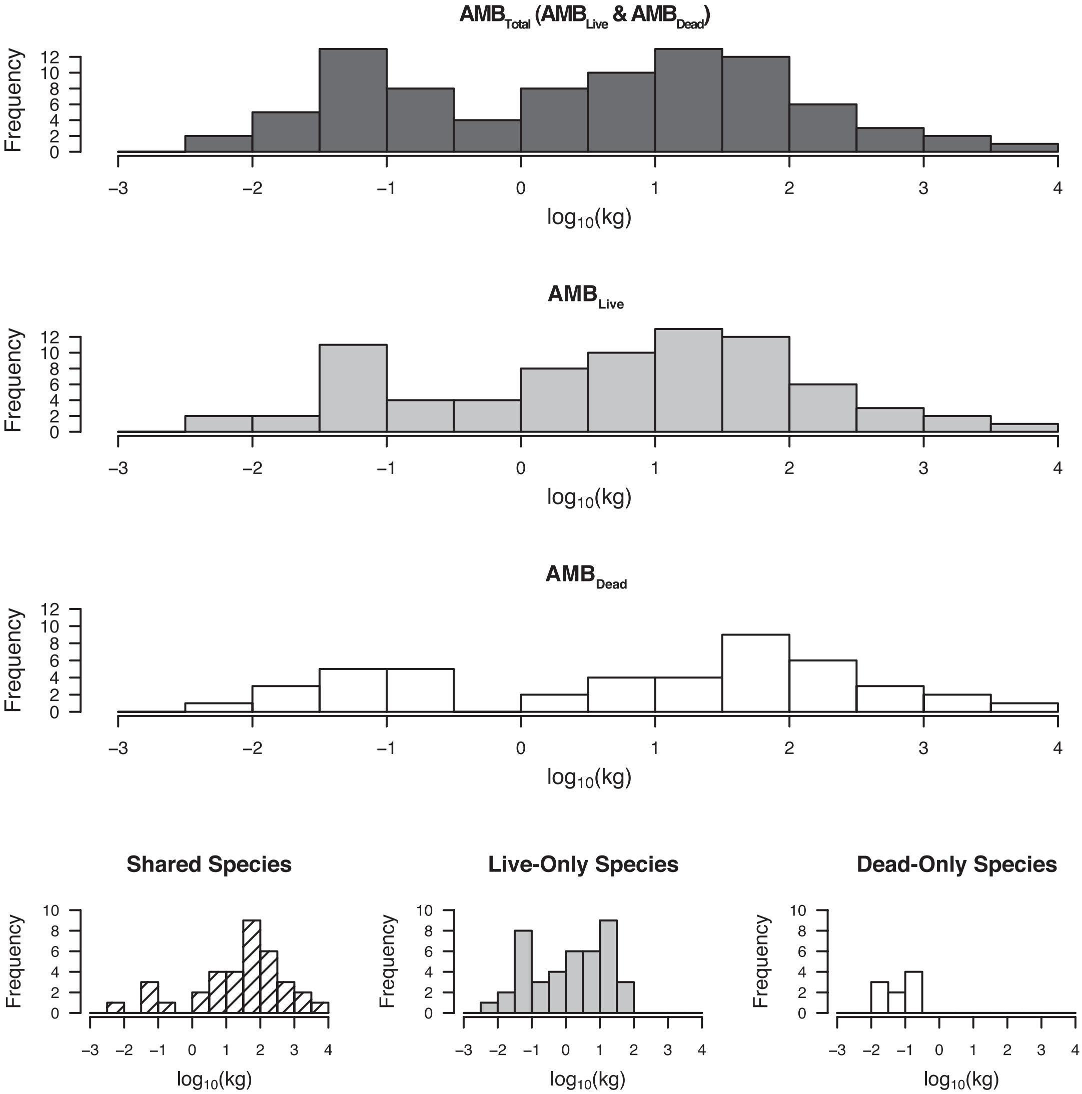

FIGURE 2. Log-transformed body-size (kg) frequency distributions of non-volant mammal species found in Amboseli National Park. AMB_{Total} combines all unique species recovered from sampling the live (AMB_{Live}) and dead (AMB_{Dead}) and represents the best estimate for richness and body-size distribution of the whole time-averaged source community. "Shared Species" displays species recovered by both AMB_{Live} and AMB_{Dead}. The body-size frequency distribution of species only found in the live ("Live-Only Species") and dead ("Dead-Only Species") are also provided. Complete listing of species in Supplementary Appendix A.

biased death assemblages). For example, the body-size distribution of diurnal species is roughly bell-shaped, whereas nocturnal species are concentrated in smaller-bodied animals with a noticeable tail toward larger-bodied species (Fig. 4). Species sheltering in "Underground Cavities" include only those less than 100 kg (and are most commonly species up to 30 kg), whereas species preferring to shelter in "Aboveground Cavities" are largely those of the smallest body sizes (less than 0.1 kg).

Although the ranges of body sizes characterizing the 51 functional attributes are variable (Figs. 3, 4), simulations generally fail to find significant differences between observed body-size ranges of individual functional attributes and expectations based on observed species richness and randomly sorting species into those attributes. Only one attribute (the

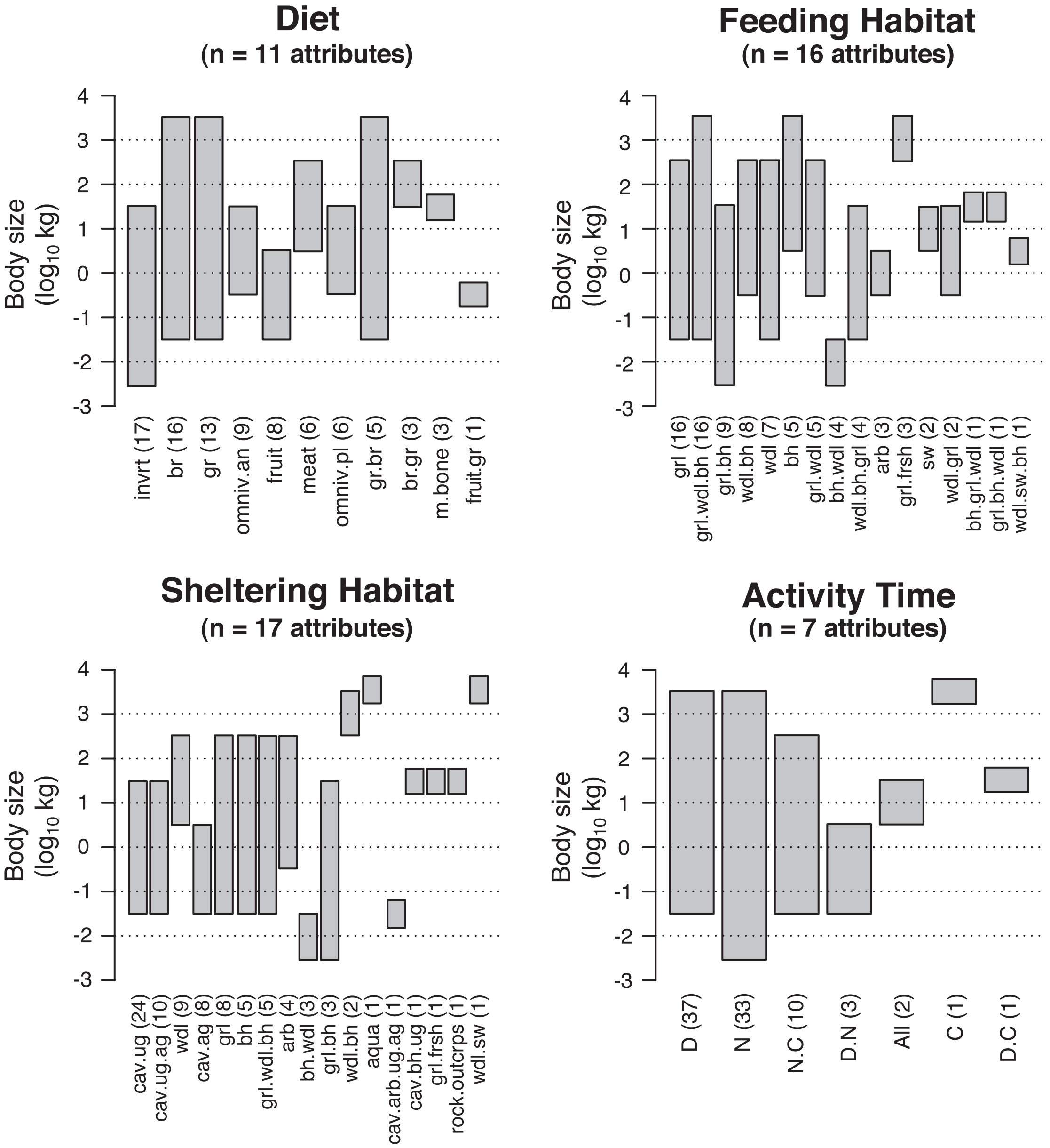

FIGURE 3. Generalized schematic of the range of body sizes (in orders of log-transformed magnitude) found in functional attributes in the Amboseli mammal community (AMB_{Total}). Attributes are ordered by their species richness (noted in parentheses; see Supplementary Appendix B). Functional attributes that include small (<1 kg) and large mammals (≥1 kg) can be identified by bars crossing $\log_{10} = 0$. Most of the functional attributes include mammals from multiple orders of body-size magnitude. For visual simplicity, note that small increments of body size are plotted halfway between the major $\log_{10}$-scale intervals on the y-axis (e.g., 0.9 or 0.3 kg are plotted halfway between –1 and 0).

"underground cavities" Sheltering Habitat) had an observed body-size range outside null expectations (in this case, smaller than expected; Supplementary Fig. S1), illustrating that sheltering in underground cavities comes with certain body-size restrictions (an intuitive finding). Overall, however, the body-size ranges of species sharing functional attributes (AMB_{Total}) follow null expectations.

Capturing the Diversity and Structure of Functional Ecological Traits.—The death assemblage (AMB_{Dead}) captures the majority of

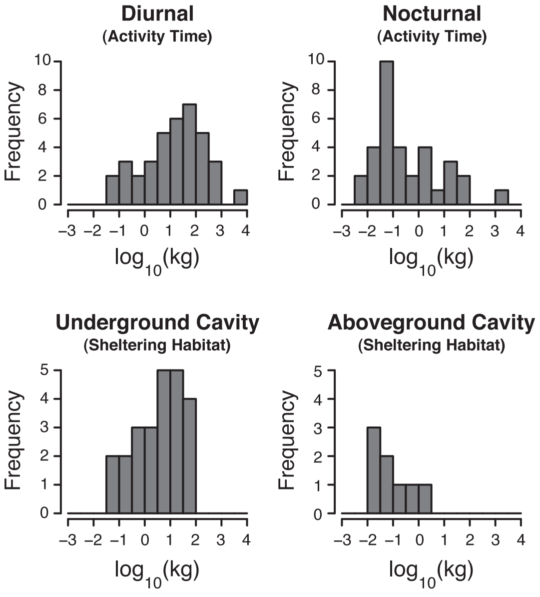

FIGURE 4. Body-size frequency distributions for selected functional ecological attributes found in $\mathrm{AMB}_{\mathrm{Total}}$. A variety of distributions occur across functional attributes (Supplementary Appendices A and B) and none are uniformly distributed across body size, suggesting that size biases could affect the representation of a community's functional ecology.

functional ecological attributes found in $\mathrm{AMB}_{\mathrm{Total}}$ (86%: 44 of 51 attributes were recovered). All 11 Diet attributes were recovered, as well as 13 of 16 Feeding Habitats, 15 of 17 Sheltering Habitats, and 5 of 7 Activity Times (Fig. 5 [see Fig. 3 for attribute identification], Supplementary Appendix B). The live ($\mathrm{AMB}_{\mathrm{Live}}$), which misses only nine species from $\mathrm{AMB}_{\mathrm{Total}}$, recovers all but two functional ecological attributes: one Diet preference (mixed frugivore-grazer) and one Sheltering Habitat (arboreal cavities; Fig. 5). The high correspondence between $\mathrm{AMB}_{\mathrm{Dead}}$, $\mathrm{AMB}_{\mathrm{Live}}$, and $\mathrm{AMB}_{\mathrm{Total}}$ in representation of functional attributes is also evident in their high Jaccard similarity values (generally at or approaching 1.0; Table 1). $\mathrm{AMB}_{\mathrm{Dead}}$ also shows highly positive (and strongly significant) rank-order fidelity to attribute abundances within functional traits ($\mathrm{AMB}_{\mathrm{Dead}}$ vs. $\mathrm{AMB}_{\mathrm{Live}}$ and $\mathrm{AMB}_{\mathrm{Dead}}$ vs. $\mathrm{AMB}_{\mathrm{Total}}$). Both $\mathrm{AMB}_{\mathrm{Dead}}$ and $\mathrm{AMB}_{\mathrm{Live}}$ closely record overall evenness (PIE) of attribute frequencies within the four functional traits (Table 2), showing estimates within 2.5% of $\mathrm{AMB}_{\mathrm{Total}}$ for all samples except the $\mathrm{AMB}_{\mathrm{Dead}}$ sample of Activity Time. Compared to $\mathrm{AMB}_{\mathrm{Total}}$, the $\mathrm{AMB}_{\mathrm{Dead}}$ sample of mammalian Activity Time is more strongly dominated by diurnal species (reducing evenness; Fig. 5).

Resampled $\mathit{AMB}_{\mathit{Dead}}$ *and* $\mathit{AMB}_{\mathit{Total}}$.—How would a random sample of species from $\mathrm{AMB}_{\mathrm{Total}}$ reflect the overall functional ecology of $\mathrm{AMB}_{\mathrm{Total}}$, and how does that reflection change with increased sample size? Monte Carlo simulations show that, compared to $\mathrm{AMB}_{\mathrm{Total}}$, the recovery of functional attributes based on randomly sampling species (Jaccard; Fig. 6, dark polygons, top row) generally quickly escalates towards 1.0 and occurs within a narrow range of values for any given sample size. For Diet, Feeding Habitat, and Sheltering Habitat, recovery of all available functional attributes (i.e., 95% confidence intervals include 1.0) occurs well before sampling the full complement of the 87 species in $\mathrm{AMB}_{\mathrm{Total}}$, ranging from 22 species for Diet (24% of $\mathrm{AMB}_{\mathrm{Total}}$) to 52 species for Sheltering Habitat (60%). The null expectation of functional attribute acquisition for Activity Time is more step-like because of the reduced number of attributes. Simulated expectations for rank-order agreement of attributes within functional traits (Fig. 6, middle row, dark-gray polygons) encompass much higher vertical variability than Jaccard, particularly at low sample sizes. This is especially apparent for Diet, Feeding Habitat, and Sheltering Habitat. The null expectation for evenness, including ΔPIE (Fig. 6, dark-gray polygons, bottom row) and raw PIE (Fig. 6, dark-gray polygons, bottom row inset) is highly sensitive to small increases in species sampling and quickly stabilizes to the observed $\mathrm{AMB}_{\mathrm{Total}}$ value.

How do the functional ecological data contained in $\mathrm{AMB}_{\mathrm{Dead}}$ reflect $\mathrm{AMB}_{\mathrm{Total}}$, and how is that different from the pattern generated from randomized sampling of species? Using the 95% confidence intervals defined by resampling $\mathrm{AMB}_{\mathrm{Total}}$ ($\mathrm{AMB}_{\mathrm{Total}}$–$\mathrm{AMB}_{\mathrm{Random}}$, Fig. 6, dark-gray polygons), at 45 species (the number of species recovered from $\mathrm{AMB}_{\mathrm{Dead}}$), nearly all $\mathrm{AMB}_{\mathrm{Dead}}$ vs. $\mathrm{AMB}_{\mathrm{Total}}$ comparisons (cross-hairs of all plots in Fig. 6, Tables 1 and 2) lie within null expectations. Only evenness for Activity Time lies slightly outside the 95%

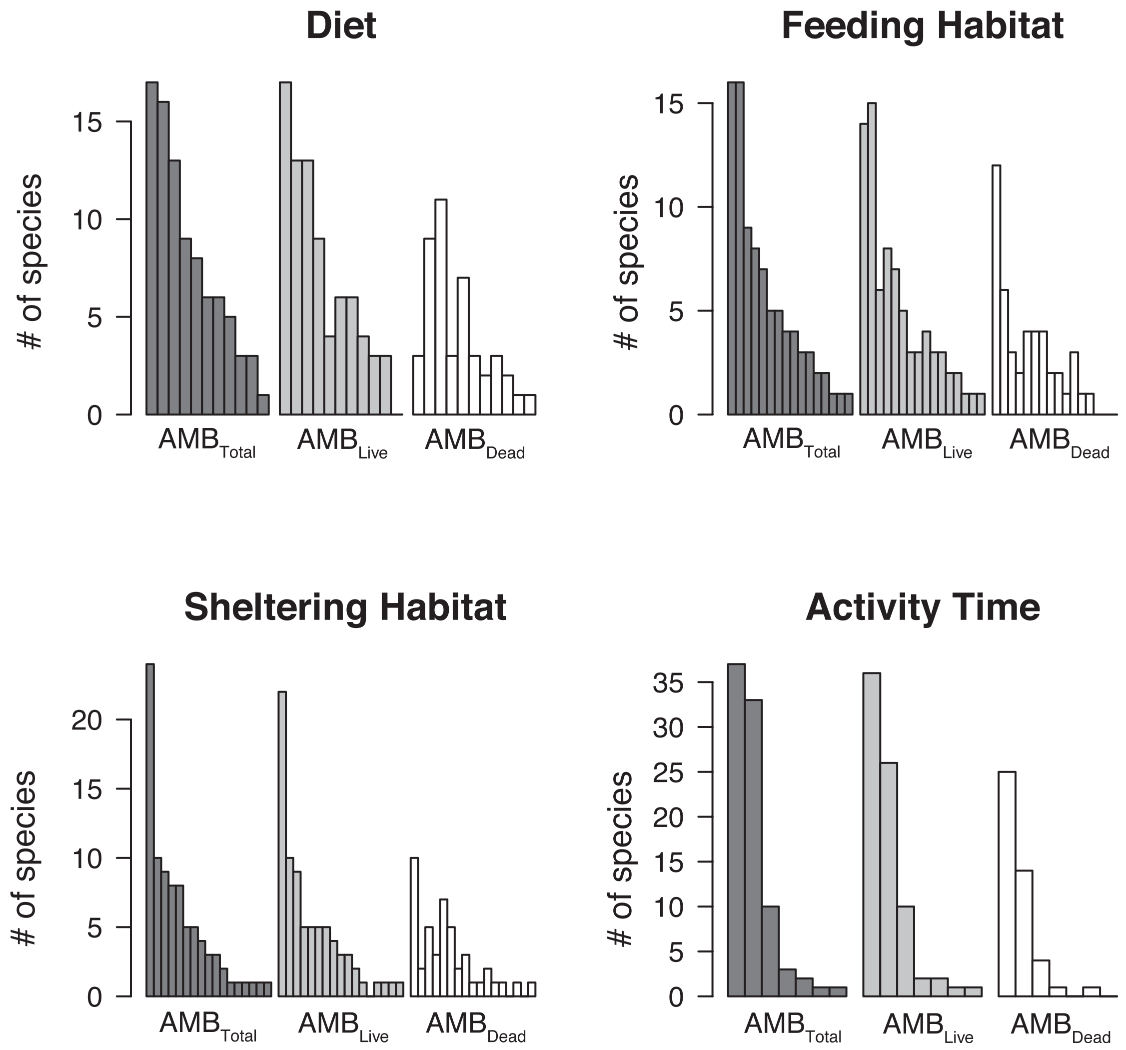

Figure 5. Species frequency distributions for attributes of four functional ecological traits (Diet, Feeding Habitat, Sheltering Habitat, and Activity Time) of Amboseli mammals as recorded by $\mathrm{AMB}_{\mathrm{Total}}$ (darkly shaded bars), $\mathrm{AMB}_{\mathrm{Live}}$ (lightly shaded bars), and $\mathrm{AMB}_{\mathrm{Dead}}$ (white bars). Each bar represents the number of species sharing a single functional ecological attribute. Attributes within the functional traits are ordered as in Figure 3 and Supplementary Appendix B.

Table 1. Comparisons of the composition and abundance structure of functional attributes within four ecological traits (Diet, Feeding Habitat, Sheltering Habitat, and Activity Time) as documented by species recovered in $\mathrm{AMB}_{\mathrm{Dead}}$, $\mathrm{AMB}_{\mathrm{Live}}$, and $\mathrm{AMB}_{\mathrm{Total}}$. All Jaccard similarity comparisons are high, evidence that $\mathrm{AMB}_{\mathrm{Dead}}$ and $\mathrm{AMB}_{\mathrm{Live}}$ both do a good job of capturing overall attribute composition of traits from $\mathrm{AMB}_{\mathrm{Total}}$. All Spearman rho values are highly positive (and significant), indicating high agreement among groups in rank-order of attribute abundances within each trait.

	$\mathrm{AMB}_{\mathrm{Dead}}$–$\mathrm{AMB}_{\mathrm{Total}}$		$\mathrm{AMB}_{\mathrm{Live}}$–$\mathrm{AMB}_{\mathrm{Dead}}$		$\mathrm{AMB}_{\mathrm{Live}}$–$\mathrm{AMB}_{\mathrm{Total}}$	
	Jaccard	rho	Jaccard	rho	Jaccard	rho
Diet	1.00	0.79 **	0.91	0.71 *	0.91	0.96 ***
Feeding habitat	0.81	0.89 ***	0.81	0.86 ***	1.00	0.97 ***
Sheltering habitat	0.88	0.86 ***	0.82	0.83 ***	0.94	0.99 ***
Activity time	0.71	0.88 **	0.71	0.85 *	1.00	0.99 ***

* $p < 0.05$; ** $p < 0.01$; *** $p << 0.001$.

TABLE 2. Probability of Interspecific Encounter (PIE; evenness) for abundance distributions of attributes within functional ecological traits (AMB_{Dead}, AMB_{Live}, and AMB_{Total}). All PIE values for AMB_{Dead} and AMB_{Live} are within 2.5% of AMB_{Total} except for Activity Time of AMB_{Dead}, which is more strongly dominated by diurnal species (Fig. 5).

	AMB_{Total}	AMB_{Live}	AMB_{Dead}
Diet	0.88	0.87	0.87
Feeding habitat	0.90	0.90	0.89
Sheltering habitat	0.88	0.88	0.90
Activity time	0.67	0.67	0.60

confidence interval of AMB_{Total}–AMB_{Random} (Fig. 6, dark-gray polygons). The composition and distribution of functional traits largely accumulates within expectations of randomized sampling of AMB_{Total}. High similarity between AMB_{Dead} and AMB_{Total} is accentuated in comparisons of Feeding and Sheltering Habitats, for which resampled-AMB_{Dead} curves (Jaccard, Spearman rho, PIE) tightly follow patterns of resampled AMB_{Total}. In fact, between resampled AMB_{Total} and resampled AMB_{Dead}, only rank-order correlations of Diet and the evenness of Activity Time show potentially meaningful deviations from expectations. A companion analysis testing null expectations of all AMB_{Live} and AMB_{Dead} comparisons shows that AMB_{Dead} falls within expectations generated from randomized sampling of the functional ecological data in AMB_{Live} (Supplementary Fig. S2).

Because the functional ecological attributes we used to characterize the Amboseli mam-

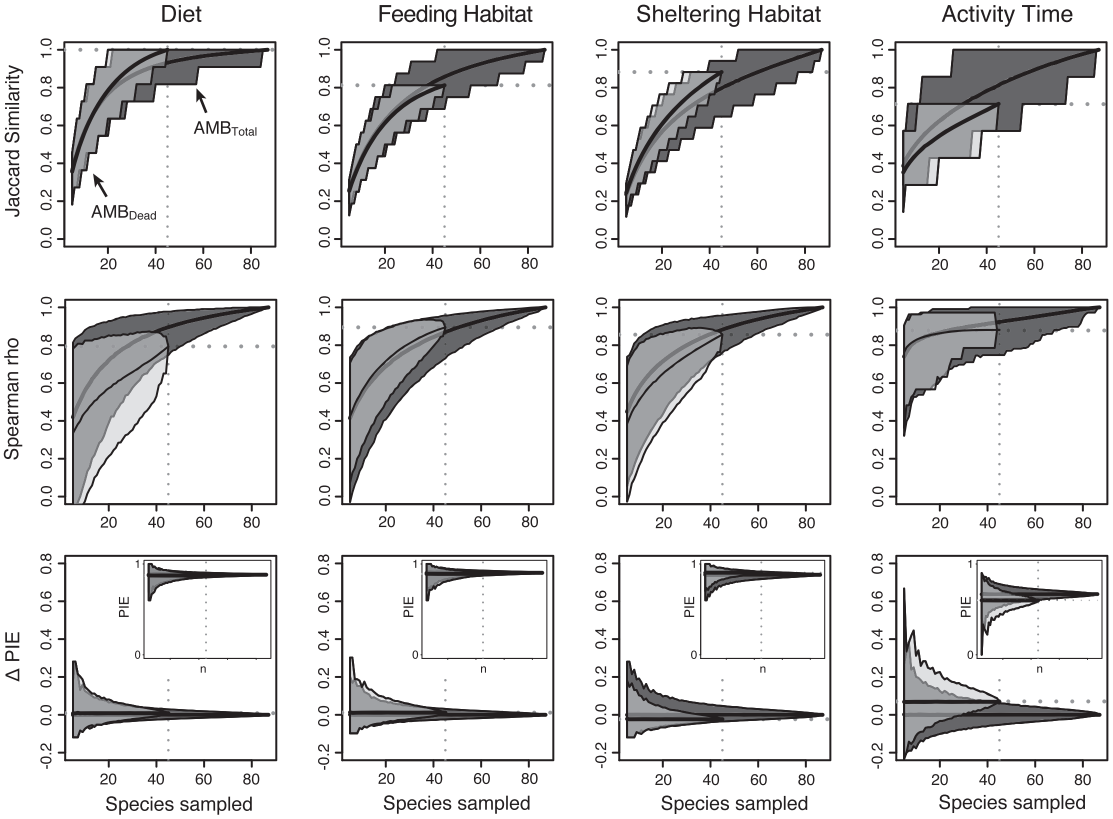

FIGURE 6. Results from Monte Carlo simulations modeling the recovery of functional ecological data from AMB_{Total} and AMB_{Dead}. Simulations are randomized iterative comparisons of the composition and abundance structure of functional attributes between AMB_{Total} and subsamples of AMB_{Total} (dark-gray polygons) and between AMB_{Total} and subsampled AMB_{Dead} (light-gray polygons). Three ecological metrics are used for comparing functional attribute composition and structure: Jaccard similarly, Spearman rank-order correlation (rho), and PIE (evenness). Cross-hairs indicate number of species recorded by AMB_{Dead} (x-axis) and the associated metric value for each analysis (y-axis). At 45 species (the richness of AMB_{Dead}), ecological metrics of AMB_{Dead} fall within the confidence intervals of randomized subsamples of AMB_{Total}. The evenness (PIE) of Activity Time is the one exception.

mal community were hierarchical (i.e., grazer-browsers are differentiated from "grazers" because they also browse), we can collapse those hierarchies to test whether the number of ecological attributes used in our analyses influenced our results. Collapsing more specified attributes to their primary (dominant) characteristic (e.g., browser, grazer, invertivore; resulting in 7 Diet attributes, 5 Feeding Habitats, 7 Sheltering Habitats, 3 Activity Times, Supplementary Appendix C) may also be more akin to data available in the fossil record. Monte Carlo results based on this condensed attribute set are consistent with previous findings; empirical AMB_{Dead}–AMB_{Total} comparisons are within null expectations of randomized AMB_{Total} (Supplementary Fig. S3).

A Gap in Ecological Data Recorded by AMB_{Dead}.—To examine the functional ecological fidelity of AMB_{Dead} in multivariate space, we projected the dead species onto an ordination (NMDS) of the functional ecological space generated by AMB_{Total} (Fig. 7). Visually, AMB_{Dead} appears to capture a wide array of the functional ecospace of AMB_{Total}. The modified HMD test reveals that the dispersion of AMB_{Dead} is significantly larger than AMB_{Live} ($p < 0.05$; Supplementary Table S4), which is noteworthy given that AMB_{Dead} is composed of roughly 40% fewer species. Although this indicates that AMB_{Dead} is an efficient recorder of the functional extremes contained in AMB_{Total}, randomization simulations show that the AMB_{Dead} centroid is significantly more offset from the global centroid than expected (the offset of the AMB_{Live} centroid is within expectations; Supplementary Table S5). Thus, there is an indication of bias in the functional ecological data recorded by AMB_{Dead}. The centroid offset of AMB_{Dead} is away from the lower-right quadrant of the NMDS (Fig 7, dotted square). In fact, rerunning the simulations after excluding species in this quadrant reveals that previously observed differences between the AMB_{Dead} and AMB_{Total} (global) centroids are no longer found (Supplementary Table S5). Relative to the rest of AMB_{Total}, this quadrant is enriched in species that (a) shelter in underground cavities, (b) consume animal products (including invertebrates, mammal meat, bone), and are (c) active during multiple periods of the day (Supplementary Fig. S4). Examples of such species include marsh mongoose, elephant shrew, ratel, and striped hyena. Importantly, the species in this quadrant are not a biased body-size subset relative to the rest of AMB_{Total} (Wilcoxon test: $W = 620$, $p = 0.57$). Instead, these findings indicate that AMB_{Dead} has an underlying bias against species in this region of ecospace based on aspects of their ecology other than body size.

Although the AMB_{Live} centroid is not significantly offset relative to the global centroid (Supplementary Table S5), we note that the majority of species not recovered by AMB_{Live} (seven of nine species) are in the upper right quadrant of the NMDS (Fig. 7; x's not enclosed by circles). All species in this quadrant of ecospace are nocturnal, a functional ecological attribute that often challenges surveys of living species.

Imposing an Analytical Size Bias.—Although analyses focused on the NMDS (Fig. 7) reveal that undersampling of functional ecospace by AMB_{Dead} does not appear linked to body-size bias, the effect of size bias is of general concern to paleobiologists. Resampling AMB_{Total} using our analytically imposed size bias (AMB_{Biased}, Fig. 8; light-gray polygons) does not produce major deviations in representation for any of the functional ecological traits. Presence-absence, rank-order correlation, and evenness of functional ecological attributes all show behavior nearly identical to the randomized resampling of AMB_{Total} (Fig. 8 dark-gray polygons). Thus, as previously suggested (Fig. 7, Supplementary Table S5) deviations observed between AMB_{Dead} and AMB_{Total} are likely caused by more nuanced and ecologically specific biases, such as reduced representation of cavity-dwelling predators with complex activity times (Fig. 7, Supplementary Fig. S4).

Discussion

We find that many aspects of the functional ecological setting recorded by AMB_{Dead} are in strong agreement with those of AMB_{Total} (Tables 1, 2). Moreover, although AMB_{Dead} is significantly size-biased (Supplementary Ta-

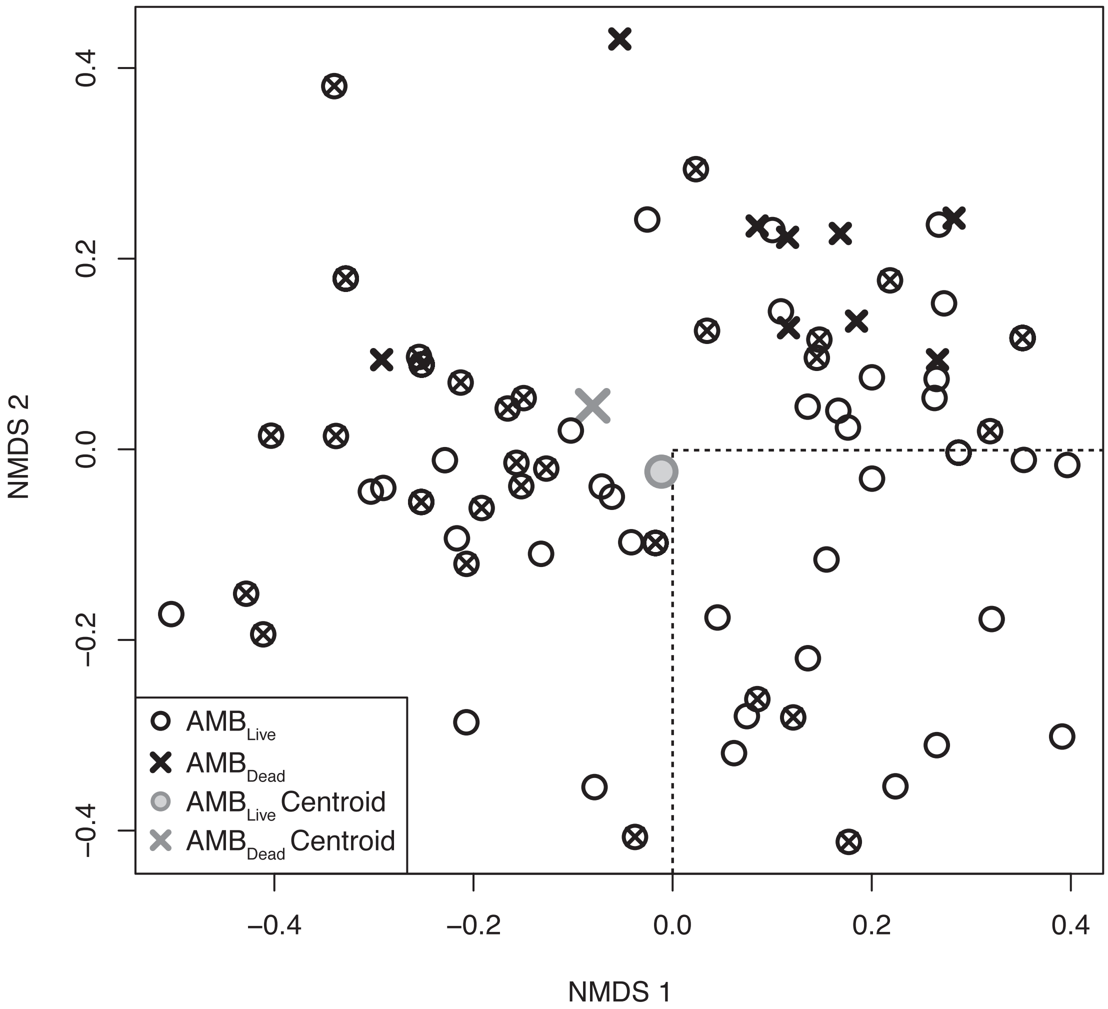

FIGURE 7. Nonmetric multidimensional scaling of four ecological traits for the total Amboseli mammal community (AMB_{Total}; Stress = 0.125). Species recorded by AMB_{Dead} are small X's. Species documented in AMB_{Live} are open circles. Though not demarcated, the global (AMB_{Total}) centroid is located at [0, 0]. A gap in coverage by AMB_{Dead} in the lower-right quadrant (dashed box) corresponds to ecospace constructed by species that (1) consume other animals (invertebrates, meat, bone), (2) shelter in underground cavities, and (3) are active during many periods of the day (Supplementary Fig. S2).

bles S1, S2), simulations indicate that the recovered AMB_{Dead}–AMB_{Total} agreement is within expectations based on randomized samples of the source community (Figs. 6, 8). This suggests that the ecological fidelity of fossil vertebrate communities is potentially sufficient to allow analysis of ecological variables beyond traditional measures of biodiversity (e.g., taxonomic richness, relative abundance) and may include detailed data on the functional ecology of the community.

Modern analogues are important references for assessing diversity bias in the fossil record, and an initial goal of this research was to compile a complete reference list of mammalian species from one modern, tropical ecosystem. For our study system, this proved to be more challenging than expected. Although some species in the Amboseli ecosystem have been studied in great detail, knowledge of smaller-bodied species is more limited. Brief small-mammal trapping surveys in 2003–2004 (Kanga et al. 2004), combined with examination of raptor pellets (Reed et al. 2006), boosted the known richness of the Amboseli non-volant community by 18% (seven new

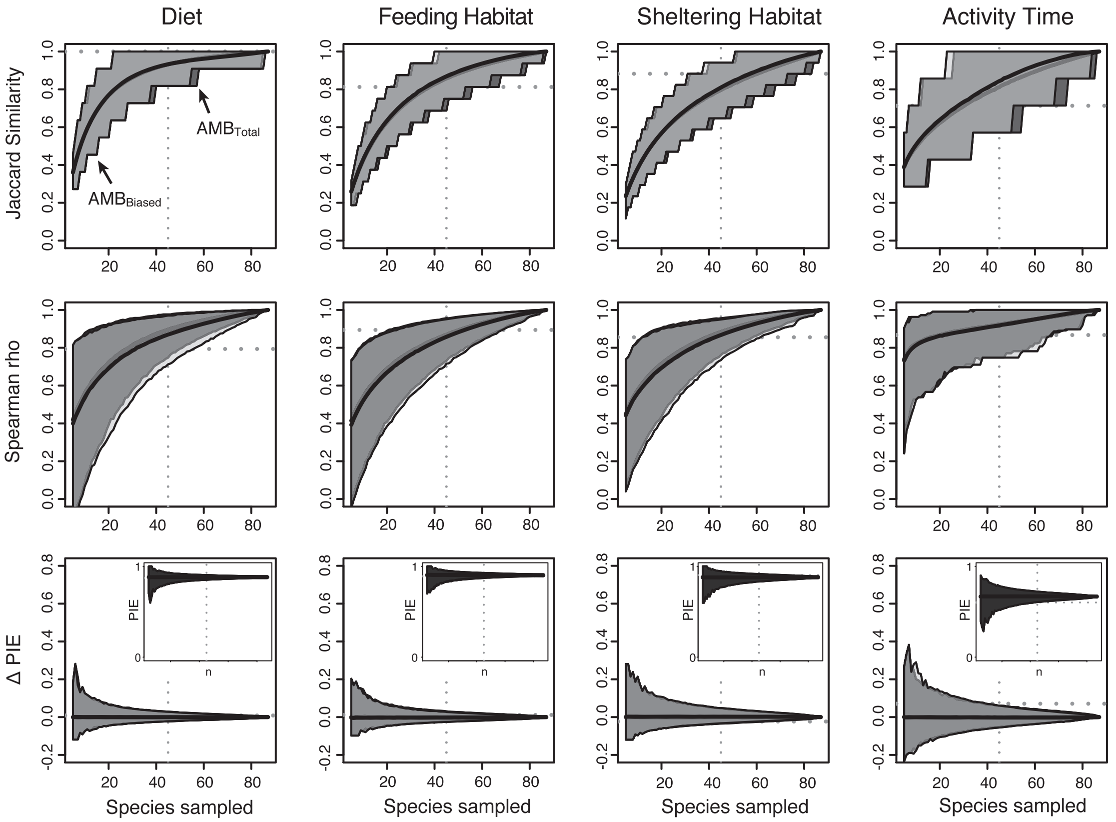

FIGURE 8. Results from Monte Carlo simulations modeling the recovery of functional ecological data from $\mathrm{AMB_{Total}}$ with an imposed size bias. The simulated size bias is parameterized by fitted recovery probabilities from the logistic regression modeling species recovery in $\mathrm{AMB_{Dead}}$ as a function of body mass (Supplementary Tables S2, S3). Expectations of functional fidelity for this analytically imposed size bias ($\mathrm{AMB_{Biased}}$; light-gray polygons) are within confidence intervals of randomly subsampled $\mathrm{AMB_{Total}}$ (dark-gray polygons) for all ecological metrics and functional traits. High similarity between sampling curves suggests that body size is not a major driver of bias in functional ecological representation for $\mathrm{AMB_{Dead}}$.

species known only from $\mathrm{AMB_{Live}}$ and nine species known only from $\mathrm{AMB_{Dead}}$). Although inequalities in sampling effort (particularly between large and small species in both $\mathrm{AMB_{Live}}$ or $\mathrm{AMB_{Dead}}$) are present, and it is likely that additional sampling of both $\mathrm{AMB_{Live}}$ or $\mathrm{AMB_{Dead}}$ will continue to reveal species (particularly rare species), comparisons of body-size frequency distributions between $\mathrm{AMB_{Total}}$ and four other savanna ecosystems in Kenya and Tanzania (Nairobi Game Park, Shompole National Park, Masai Mara National Park, and Serengeti National Park: Sinclair and Arcese 1995; Byrom et al. 2014; Tóth et al. 2014) suggest that our current estimate of the Amboseli community ($\mathrm{AMB_{Total}}$) is not strongly different in body-size composition from other well-studied ecosystems (Wilcoxon and Kolmogorov-Smirnov tests; all p-values > 0.05; Supplementary Table S6, Supplementary Fig. S5). That is, we do not appear to be significantly undersampling small-mammal richness. Comparisons to the Serengeti are particularly germane, as it has been the focus of substantial small-mammal survey efforts for both the live and the dead (Reed et al. 2006; Reed 2007; Byrom et al. 2014). The combined total of 87 mammal species represents the best current estimate for wild, non-volant species richness of the Amboseli mammal community across the last 50 years.

Size Biases and Biological Records.—Paleobiologists have long been concerned with the effect of size bias on paleoecological reconstructions of the fossil record. Although we document good evidence for a positive size bias in $\mathrm{AMB}_{\mathrm{Dead}}$ (Supplementary Tables S1, S2), we also find strong evidence that biological records for modern ecosystems can be similarly challenged (Supplementary Tables S1, S2). Amboseli National Park has been subjected to intensive ecological research over many decades, yet recent study (Reed et al. 2006) of the raptor pellets ($\mathrm{AMB}_{\mathrm{Dead}}$) added nine species to the non-volant community (all less than 1 kg)—a 12% increase in known alpha diversity. In addition to raw richness, species from $\mathrm{AMB}_{\mathrm{Dead}}$ added two functional ecological attributes to our understanding of the ecosystem, including one Diet attribute (frugivore-grazer) and one preferred Sheltering Habitat (arboreal cavities). Such discoveries highlight the challenges of obtaining a total census of species in a modern community and demonstrate how death assemblages can contribute to modern ecological surveys.

Functional Ecological Attributes are Distributed Broadly Across Body Sizes.—The high fidelity with which $\mathrm{AMB}_{\mathrm{Dead}}$ captures many aspects of the functional ecological setting of $\mathrm{AMB}_{\mathrm{Total}}$ (particularly trait presence; Jaccard), in spite of a significant size bias, appears to result from single functional traits being shared across species with wide-ranging body sizes (Figs. 3, 4). This includes the high proportion of functional attributes shared by small- (<1 kg) and large-bodied (≥ 1 kg) species (28; 72% of attributes occurring in multiple species, Fig. 3). Of the 51 total functional ecological attributes in $\mathrm{AMB}_{\mathrm{Total}}$, 21 (41%) are found in species over 100 kg—the body-size range where $\mathrm{AMB}_{\mathrm{Dead}}$ completely samples the richness of $\mathrm{AMB}_{\mathrm{Total}}$. Moreover, 17 (81%) of these traits are found across four or more orders of body-size magnitude. In terms of overall differences in attribute distribution between small and large mammals, 47 (92% of all functional attributes) occur in species larger than 1 kg. On the other end of the body-size spectrum, 32 attributes (63%) are found in species less than 1 kg and 28 (88%) of these in both small and large species. Thus, in terms of raw trait richness (e.g., Jaccard), even when targeting only "small" or "large" mammals, many of the broad characteristics by which paleobiologists often bin species (e.g., grazer, browser) are shared across large portions of the total community. This biological redundancy (at least at the coarse scales typically available in the mammalian fossil record) makes it possible to recover important aspects of community ecology even with limited samples.

Although simulations show that the range of body sizes incorporated into individual functional attributes follows null expectations (Supplementary Fig. S1), some aspects of functional traits do have important links to body size. For example, there is a natural upper boundary for tree-dwelling species (~30 kg, Supplementary Appendix A), and grazing is strongly dominated by species between ~30 and 300 kg (Supplementary Appendix A). It is common for researchers to concentrate on particular body-size subsets of a community or fossil assemblage (e.g., when only one body-size group is available or feasible for sampling). While there is indication of functional redundancy across body sizes, different portions of the body-size spectrum do contain unique information about the community's overall functional ecology (Figs. 3, 4). More restrictive size biases than found in $\mathrm{AMB}_{\mathrm{Dead}}$ could filter out some of these ecological signals. Previous work (Soligo and Andrews 2005; Andrews 2006; Le Fur et al. 2011) also indicates that strong body-size biases can produce significant distortions in how functional trait data record community ecology and environmental preferences.

Reevaluating the Importance of Body Size Bias.—Although large-bodied species are significantly more likely to be captured in $\mathrm{AMB}_{\mathrm{Dead}}$ (Supplementary Tables S1, S2), the full spectrum of $\mathrm{AMB}_{\mathrm{Total}}$ body sizes is represented. The substantial number of small-bodied species in $\mathrm{AMB}_{\mathrm{Dead}}$ is largely because data from surface bone surveys were supplemented by remains from owl pellets. Our logistic model of presence-absence in $\mathrm{AMB}_{\mathrm{Dead}}$ and body size reveals that the predicted recovery probability for Amboseli's smallest-bodied species (white-toothed shrew) is over 25% (Supplementary Table S3). Given this seemingly high probability of recovery (based on body size alone), it is not surprising that our analytically imposed size bias has such a limited effect on ecological recovery. This suggests that (1) when different data collection strategies are imposed (e.g., targeted sampling of both large- and small-bodied species), size biases in death assemblages may be at least partially mitigated, and (2) size bias alone (at least when the bias is not severe enough to eliminate entire body size subsets) may not be the most influential force behind ecological bias in death or fossil assemblages. Particularly when both macro- and micro-vertebrate sampling is possible (Fortelius et al. 1996; Fernandez-Jalvo et al. 1998; Harrison 2007; Reed and Denys 2011; Geraads et al. 2012; Reed and Geraads 2012), the available data may overcome many issues relating to body-size bias; however, the biological ramifications of remaining biases must still be carefully considered.

Our data also suggest that biases other than body size can be important for skewing ecological representation. For example, 57% (24 of 42) of the species not recovered from the death assemblage include species in the lower-right quadrant of the NMDS (Fig. 7), which are generally composed of carnivorous cavity dwellers. If the death assemblage's bias against this group is as closely allied to its ecology as it appears (e.g., cavity dwelling), that would suggest the ecological biases observed in $\mathrm{AMB}_{\mathrm{Dead}}$ are more complicated and biologically interesting than a simple correlate of body size. Further work is needed to differentiate the ecological biases acting on skeletal accumulations, particularly with reference to species abundance (which is often unavailable for populations of modern small- and medium-bodied mammals). Thus, direct tests of the interactions of abundance, body size, and functional ecology will require more concerted ecological sampling in the future.

At least during the initial taphonomic stages in the development of a terrestrial mammalian death assemblage, our data indicate that body size may have a nuanced and even limited role in biasing some forms of ecological data from a source community. Later diagenetic changes, of course, could impose additional body-size-linked taphonomic filters. Additionally, particular sorting and collecting agents may also impose dramatic size biases and generate body-size subsets of the ecosystem (e.g., owl roosts, hyena dens, perhaps fluvial processes [Voorhies 1969; Lansing 2009; Terry 2010a]).

Do Cavity Dwellers Hide from Bone Surveys?—Half of all species in $\mathrm{AMB}_{\mathrm{Total}}$ shelter in some form of cavity (44 of 87; Supplementary Appendix A, Figs. 3, 5). Although cavity-dwelling species correctly represent the dominant sheltering habitat of species found in $\mathrm{AMB}_{\mathrm{Dead}}$ (16 of 45; 36%; Supplementary Appendix A, Fig. 5), they are somewhat depauperate compared to the source community and poorly represented in a region of ecospace that is enriched in cavity dwellers (Fig. 7). Recent work has shown that death assemblages can offer high-quality spatial data and can be used to reconstruct season-specific landscape use, birthing grounds, hunting grounds, and even ecological gradients (Tomašových and Kidwell 2009b; Terry 2010a; Miller 2012; Miller et al. 2013). It is not surprising that bone surveys, which record bones visible on landscape surfaces or at roosting sites, may have difficulty recovering species that spend significant portions of their lives in burrows, tree hollows, or other protected places. Although not a direct test, this may also speak to the spatial fidelity of landscape bone records and provide further insight into how well behavioral patterns reveal themselves in modern death assemblages. Future directed sampling of these kinds of habitats and structures (e.g., tree hollows, underground burrows) could test whether this undersampled ecological trait can be more competently recovered from a modern death assemblage. Interestingly, the fossil record has many examples of cavity dwellers, including the preservation of individuals within their burrows (Voorhies 1975; Brain 1980; Hunt et al. 1983; Smith 1987; Potts et al. 1988; see also Behrensmeyer and Hook 1992). Thus, although surface bone surveys may be biased against an important ecological mode, this does not necessarily translate to a bias in the fossil record.

Fidelity in Proportional Abundance of Functional Ecological Traits.—Although $\mathrm{AMB}_{\mathrm{Dead}}$ includes approximately 50% of available species from $\mathrm{AMB}_{\mathrm{Total}}$, this size-biased sample records many ecological details within expectations of a randomized collection of species.

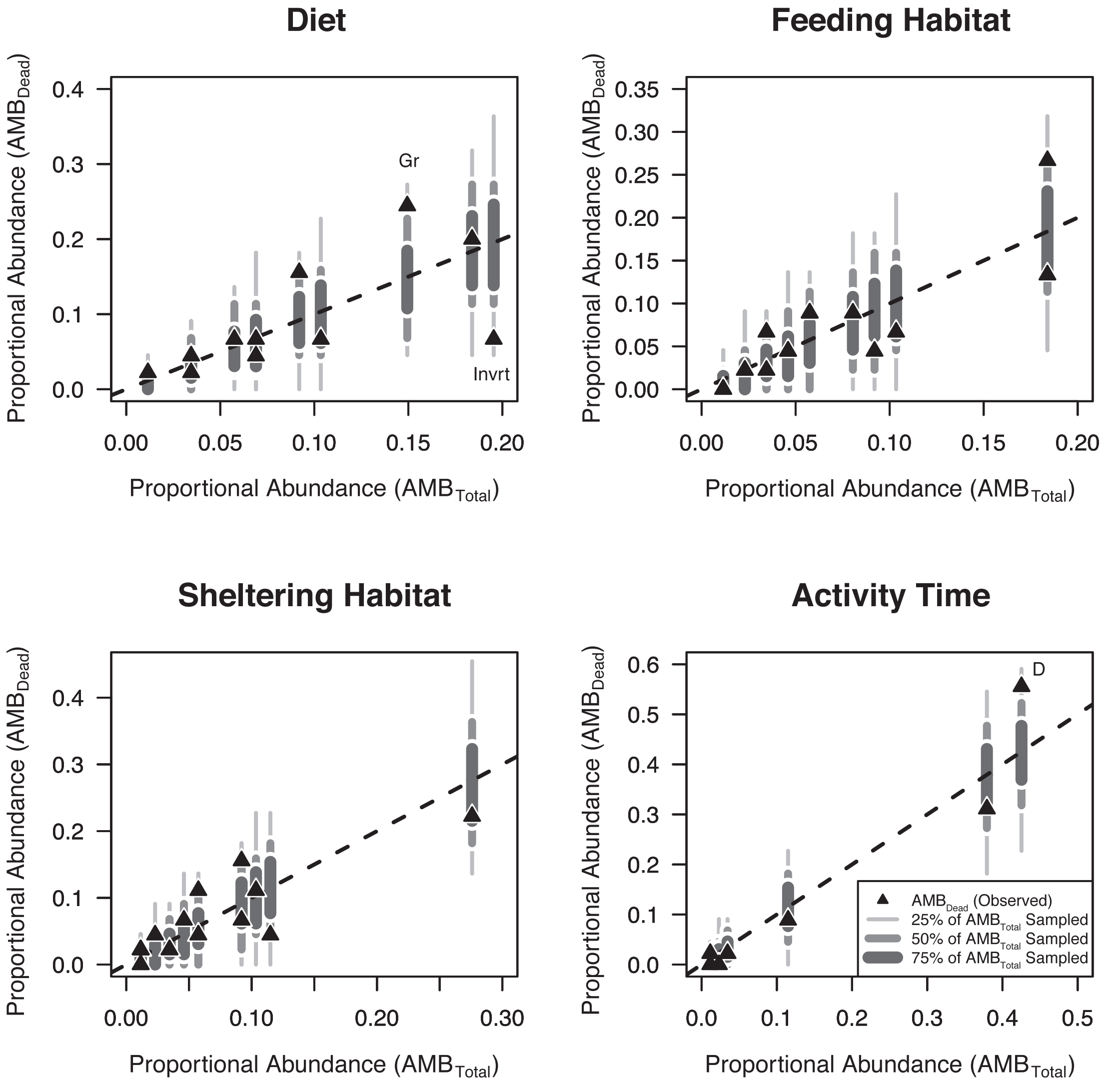

FIGURE 9. Proportional abundances of attributes within each functional ecological trait as recovered by AMB_{Dead} and as simulated through randomized sampling of AMB_{Total}. Error bars are 95% confidence intervals based on Monte Carlo simulations for sampling AMB_{Total} at increasing levels of community completeness (i.e., sampling 25%, 50%, and 75% of all available species). Dashed line shows one-to-one correspondence, representing ideal agreement between AMB_{Total} and AMB_{Dead}. Based on a simulated sampling intensity equal to AMB_{Dead}'s species richness ($S = 45$, 52% of AMB_{Total} richness sampled, Supplementary Table S7), AMB_{Dead} records the proportional abundances of nearly all function attributes within null expectations. Only three functional attributes fall outside expectations: diurnality (D), invertivory (Invrt), and grazing (Gr). These misrepresentations are consistent with AMB_{Dead}'s undersampling of invertebrate-consuming predators (which have complex Activity Times; Fig. 7, Supplementary Fig. S4) and oversampling of large diurnal grazers.

In fact, high-quality retrieval of functional properties includes the capture of proportional abundances of individual attributes within functional traits. Using Monte Carlo simulations, we can calculate the 95% confidence intervals with which a randomized sample of AMB_{Total} will characterize the proportional abundance of each functional attribute at different sampling intensities (e.g., sampling the community at varying degrees of completeness; Fig. 9). Comparing the proportional abundances of functional ecological attributes found in AMB_{Dead} with simulated expectations, we find that 48 attributes (94%) fall within expectations of a randomized sample of 45 species (the number of species in $\mathrm{AMB}_{\mathrm{Dead}}$) (Fig. 9, Supplementary Table S7). This includes all seven functional attributes not recovered from $\mathrm{AMB}_{\mathrm{Dead}}$ (which are all rare in the living community and found in only one or two species) and the 12 traits recovered as singletons in the death assemblage. Thus, with sufficient sampling, the rarity of traits recovered from skeletal remains may be suggestive (and even indicative) of rarity in the source community.

The functional traits recovered in $\mathrm{AMB}_{\mathrm{Dead}}$ that fall outside of randomized expectations are diurnality (overrepresented in $\mathrm{AMB}_{\mathrm{Dead}}$ relative to $\mathrm{AMB}_{\mathrm{Total}}$), invertivory (underrepresented), and grazing (overrepresented) (Fig. 9, Supplementary Table S7). These misrepresentations are all consistent with $\mathrm{AMB}_{\mathrm{Dead}}$'s undersampling of animal-consumers with complex activity times (e.g., not diurnal) and oversampling of diurnal grazers (Fig. 7, Supplementary Fig. S.4). This particular gap in $\mathrm{AMB}_{\mathrm{Dead}}$ represents the largest meaningful deviation in the dead's ecological representation of the source community, with the remaining missing 18 species (21% of $\mathrm{AMB}_{\mathrm{Total}}$) potentially reflecting random noise of species retrieval from the source community. By and large, this work and others (Behrensmeyer et al. 1979; Behrensmeyer and Miller 2012; Kidwell 2001, 2002, 2007, 2013; Tomašových and Kidwell 2009a,b; Western and Behrensmeyer 2009; Terry 2010a; Miller 2011, 2012; Miller et al. 2013) show that even at fine scales (i.e., proportional abundances of functional ecological attributes), death assemblages can provide biologically informative data about their source communities. Our findings also strengthen earlier indications that proportional representation of some dietary attributes of Amboseli herbivores are faithfully recorded in the death assemblage (Western and Behrensmeyer 2009). Additionally, although species abundance data are not always readily available in fossil records, the simple presence of species and their functional ecological traits may provide meaningful insight into landscape ecology. Isotopic and morphological data can add valuable quantitative dimensions to such work, particularly when functional aspects of fossil species cannot be confidently extracted from recent populations or related species.

Conclusions

We find that even in the face of a statistically significant body size bias (i.e., overrepresentation of large-bodied species), $\mathrm{AMB}_{\mathrm{Dead}}$ captures the functional ecological structure of $\mathrm{AMB}_{\mathrm{Total}}$ within expectations of randomized sampling. If a collection of bones from ~50% of the species in a modern ecosystem provides a relatively high level of ecological fidelity with respect to the overall community, then this could also hold true for fossil assemblages representing extinct ecosystems. In the Amboseli death assemblage, size bias alone does not cause major deviations in the recording of the source community's functional ecology. Furthermore, simulations show that sampling the functional data of $\mathrm{AMB}_{\mathrm{Total}}$ with an analytically imposed size bias (parameterized on characteristics of $\mathrm{AMB}_{\mathrm{Dead}}$) recovers functional ecological data that deviate remarkably little from null expectations. Analysis of $\mathrm{AMB}_{\mathrm{Total}}$ suggests that this is largely because many functional ecological attributes are shared across wide ranges of body sizes. Thus, even when death assemblages have an underlying body-size bias, they can record many functional attributes that also exist in more poorly sampled regions of the community. When body-size biases are extreme and preservation or collection results in body-size subsets of the original community, the effect on functional ecological data is likely more severe, though this effect remains unquantified. Ecological bias in death assemblages undoubtedly occurs, but our results indicate that this can be driven less by body size than by interactions between species' functional ecology and the taphonomic setting responsible for accumulating the skeletal remains. Although the redundancy of functional attributes across body-sizes is encouraging, it is also likely that a more accurate representation of functional ecology will result from recovery of skeletal materials across the body-size spectrum for any given fossil (or modern) community.

The recovery of nine species (and two functional traits) from the Amboseli death assemblage that were previously unknown from the living community (i.e., not observed in the more than 50 years of active ecological monitoring in Amboseli) underscores the value of including death assemblage surveys in ecologists' methodological toolkit for obtaining more complete biological data on modern ecosystems.

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