Implications of Time-Averaged Death Assemblages for Ecology and Conservation Biology

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Abstract

Biologists increasingly appreciate the importance of community-level attributes in the functioning and temporal turnover of ecosystems, but data other than species richness are difficult to acquire over the habitat-to-regional and decadal-to-millennial scales needed to recognize biodiversity change, discriminate between natural and anthropogenic drivers, and inform theoretical and applied ecology. Death assemblages (DAs)—the actively accumulating organic remains encountered in present-day seabeds and landscapes, as distinct from permanently buried fossil assemblages—are an underexploited source of historical information at precisely these scales. Meta-analyses, dynamic modeling, and individual case studies, particularly of mollusks and mammals, reveal that DAs differ from censused living assemblages (LAs) primarily because they are temporally coarse, time-averaged samples, contrary to concerns that postmortem bias dominates. Temporal pooling predictably damps the ability of DAs to detect small-scale variation, but promotes their ability to inventory rare species; estimate the abundance structure of the metacommunity; document range changes; evaluate historic habitat use; and identify now-absent species, community states, and anthropogenically shifted baselines.

1. INTRODUCTION

Metacommunity:
a network of local
communities linked by
dispersal; the regional
species pool

**Death assemblage
(DA):** a set of dead,
taxonomically
identifiable organic
remains that is present
on or in the surficial
mixed layer of a
landscape or seabed

Over the past several millennia, accelerating with the Age of Discovery, the Industrial Revolution, and late-twentieth-century globalization, humans have come to dominate ecosystems in diverse ways and at many scales, from individual species to key habitats and entire biomes (Vitousek et al. 1993, Jackson et al. 2001, MEA 2005, NRC 2005, Watling 2005, Lötze et al. 2006, Willis & Birks 2006, Worm et al. 2006, Halpern et al. 2008, Jackson & Hobbs 2009, Waycott et al. 2009, Tittensor et al. 2009, Fisher et al. 2010, Strong & Frank 2010). Biologists, managers, and policy makers increasingly recognize the need for a broad-based science of biological diversity to understand the dynamics of species, communities, and ecosystems under both natural and human perturbation (Soulé 1985, Loreau 2010, NRC 2012). However, two large information gaps have emerged and gained renewed urgency as conservation efforts have shifted focus from single species to habitats and regions.

First, community-level information beyond species richness, such as species composition and community structure, is scarce. From theoretical, experimental, and macroecological approaches, it is becoming clearer that community-level attributes are most relevant to the functioning and temporal turnover of ecosystems and that the dynamics of extinction and speciation are determined to a significant extent by broad, regional-scale parameters such as habitat extent, connectivity, fragmentation, and temporal variability (e.g., Chave et al. 2002, Leibold et al. 2004, Ricklefs 2008, Gravel et al. 2010). Analyses of community and ecosystem dynamics as well as extinction risk are increasingly focusing on multiple scales and on unified explanations of multiple community-level attributes (e.g., Hubbell 2001, Leibold et al. 2004, Babcock et al. 2010, McGill 2010).

The second challenge is to acquire such information on the relatively large temporal scales necessary to recognize biodiversity change, thresholds, and natural baselines, and to evaluate drivers. Historic perspectives are also required to validate theoretical models of community and ecosystem dynamics (McGill et al. 2005, Reymond et al. 2011, Bode et al. 2012). The minimum requirement is decadal to centennial information on landscape and seascape scales, thereby placing the target species or community in the context of its metacommunity (e.g., Pelc et al. 2010, Shackell et al. 2012). However, owing to the direct and indirect effects of long-standing human activity in most regions, including the open ocean, the temporal perspective usually should encompass several centuries or millennia (see citations in first paragraph).

Unfortunately, windows of direct observation are commonly shorter than the life spans of key species and biotically constructed habitats (e.g., tree stand, reef, seagrass meadow). In addition, longer, decadal-scale monitoring that can generate formal time series typically focuses on spatially limited plots and/or areas where one or more human stresses are already under way. As a result, for almost all groups and regions, we lack data on long-term rates of change even for richness, much less temporal changes in abundance, taxonomic composition, geographic range, and beta diversity (e.g., Srivastava & Vellend 2005, Storch et al. 2007, Stachowicz et al. 2008, Magurran 2012, and other papers by Solan et al. 2012, Dornelas et al. 2013, Pereira et al. 2013). These shortages generally lead to an underestimation of human impacts and conservation risks. Short temporal perspectives also make it difficult to exonerate human agency (e.g., pollen data showing that suspected invasives are instead native; Burney et al. 2001, van Leeuwen et al. 2008).

Historical archives, archeological evidence, and paleontological information extracted from cores and other sedimentary records can all be excellent sources of robust and otherwise unob-tainable data, prompting a general call that they become part of the standard tool kit of conservation biology (e.g., Swetnam et al. 1999, Lyman & Cannon 2004, Hayashida 2005, NRC 2005, Willis & Birks 2006, Smol 2010, Dietl & Flessa 2011, Brewer et al. 2012, Conserv. Paleobiol. Workshop 2012, Rick & Lockwood 2013). Here we focus on death assemblages (DAs), which are naturally

accumulated biological remains drawn exclusively from the top increment of sedimentary records, as unique and under-exploited sources of historical data.

1.1. Death Assemblages (DAs)

DAs are the dead organic remains that are encountered in still largely unburied form on landscapes and seafloors, and thus are distinct from the permanently buried fossil record, such as extracted from sedimentary cores and geological outcrops. DAs comprise taxonomically identifiable individuals from the past generations of extant or recently extinct species at a site, most often dominated by biomineralized or otherwise refractory tissues such as shells and other calcareous skeletons, bones, leaf litter, deadwood, and diaspores (**Table 1**). They can be sampled using many of the same methods used to census living individuals, such as counts in quadrats and along transects or sieving sediment samples. Although DAs are regularly overlooked or discarded during biological surveys, the DAs of metazoans and higher plants have been the focus of intense paleontological analysis since the 1970s as possible analogs of deeply buried fossil assemblages (see reviews by Kidwell & Bosence 1991, Behrensmeyer et al. 2000, Kidwell 2013). Insights into the resolution, fidelity, and dynamics of DA accumulation now provide a confident basis for using DAs to evaluate the recent history of modern-day systems.

DAs are sources of biological information whose most important feature is that they are time-averaged, temporally coarse accumulations in which noncontemporaneous individuals co-occur. While accumulating on and within the uppermost, mixed layer of a landscape or seafloor, dead individuals are subject to physical reworking, bioturbation, scavenging, disintegration, and other postmortem processes, which together tend to remove individuals from the assemblage. The DA also continues to receive newly dead individuals from local standing populations, known as the living assemblage (LA). DAs thus remain dynamic, open systems within the window of time-averaged accumulation, much like seedbanks that both acquire new diaspores and lose older ones to disintegration or deeper burial. DAs thus tend to be temporally autocorrelated with local LAs. However, compared with conventional "snapshot" samples of the LA, DA samples have lower temporal resolution. The total duration of time averaging for a given DA is a function of the inherent durability of organic remains to exposure and reworking at the site of accumulation, the net rate of sediment accumulation (burial rate below the sediment-air or -water interface), and the depth of reworking by burrowers and physical processes, which can move dead individuals both upward and downward within the mixed layer (see discussion in Kidwell 2013). The size of the temporal window represented by DAs—and by the fossil assemblages that they eventually become upon permanent burial and isolation from the input of newly dead individuals—thus varies dramatically among settings and groups (**Table 1**).

Rigorous use of DAs for any kind of biological analysis requires understanding the effects of temporal scaling on biological information and the potential uses of temporally coarse data. Here, we begin with a review of findings from modeling and meta-analysis on how temporal scaling and postmortem bias affect community-level attributes. We then review some of the ways in which naturally time-averaged DAs can inform major questions in conservation biology and ecology. We use shallow-marine soft-sediment mollusks as a model system, but other groups and settings are also becoming well understood. This growing literature attests that DAs have much to offer any biological study in which temporal dynamics on decadal and longer scales enter the equation.

2. TEMPORAL SCALING IN THEORY AND PRACTICE

Temporal coarsening—whether achieved via the natural process of time averaging or via the analytical pooling of consecutive samples of live-collected individuals—will affect multiple

Fossil assemblage: a set of permanently buried individuals excavated from the sedimentary record, occurring below the surficial mixed layer of a modern landscape or seabed

Living assemblage (LA): a multispecies set of living individuals, such as censused by a survey

Time averaging: natural process by which noncontemporaneous individuals accumulate into a single assemblage, usually because rates of permanent burial are slow relative to generation times

Table 1 Proportion of living species in a habitat that are also present as dead individuals in the same area.[a] Last column: estimated maximum and median (50% surviving) postmortem longevity or residence time of dead remains[b]

Group	Setting(s)	% of live-collected species also present dead	Study scope	Maximum (median) postmortem age of individuals
Land snails	Hawaii, Samoa, Palau	77–100	Nine surveys of rain- or wet forest (Rundell & Cowie 2004)	≤20 years?
Land snails	Hawaii	93–100	Three surveys of dry forests (Rundell & Cowie 2004)	Tens of years?
Land snails	Bahamas	100	Three dry habitats (Yanes 2012)	~3,000 years (tens to thousands of years) (Yanes et al. 2007)
Land snails	Hungary	86–100	Four habitats (Sólymos et al. 2009a)	(Tens of years) (Pearce 2008)
Land snails	Austria	100	Three habitats (Briggs et al. 1990)	(Tens of years) (Pearce 2008)
Freshwater mollusks	Pampas, Argentina	71–100	Two lotic and two lentic areas (Tietze & De Francesco 2012)	Probably tens of years
Freshwater mollusks	Southern Brazil	75	One river stretch (Erthal et al. 2011)	Probably tens of years
Freshwater bivalves	Ohio	87–100	Seven lakes and streams (Cummins 1994)	Probably tens of years
Reefal mollusks	Seychelles	63	Three hard-bottom habitats (Zuschin & Oliver 2003)	Hundreds to a few thousand years (ten to a hundred years) (Kidwell 2013)
Reefal mollusks	Gulf of Aqaba	26–53	Six hard-bottom habitats (Zuschin & Stachowitsch 2007)	As in Seychelles mollusks
Reefal mollusks	Red Sea	68	Five hard-bottom habitats (Zuschin et al. 2000)	As in Seychelles mollusks
Reefal corals	New Guinea	54	Entire lagoon (Pandolfi & Minchin 1996)	~1,000 years (a few hundred years) (Edinger et al. 2007)
Reefal corals	Florida	60–80	Four shallow reefs (Greenstein & Pandolfi 1997)	As in New Guinea corals
Reefal corals	Florida	63–89	Four deep reefs (Pandolfi & Greenstein 1997)	As in New Guinea corals
Subtidal soft-bottom mollusks	Tropical and temperate	88 ± 6 global average	85 data sets from lagoons, estuaries, and open shelfs (Kidwell 2002)	Hundreds of years (tens of years) in estuaries; thousands of years (100 years) on shelves (Kidwell 2013)
Decapods	Texas	50	Three shoreline sites (Plotnick et al. 1990)	0.5 to tens of years?
Echinoids	Red Sea	76	11 subtidal habitats pooled (Nebelsick 1992)	As in reefal mollusks?
Sponges	Caribbean Panama	71	Entire lagoon (Lukowiak et al. 2013)	Tens of years?
Large mammals	Amboseli, Kenya	72 (1–14 kg), 95 (≥15 kg)	Six surface habitats[c] (Behrensmeyer & Boaz 1980)	Tens of years (Behrensmeyer & Miller 2012)
Large mammals	Virunga, Democratic Republic of the Congo	32 (>1 kg)	Four surface habitats (Sept 1994)	As in Kenya mammals

(Continued)

Table 1 (*Continued*)

Group	Setting(s)	% of live-collected species also present dead	Study scope	Maximum (median) postmortem age of individuals
Large mammals	Virunga, Democratic Republic of the Congo	62	33 surface transects[c] (Tappan 1995)	As in Kenya mammals
Ungulates	Wyoming	86 (≥15 kg)	Five surface habitats[c] (Miller 2011)	~100 years (tens of years) (Miller 2011)
Small mammals	Utah-Nevada	100	Two regions (owl pellets in caves) (Terry 2010a, 2010b)	~100 years (tens of years) (Terry 2010b)
Birds	Amboseli, Kenya	4	Seven surface habitats[c] (Behrensmeyer et al. 2003)	~10 years (few years)?
Playa lake beetles	Arizona	28 (% of genera)	Lake shoreline (Smith 2000)	A few years (few months)?
Deciduous leaf litter	Tropical Costa Rica and Amazon	43–70	1-hectare forest plots (Burnham 1994, 1997)	0.5 to 1 year (Vogt et al. 1986, Zheng et al. 2006)
Evergreen leaf litter	Tropical Tabasco	51–53	Nine floodplain transects (Burnham 1989)	2.4 years (Vogt et al. 1986)
Deciduous leaf litter	Temperate Maryland	68–73	Three regions, 1-hectare plots (Burnham et al. 1992)	10–20 years (3–4 years) (Lousier & Parkinson 1976)
Conifer leaf litter	Temperate Alberta and Mediterranean	No data	No studies?	20–30 years (5 years) (Prescott et al. 1989, Kurz et al. 2000, Kavvadias et al. 2001)
Standing deadwood	Tropical Panama	No data	No studies?	<20 years (snag numbers do not change with forest age) (DeWalt et al. 2003)
Standing deadwood	Boreal Québec	No data	No studies?	25 to ≥50 years (15–26 years) (Angers et al. 2010)

[a]Findings based on a single census, which is a useful gauge of the intrinsic preservation potential of a group (first four columns).

[b]Most estimates are based on analysis of a different but analogous study area than was used to test the live-dead agreement reported in other columns; unreferenced estimates are based on geological reasoning (S.M. Kidwell & A. Tomasovych, unpublished findings).

[c]Denotes dead data pooled across a multihabitat region and then compared with live-census data pooled from multiple surveys of the same region.

fundamental attributes of communities, most obviously an increase in species richness as shown by empirical species-time accumulation curves (Fürsich & Aberhan 1990, Rosenzweig 1998, Fridley et al. 2006, White 2007, McGlinn & Palmer 2009, Tomasovych & Kidwell 2010a). The critical issue for using naturally time-averaged DAs is whether the observed richness and other community-level patterns of DAs (*a*) fall within the range of values expected from temporal coarsening of successive LAs alone or (*b*) must be attributed to taphonomic bias arising from interspecies differences in skeletal production, which can decouple the abundance of dead shells from the standing abundance of LAs, and in postmortem skeletal destruction and transport, which can selectively remove individuals. This is equivalent to bias from interspecies differences in detectability in ecological monitoring studies.

Empirical studies of DAs demonstrate that the absolute scale of time averaging, which is determined by natural processes and assessed using radiometric and other paleontologic methods,

Taphonomic bias: postmortem distortion of biological information, due to interspecies differences in population turnover (or molt frequency), durability of tissues, and out-of-habitat transport

varies among groups and settings (**Table 1**). For groups with biomineralized or refractory tissues, taxonomically identifiable individuals may persist postmortem for a maximum of a few decades up to several thousand years under favorable conditions (median values in **Table 1**). Thus, the temporal resolution of naturally time-averaged DAs is commonly coarser than what could be achieved by analytically pooling even long time series of direct observations. However, most individuals in a DA are from the youngest (most recent) few cohorts, sharpening the effective temporal acuity of the DA (median values in **Table 1**) (Kidwell 2013 and references therein), in contrast to analytically pooled assemblages in macroecological studies where all age cohorts contribute equally.

2.1. Temporal Scaling: Predicted Effects and Implications of Time Averaging

With increasing length of time or area sampled, species accumulate in an assemblage because the probability of immigration by species increases and new habitats or environmental conditions are added (Preston 1960, Adler & Lauenroth 2003, Adler et al. 2005). Temporal scaling effects can be quantified either by empirical pooling of LAs observed in a time series (Peterson 1977, Staff & Powell 1988, Martin et al. 2002) or by dynamic models that are constrained by parameters derived from either spatially or temporally replicate samples of LAs (size of the local community, migration rate between local communities and the source regional species pool, abundance structure of that pool) (Tomasovych & Kidwell 2010a,b, 2011).

In dynamic models of DAs, the effects of time averaging are assessed over several years to several millennia, representing a realistic time frame for molluscan DAs in shallow marine systems. The rules of our within-habitat models (Tomasovych & Kidwell 2010a,b, 2011) mostly follow those of metacommunity models routinely used in ecological studies: Communities assemble by species colonization that is dispersal limited and individual based; neutral models assume that species do not differ in their per-individual vital rates, and non-neutral models add interspecies differences in fecundity and mortality as well as density dependence (Chave et al. 2002, Leigh 2007, Rosindell et al. 2011). All of these models have quantified temporal scaling in single habitats; the consequences of time averaging under a dynamic that allows species sorting into habitats according to their evolved niche preferences are still poorly explored. In addition to these rules of within-habitat metacommunity dynamics, our models of DA formation keep track of dead individuals that are subjected to sampling, destruction, or burial, and they assess the magnitude of the effects of time averaging by comparing increasingly averaged DAs for the same sample size.

Using molluscan LAs from 31 different shallow-marine habitats to parameterize models, time averaging has predictable effects on community-level attributes, and these mostly arise within the first few decades or centuries (**Figure 1**) (more results in **Supplemental Table 1**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**). These results show the rates at which the effects of time averaging should emerge within DAs, and they reveal the adjustments (scaling factors) needed to compare LAs and DAs or merge their data into a single time series. These models are neutral in terms of preservation: They assume that all species have the same (stochastic) per-individual rate of shell destruction or removal from the DA. For modeling purposes, the definition of "within-habitat" is limited to random demographic variability: Faunal changes related to seasonal habitat fluctuations are treated as between-habitat variability.

2.1.1. Richness and rarity. Species composition in a habitat can change over time, owing to the increasing probability of immigration from the regional metacommunity, local-scale drift from demographic and environmental stochasticity, and, in non-neutral models, changes in habitat conditions. Such temporal changes in the identities of species, when summed by time averaging, inevitably increase richness. In particular, most empirical and modeling studies find that abundant
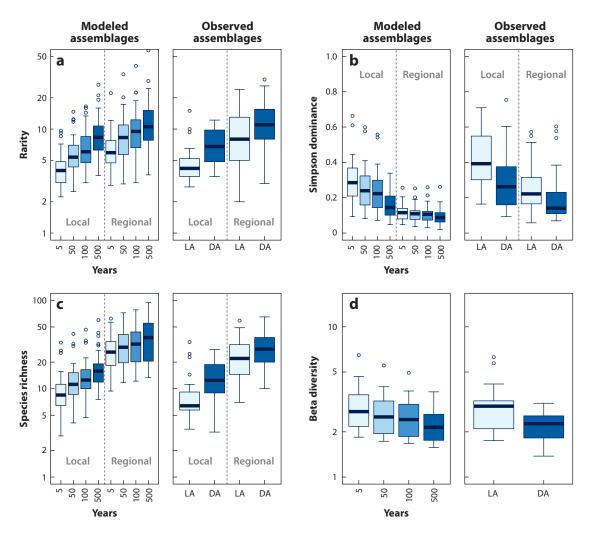
Figure 1

In settings with little or no human activity, observed differences in the community-level attributes of molluscan death assemblages (DAs) and living assemblages (LAs), both collected during a single survey, can be explained largely by differences in time averaging (i.e., temporal resolution). (*Left columns*) Within-habitat metacommunity models, parameterized using the rank-abundance curves of molluscan LAs from 31 shallow-marine habitats, show that by increasing time averaging from 5 to 500 years, (*a*) rarity—the number of species with one or two individuals—increases, (*b*) Simpson dominance decreases, and (*c*) species richness increases. They also show that these changes in community-level attributes are stronger at local than at regional spatial scales. (*d*) Between-assemblage spatial variation (multiplicative beta diversity expressed by regional-scale richness divided by local-scale richness) also declines with increased time averaging. (*Right columns*) Observed attributes of nonaveraged molluscan LAs and naturally time-averaged DAs from the same 31 habitats shown in the left columns: These observed live-dead differences are both qualitatively and quantitatively similar to those expected from temporal coarsening alone (compare *right* and *left columns*), with higher rarity and richness and lower dominance and beta diversity of DAs relative to LAs and stronger differences at local than at regional scales, leaving little live-dead discrepancy that needs to be explained by taphonomic bias. Each colored rectangle spans the first to third quartiles of values (interquartile range) with a thick dark line denoting the median value; whiskers encompass values up to 1.5 times the interquartile range; open circles represent extreme values. Based on replotting of data and results from Tomasovych & Kidwell (2010a, 2011).

species remain the same over time but that rare species replace each other at local scales (Hanski 1982, McGill 2003, Magurran 2007, Magurran & Henderson 2010). As a result, with progressive time averaging, the number of rare species increases, each of the rare species becomes rarer (constitutes a smaller proportion of all individuals), and local-scale richness increases, even when sample size is held constant (Tomasovych & Kidwell 2010a) (**Figure 1**). *Implications: Even at small sample sizes, naturally time-averaged DAs should be efficient samplers both of richness and of rare species in the habitat or metacommunity. In addition, many rare species will occur consistently in DAs but not in LAs, suggesting that they may be locally extinct when they actually persist in the metacommunity. Habitat-scale DA richness data are more robust than local-scale data for comparisons among areas or over time, because they undergo a smaller change in the proportion of rare species with temporal coarsening.*

2.1.2. Dominance. Although abundant species are more likely than rare species to occur continuously, their probability of switching in dominance at local scales increases with increasing time, either through stochastic demographic drift or by changing habitat quality: Species with different habitat optima replace each other locally as the dominant taxon. This switching among the most common species decreases dominance of a DA by any single species and increases evenness in the distribution of individuals among species (**Figure 1**) (Tomasovych & Kidwell 2010a). *Implications: Unless a single species dominates over the duration of time averaging (as in some highly stressed and human-controlled systems), short-term instability in a community will be underestimated. More positively, the dominance of the DA approximates the shared dominance of multiple species in the metacommunity.*

2.1.3. Abundance structure. As a result of these effects on both rare and abundant species, the rank-abundance distribution is flattened significantly at small spatial scales: The most abundant taxa do not dominate as strongly as they do in LAs, more species have moderate abundance, and the tail of rare species is lengthened, even with constant sample size (Tomasovych & Kidwell 2010a). This flattening is inevitably coupled with the higher species richness of DAs at small spatial scales, which arises within the first few decades to centuries of time averaging. *Implications: The rank-abundance distributions of DAs approximate that of the single-habitat metacommunity and tend to underestimate how strongly a single species may temporarily dominate a local community. Past levels of stress and variability in stress will thus be underestimated.*

2.1.4. Regional-scale diversity. As a result of flatter rank-abundance distributions, time-averaged assemblages at small spatial scales capture a larger proportion of regional richness than do nonaveraged assemblages (Tomasovych & Kidwell 2010a). This effect corresponds to an increase in the y-intercept and a decrease in the slope of the species-area relationship of DAs relative to LAs. *Implications: Local-scale DAs sample the habitat-level metacommunity more completely than do LAs, although they do not fully reach metacommunity values; this should also be true for habitat-scale DA sampling of the multiple-habitat, regional metacommunity. Compared with nonaveraged LAs, DAs are more efficient samplers of both metacommunity richness and species composition.*

2.1.5. Beta diversity. Beta diversity is the variation or turnover in composition among assemblages on a landscape (see Anderson et al. 2011). It declines with time averaging because each local assemblage is increasingly likely to (*a*) be colonized by species from the shared species pool and (*b*) experience habitat conditions that occur in spatially adjacent communities, thus reducing spatial variation in species identity and species abundance (**Figure 1**) (Tomasovych & Kidwell 2009a,b). Empirical studies show that beta diversity declines among DAs sampled inside a single habitat as well as among DAs sampled from multiple habitats, although the potential for complete homogenization of assemblages from multiple habitats is small. Compared with LAs, temporal turnover

among DAs is also reduced, thereby generating a relatively shallower slope in the species-time relationship of DAs (Tomasovych & Kidwell 2010b). *Implications: Diversity is transferred from the beta to the local scale with time averaging; thus, spatial and temporal comparisons of beta diversity and diversity partitioning are sensitive to temporal scale.*

2.1.6. Metacommunity species composition and structure. Local-scale DAs become increasingly similar to each other and to the source metacommunity both in species' presence/absence and in rank abundance, owing to the changes in diversity and abundance structure described above, and these changes arise within the first few decades to centuries (Tomasovych & Kidwell 2010a,b, 2011; also see the modeled robustness of rank-abundance data by Olszewski 2012). The average composition of time-averaged DAs (defined by the centroid of assemblages in multivariate space) can shift significantly from the average composition of short-term LAs, owing to increased species richness, especially the increased proportion of rare species. The location of the DA centroid thus captures more of the composition of the regional metacommunity than does the average composition of multiple local LAs at any instant in time. *Implications: DAs approximate the identity and relative dominance of species in a larger encompassing area, even at low time-averaging levels. The taxonomic composition of a fauna is sensitive to its temporal scale.*

2.1.7. Variability in general. Time averaging reduces the range of variability among samples of all biological attributes listed above in both space and time (Tomasovych & Kidwell 2009a, 2010a,b, 2011; for an early discussion, also see Peterson 1977). A series of time-averaged samples (DAs or fossil assemblages) will underestimate the magnitude of swings in community composition and structure and thus will underestimate the historic range of variability in a system; modern-day states and variability in states, based on nonaveraged LA data, will tend to appear unprecedented (Tomasovych & Kidwell 2010b). *Implications: Time averaging limits the size of an environmental or biological perturbation that can be detected paleontologically and limits the detection of changes occurring at small spatial scales or over short intervals of time. Analyses testing the match between observations and models need to scale model predictions to the temporal resolution of assemblages. By contrast, coarsened temporal resolution permits the detection of turnover and diversity of metacommunities and of the large-scale processes that determine metacommunity evolution.*

2.1.8. Relationships between species and environments. With time averaging, local-scale DAs along a spatial or environmental gradient become more similar to each other but do not become identical: Significant spatial variation in the species composition of DAs is explained by environmental characteristics, comparable with that observed among LAs along the same gradient (Tomasovych & Kidwell 2009b). A local DA is most strongly autocorrelated with the habitat-level species pool that served as the most recent source of individuals, thus reducing the potential for complete among-habitat homogenization in species composition at local scales. Unless rates of sediment aggradation (and thus burial) are extremely low, a limited number of habitats will be averaged locally. *Implications: DAs capture relationships between species abundance and environmental variation and can reveal habitat preferences where such preferences exist in the LA. Thus, they can inform species-distribution modeling that ranks models according to their ability to predict spatial variation in species identity and abundance.*

2.2. Temporal Scaling: Observed Effects in Death Assemblages

The key finding from meta-analyses of molluscan LAs and DAs is that, in settings with little or no human activity, the majority of observed live-dead differences in community-level attributes

closely match the expectations of time-averaging models that do not permit taphonomic bias: Observed live-dead differences can be explained largely by differences in the temporal scales of nonaveraged LAs and time-averaged DAs (compare right and left columns in **Figure 1**) (also see **Supplemental Table 2**; see review by Kidwell 2013). Information on a community-level attribute such as richness or dominance that is derived from molluscan DAs is appropriate for a temporally coarse sampling of random, within-habitat variability in the composition of the LA.

The ability of natural, within-habitat variability among LAs to encompass observed live-dead differences is impressive, given the duration of time averaging for most molluscan DAs (**Table 1**) and the array of postmortem processes with potential to alter species abundances during shell residence in the uppermost mixed layer of the seabed. The net effect of taphonomic biasing processes on community-level attributes during time averaging is apparently minor for soft-sediment shallow-marine mollusks (Tomasovych & Kidwell 2009a, 2010a, 2011; Weber & Zuschin 2013). Taphonomic biases within community-level data are apparently so numerous and operate in such varied directions that they primarily introduce nondirectional noise both within habitats and across landscapes (Kidwell 2013). [For an early case study recognizing the importance of time averaging rather than postmortem transportation and other processes in creating observed live-dead differences, see Warme (1969).] Comparably good live-dead agreement is being found in other groups, such as ungulate and other "large-mammal" assemblages (see review by Behrensmeyer & Miller 2012); small-mammal assemblages (e.g., Jorgensen et al. 1998; Hadly 1999; Reed 2007; Terry 2010a,b); freshwater and terrestrial mollusks (e.g., Rundell & Cowie 2004, Erthal et al. 2011, Tietze & De Francesco 2012, Yanes 2012); lake ostracodes (Michelson & Park 2013); and, for some diversity attributes, reef corals (see review by Greenstein 2007) and hard-substratum mollusks (e.g., Zuschin et al. 2000, Zuschin & Stachowitsch 2007, Albano & Sabelli 2011). This high level of fidelity is not expected for all groups, particularly ones with strong interspecies differences in body size and other features affecting intrinsic durability (e.g., all birds as opposed to passerines) (Behrensmeyer et al. 2003, Turvey & Blackburn 2011; for a general discussion, also see Kidwell 2013).

"Residual" live-dead differences that cannot be explained by within-habitat time averaging may reflect true taphonomic bias but are as likely to reflect local directional change in environmental conditions (and LAs along with them) (Tomasovych & Kidwell 2011). For example, rare dead shells of intertidal or estuarine species encountered in subtidal DAs have generally not been transported there, but instead are relicts of populations that lived at those approximate locations during earlier stages of postglacial sea-level rise (e.g., Flessa 1998; see reviews by Kidwell & Bosence 1991, Kidwell 2013). Globally, the strongest correlate of live-dead mismatch in molluscan data sets turns out to be human activity in the study area, which is capable of shifting the LA from its natural baseline in recent time, thus causing the time-averaged DA to disagree with a snapshot of the LA today (Kidwell 2007) (also see Section 3.5).

Molluscan DAs accurately discriminate habitats at spatial scales of tens to hundreds of meters and over a temporal window of a few decades to centuries, with some shells as old as several millennia, depending on the setting. The temporal and spatial resolution of land mammal DAs, reef corals, reef mollusks, reef larger foraminifera, and open-shelf brachiopods is generally on the same order or finer (Behrensmeyer et al. 2000, Krause et al. 2010, Behrensmeyer & Miller 2012, Kidwell 2013) (**Table 1**). In contrast, the standard spatial resolution of samples for most ecological analysis including regional surveys is a local site (meter-scale point, quadrat, plot), and, even for multiyear studies, the usual standard for temporal resolution of a sample is a single season or less.

Thus, the consistently coarser spatial and temporal scale of DA data is the primary opportunity—and challenge—for using DAs in ecology and conservation biology as well as for integrating DA (and fossil assemblage) data with conventional live-collected data. Most other

"data-quality" concerns are shared: For example, both LA and DA data are subject to problems related to sample size and statistical power, methodological and other observer biases such as census corrections for hard-to-capture species, the matching of space and time frames to the question at hand, and taxonomic and functional scope (e.g., focus on small mammals rather than all metazoan granivores in a community, focus on breeding passerines rather than all birds that occupy a habitat).

3. APPLICATIONS

3.1. Inventory and Structure of Regional Diversity

DAs should be more efficient than LAs as samplers of regional diversity because time averaging transfers a significant portion of beta diversity to the local scale. For example, among 11 large molluscan live-dead data sets, local DAs, on average, capture 80% of regional richness (expressed by the total Shannon entropy of all DAs pooled), whereas LAs capture only 60%, holding sample size constant (Tomasovych & Kidwell 2009a). Multiple samples of DAs will generally be needed to estimate the regional-scale composition accurately in a region with multiple habitats, owing to limits on the postmortem transportation of shells among habitats and despite the potential for habitat migration during the prolonged windows of time averaging in some settings. For example, in a single set of samples from a survey of the southern California shelf in 2003, 63 bivalve species occurred alive and these plus an additional 31 species were encountered dead, out of a cumulative regional checklist of 100 species (expected under a comparable sample size) based on several decades of biomonitoring subtidal LAs. Warwick & Light (2002) suggested using taxonomic distinctness (average step between species in a Linnean classification or phylogenetic tree) and variation in distinctness as less sample-dependent measures of diversity. Doing so, they found that a single intertidal sample of the largely epifaunal gastropod DA in southwest Britain matched a regional species checklist fairly well but that a comparable sample of the largely infaunal bivalve DA underestimated regional richness (presumably because that DA reflected less postmortem transportation). Pooling two local intertidal samples of molluscan DAs on Australian rocky headlands, in contrast, consistently yielded estimates of taxonomic distinctness that were well within the 95% confidence intervals of the taxonomic distinctness of the regional molluscan checklist (Smith 2008).

To serve as proxies or surrogates of regional species pools, DAs need not capture all species present if we have a reasonable estimate of the proportion of diversity that they typically do capture in analogous settings (see Kidwell 2013 for more cross-scale estimates) (for the ability of DAs to estimate habitat-scale diversity, also see **Table 1**). This finding, long assumed in malacology, should encourage researchers to use molluscan DAs to recognize diversity gradients and hot spots (for the power of live-collected mollusks as surrogates of total macrobenthic diversity, see Magierowski & Johnson 2006; for the use of standing deadwood diversity to estimate saproxylic insect diversity, see Lassauce et al. 2011). Given the probable extinction rates today and in the near future (Barnosky et al. 2011), DAs are valuable alternatives for estimating regional species pools.

Moving beyond richness and presence-absence data, meta-analyses demonstrate that a local time-averaged molluscan DA also captures the relative abundance of species in the larger species pool and thus the structure of the metacommunity (Tomasovych & Kidwell 2009a, 2010a,b, 2011). Such information can rarely be acquired by conventional live-collection methods, yet it is far more important than local-scale data for evaluating resources and possible resilience in a system (e.g., Magurran 2012). Inventories of rare species are similarly critical for conservation efforts as well as

for theories of community assembly, and the high temporal variability of rare species is becoming increasingly clear from repeat-sampling studies (e.g., Magurran & Henderson 2010, Hercos et al. 2013). Molluscan DAs are especially good at capturing rare species. For example, Bouchet et al. (2002) encountered 2,738 species of shelled mollusks in a single New Caledonia lagoon, of which 783 (28%) were dead-only, almost all of which were numerically rare (occurring as singleton or doubleton individuals). These authors suspected but could not confirm that their dead-only species were still part of the living fauna. On the basis of the modeled effects of temporal coarsening (above), the entire set of rare dead-only species, along with the smaller number of live-only rare species, is probably part of the extant metacommunity missed by sampled LAs (see also Zuschin et al. 2000, Zuschin & Oliver 2003). Land-snail surveys also typically find that 30% or more of all species, especially rare species, are dead-only, despite relatively harsh postmortem conditions that should mitigate against postmortem persistence (Rundell & Cowie 2004; Sólymos et al. 2009a,b; Yanes 2012). Note that live-only and dead-only species can also have conservation significance as evidence of new invasion and local extirpation (see Sections 3.2 and 3.3) (also see **Supplemental Table 2**).

These advantages are not limited to molluscan DAs. For example, the species richness of small-mammal DAs, concentrated under raptor roosts, is indistinguishable from that produced by seasonal sampling of LAs over several years to decades in the surrounding landscape of varied habitats, and prey species are documented in correct proportional abundance to the source LAs (Terry 2010a,b). Passive accumulations of dead remains can also be effective samplers of regional diversity. For example, Pyenson (2010, 2011) found that the richness, species composition, and relative abundances of cetacean species inferred from beach carcasses agreed remarkably well with open-ocean censuses of living populations (also see Liebig et al. 2003, 2007). Pollen assemblages from ponds and lakes provide accurate samples of wind-pollinated species at a landscape scale that is proportional to the surface area of the water body (Jackson 1994), and leaf litter correctly captures the relative abundance of standing vegetation (Burnham 1989, 1994, 1997). The transport of specimens in all of these examples—by predators, currents, and wind—coarsens the spatial resolution of the biological information preserved by a local, time-averaged DA but that information is nonetheless faithful to species composition across the source landscape.

The ability of DAs to reflect diversity at larger temporal and spatial scales depends on the inherent postmortem durability ("longevity") of their tissues (**Table 1**). DAs tend to underestimate true richness even of biomineralized animals if the fine morphologic detail needed to discriminate species is rapidly lost postmortem, a problem that is most acute for rapidly disarticulated skeletons of echinoderms, barnacles, and sponges. For example, the richness and species composition of coral DAs agree closely with standing populations in the relatively low-diversity Caribbean Sea, but they underestimate diversity in the Indo-West Pacific, where the coral genus *Acropora* includes many species that are differentiated by fine-scale skeletal features that quickly disintegrate after death (Greenstein 2007).

Moving beyond richness, the good capture of abundance information by land-mammal and soft-sediment molluscan DAs may not apply to other groups: Where inherent durability (e.g., body size, robust shape) or life span is significantly negatively correlated with species' abundances in the LA, relative abundances in the DA can be strongly distorted (see general discussions in Edinger et al. 2001, Kidwell & Rothfus 2010). To circumvent such issues, single groups subject to strong postmortem distortion can be analytically omitted from comparisons among sites or the analysis could be coarsened taxonomically, much as biologists may subsume cryptic species into a single species complex or coarsen taxonomic resolution to the level of families or functional groups (e.g., Warwick 1993). In live-dead comparisons in tropical settings with large numbers of rare live-only and dead-only species, omitting rare species greatly improves the resemblance of

the DA to the LA (e.g., Zuschin et al. 2000). Although it should be done with care, such analytic truncation is comparable to the removal by ecologists of rare species from large data sets to reduce zeros in matrices or to avoid problems in taxonomic identification (e.g., Gauch 1982, Gobet et al. 2010).

3.2. Range Expansion and Contraction

Some of the deepest ecological insights derived from paleontological analysis come from the recognition of large, rapid, and individualistic changes in the geographic ranges of plants and animals in response to climate change since the Last Glacial Maximum, resulting in no-analog communities, high resilience, and other "ecological surprises" (Jackson & Williams 2004, Graham 2005, Williams & Jackson 2007, Pinsky et al. 2010, Bhagwat et al. 2012, Pardiñas & Teta 2012, Veloz et al. 2012). Information on the past ranges of extant species can also be inferred from DAs alone. For example, woodrat middens sample macroflora with ~100 m of spatial resolution and are protected from subsequent destruction and mixing with younger material (Lesser & Jackson 2011). Regional arrays of radiocarbon-dated middens can thus track the migration of tree species over thousands of years with 100–500-year resolution, thereby revealing responses to progressive warming (e.g., Lyford et al. 2002, Jackson et al. 2009).

Seafloor DAs are typically more time averaged, but they can still yield valuable evidence of the former existence of extant species outside of their present range. For example, dead colonies of *Acropora* exposed on the shallow-water Atlantic seafloor of Florida show that well-developed reefs grew as far north as West Palm Beach (~150 km north of the documented range of living colonies in modern times) as recently as 6,000 years ago (Precht & Aronson 2004). Driven by secular warming, populations have started to reoccupy this range in the past few decades (for similar range-dynamic analysis along Western Australia, also see Greenstein & Pandolfi 2008).

In prolonged time averaging of molluscan shells on continental shelves, most shells date from the past few decades to the past century and a long tail of rare shells dates back multiple millennia (see Kidwell 2013). Accordingly, even millennial-scale climate "flickers" can produce thermally anomalous mixtures of species, especially at locations near provincial boundaries where small northward or southward incursions of temperature-sensitive species can alter LA (and thus DA) composition (Roy 2001). Sclerochronology, isotopic, and geologic age dating of individual shells can deconvolve such histories from time-averaged DAs and should be amenable to evaluating shorter-lived climate changes including interannual El Niño cycles, interdecadal phase shifts such as the NAO and PDO, and secular warming since the mid-nineteenth century and the 1970s. For example, notwithstanding millennial-scale time averaging of molluscan DAs, age-dated bivalve shells of a now strongly dwindled bivalve species were used to develop a chronology of how dams changed the Colorado River's water flow to the upper Gulf of California since the 1930s, resulting in strongly reduced productivity (Kowalewski et al. 2000, Flessa 2009 and references therein). Analysis of otoliths from middens in the same region shows that, owing to slower growth rates, the endangered fish *Totoaba macdonaldi* now attains sexual maturity several years later than it did before the dam was built: As a result, changes in fishery management will not suffice for its recovery (Rowell et al. 2008).

As a general caveat, it is important to note that the climatically mixed assemblages created by prolonged time averaging of coral and molluscan DAs on continental shelves is a function of the slow net rates of sediment accumulation commonly found there. This contrasts with the decadal- or finer-scale resolution preserved in many lacustrine and estuarine sedimentary records that should also be evident in their core-top DAs (e.g., Brewster-Wingard & Ishman 1999, Edgar & Samson 2004, Yasuhara et al. 2012). On dry land, sediment accumulation rates are even slower,

so that bone assemblages must be parsed using weathering stage and direct age dating to achieve higher temporal resolution in species' co-occurrences (Behrensmeyer & Miller 2012; see Kidwell 2013 for more discussion).

3.3. Invasive Species and Local Extinction

DAs have not been frequently used to evaluate species invasions and extinctions. Valuable work on this topic has been either sedimentary core based (e.g., pollen evidence of problem species and habitat change) or in an archaeological context (e.g., mammal and bird extinctions; Steadman 1995, Burney et al. 2001, van Leeuwen et al. 2008, Lyman 2012, Pardiñas & Teta 2012). However, a protocol for using DAs is relatively straightforward (see **Supplemental Table 2**). Non-natives will first appear live-only and perhaps as just a few individuals, but if successful, they will quickly emerge as far more abundant alive than dead, making the ascendancy of their population evident. Similarly, a native species that has become functionally extinct, or that is strongly waning, will be observed as far more abundant dead than alive or will be abundant but dead-only. Confident interpretation of a live-only occurrence as a new arrival requires that the body type not be exceptionally fragile: Poor preservation potential would be a more conservative interpretation. Dead-only occurrences become ecologically suspicious when specimens are numerous, especially if they are in poor condition, suggesting a significant hiatus in the supply of new individuals (e.g., Simões et al. 2009). When a live-only or a dead-only species is rare, i.e., represented by very few individuals, the safest interpretation is that it is simply a rare member of the metacommunity. Yanes (2012), however, has used live-dead contrast created by numerous, individually rare living species near a port as well as strong contrast to DAs in pristine areas and the Pleistocene fossil record to suspect human-assisted arrival of several non-native land-snail species to a Bahamian island. Pardiñas et al. (2012) went directly to owl-pelleted DAs to estimate living diversity and, by comparison with a 400-year old fossil assemblage, revealed an otherwise unrecognized extinction of five small-mammal species in Patagonia. Alien arrivals and regional extinction are promising new directions for DA analysis.

3.4. Beta Diversity and Habitat Preferences

Although empirical assessments of beta diversity (turnover in species composition between samples) remain limited, ecologists are increasingly recognizing its importance to total diversity and its likely contribution to resilience: Beta diversity is almost certain to decline with increased species introductions and with habitat conversion and homogenization (McKinney & Lockwood 1999, Olden & Rooney 2006, Qian & Ricklefs 2006). DAs are one means of assessing the critical issue of beta diversity at the regional scale, where conservation and restoration efforts are usually most effective. In principle, because of the contrast in temporal resolution, beta diversity in present-day LAs should always be greater than that of co-occurring time-averaged DAs. Thus, if LA beta diversity in a region is observed to be less than, or even equal to, DA beta diversity, an alarming loss of faunal and, likely, habitat heterogeneity is indicated. This kind of live-dead mismatch in beta diversity, contrary to the mismatch expected from temporal scaling, is a promising direction in the analysis of anthropogenic impacts on regional faunas (also see Section 3.5).

Field studies consistently demonstrate that, although time averaging dampens beta diversity, DAs capture habitat-scale differences in community composition and species' habitat preferences. For example, the composition of large-mammal DAs varies in parallel with that of LAs among grassland, woodland, bush, and wetland habitats in both tropical Amboseli National Park and temperate Yellowstone National Park (Behrensmeyer & Boaz 1980, Western & Behrensmeyer 2009, Miller 2011). The DAs of corals, mollusks, and larger foraminifera also vary in parallel with
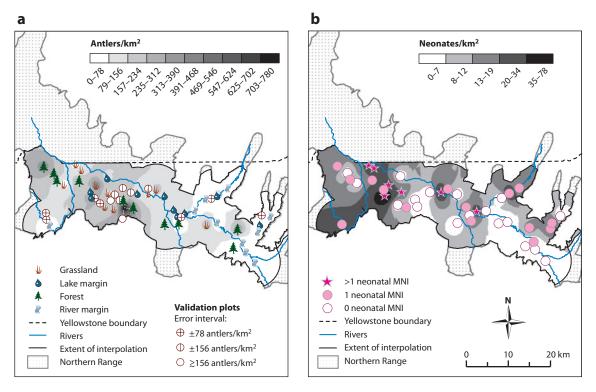
Figure 2

Bone assemblages can reveal the long-term habitat preferences of wild species, illustrated here for the wintering and calving grounds of elk on the Northern Range of Yellowstone National Park, Wyoming, based on 40 bone surveys in grasslands, forests, lake margins, and river margins. Inverse distance-weighted interpolation of bone survey data (*shaded interpolation surface*) was used to estimate past season-specific geographic preferences of living populations. (*a*) Geographic variation in the concentration of shed antlers faithfully records decadal-scale Park data on male elk wintering grounds and extends the duration over which these habitats can be studied. (*b*) Calf remains are found only within known spring calving areas (concentration expressed as minimum number of individuals, MNI/km^2). In panel *a*, 14 validation sample plots (*circles*) are also shown: Twelve of these are predicted within 20% of the interpolation and two (*open circles*) have lower accuracy. Dotted white lines show the placement of sample plots when moved for map clarity. Figure adapted from Miller (2012).

their LAs across tropical reef tracts (Miller 1988, Zuschin et al. 2000, Yordanova & Hohenegger 2002, Zuschin & Oliver 2003, Greenstein 2007). In addition, dozens of live-dead tests of tropical and temperate mollusks on soft-sediments have demonstrated the habitat-scale spatial fidelity of DAs (see the review by Kidwell & Bosence 1991 and the meta-analyses by Tomasovych & Kidwell 2009a,b). Even temporary habitat use can be detected. For example, cervid wintering and calving grounds can be identified from the concentration of shed antlers and of neonate bones, respectively (**Figure 2**). The preference of Arctic females for relatively rare riparian terraces can be similarly identified (Miller 2012, Miller et al. 2013), thereby providing guidance to habitat conservation in the absence of direct observations.

3.5. Live-Dead Mismatch as a Signal of Anthropogenic Change

A DA can change in composition during the course of time-averaged accumulation because DAs are open systems, continually receiving input from mortality in local LAs. For example, the

Bays, lagoons, estuaries

Open shelves

- AE0 — Pristine
- AE0.5
- AE1 — Eutrophied
- AE1.5
- AE2 — ↓ Severe

Taxonomic similarity (Jaccard-Chao index) — vertical axis, 0 to 1

Rank-abundance correlation (ρ) — horizontal axis
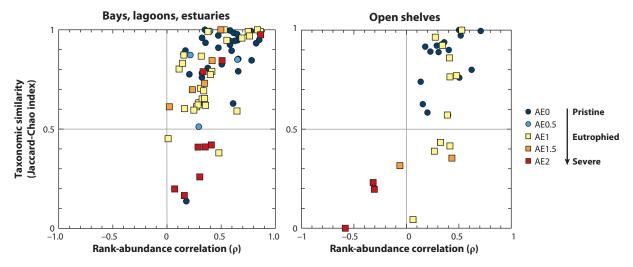
Figure 3

Per global meta-analysis of ~100 habitat-scale molluscan data sets, the largest live-dead discordances in taxonomic composition and species' relative abundance occur in study areas with known human activities, especially anthropogenic eutrophication (AE), which can be scored using independent scientific and governmental reports. Data sets from pristine areas (AE0, no human input of nutrients) consistently exhibit high live-dead agreement, falling in the upper-right quadrat of cross plots of species composition (Jaccard-Chao index of taxonomic similarity) and relative abundance (Spearman's coefficient of rank correlation ρ). Most species are present both alive and dead (similarity ≥ ~0.6), and species that are numerically dominant in one assemblage tend to dominate the other (positive ρ); live-dead differences of this small scale can be explained by differences in the temporal resolution of LAs and DAs (as in **Figure 1**). Data sets from eutrophied areas (AE0.5, uncertain human input; AE1, definite input; AE1.5, definite and possibly severe) can exhibit live-dead agreement as high as that observed in pristine areas (see overlap in *upper-right quadrant*) but range down to significantly lower values. Data sets from severely eutrophied areas (AE2, near a point source) range down to even poorer levels, with many species that occur live-only or dead-only or are otherwise much higher-ranked alive than dead or vice versa. Live-dead discordance can thus be used as a signal of anthropogenic change that has shifted the living community away from its earlier baseline, which the death assemblage remembers. Redrafted from Kidwell (2007).

composition of large-mammal DAs in Amboseli National Park have shifted significantly over the past 40 years, tracking changes in LAs driven by drought cycles and human impacts (Western & Behrensmeyer 2009). Ferguson & Miller (2007) observed a significant shift over 20 years in molluscan DA composition in a Caribbean back-reef lagoon, reflecting a shift in LA composition of an as-yet-unknown cause.

DAs can also exhibit inertia in composition, lagging behind changes in LAs, because newly dead individuals must first dilute the existing DA, which preserves a record from earlier phases of time-averaged accumulation. The greater the postmortem longevity of dead individuals, the deeper-rooted and more persistent the memory of past ecological conditions in the time-averaged DA. As shown in **Table 1**, the time frame of that memory varies among groups (a function of intrinsic postmortem durability) and settings (intensity of postmortem attack varies among environments, as does the rate at which remains are permanently buried).

This fundamental inertia of DAs can lead to strong live-dead mismatches when changes in the LA are large, rapid, and directional, providing a powerful tool for recognizing anthropogenic impacts. In the first demonstration, global meta-analysis of ~100 molluscan data sets from coastal settings found that the strongest correlate of poor live-dead agreement is human activity in the study area, especially anthropogenic eutrophication (Kidwell 2007, 2008, 2009) (**Figure 3**). More-over, the identity and functional significance of the species showing the greatest live-dead mismatch

reveal how and why the community changed. For example, seagrass-dwelling species that are more abundant dead than alive signal a loss of seagrass habitat and associated diversity, consistent with severe eutrophication (for a protocol to discriminate ecological changes from preservational and other biases, see **Supplemental Table 2**). Critically, not all habitats with known human stressors exhibit poor live-dead agreement, making live-dead discordance a conservative method—it does not produce false positives [see overlap of eutrophied data sets (coded AE1 and AE1.5) with data sets from pristine areas (AE0) in the upper-right corner of each graph in **Figure 3**]. Where stress is known to be high and live-dead agreement is quite good, the DA that archives the preimpact community may already be buried downcore, because sedimentation rates are very high and/or human impacts are so long-standing that the surficial DA has equilibrated (e.g., Erthal et al. 2011). However, the DA may also correctly recognize that human activities did not have significant ecological consequences in that area; that is, the present-day LA lies within the range of natural variability of the original community, a common finding in settings that are naturally mesotrophic or eutrophic.

The strength of the association between molluscan live-dead discordance and anthropogenic eutrophication is remarkable, given the array of natural processes, methodological issues, and scaling effects that can influence DA composition. It signifies that the impact of human activities on many benthic communities has exceeded the ecological consequences of natural changes in environmental conditions and habitat switching on decadal and longer scales. As such, we can infer such impacts with confidence for areas where historical survey data are sparse or lacking and where human stresses are unknown or contentious (Kidwell 2007, 2009).

DAs, and specifically live-dead discordance, are proving to be generally useful for recognizing strong recent changes in populations, especially human-driven changes. Miller (2011), for example, found excellent live-dead agreement in rank abundance of ungulates in Yellowstone National Park but significant disagreements in the proportional abundances of species that had undergone strong recent changes in population size. Elk, which have declined strongly since the reintroduction of wolves, are significantly more abundant in the DAs than in the LAs. By contrast, bison, whose populations have increased owing to a change in management policy, as well as mountain goats, which are a recent (re)invader, are significantly less abundant dead than alive. As another proof-of-concept study, using a 10-year time series of abundance data encompassing the invasion of an alien predatory gastropod, Chiba & Sato (2012) found high live-dead agreement of species abundances in samples collected before invasion and poor agreement afterward, reflecting known decimation of a previously dominant bivalve. Focusing on raptor-concentrated small-mammal assemblages, Terry (2010b) encountered significantly poorer live-dead agreement in richness, evenness, taxonomic similarity, and species rank abundance in a steppe landscape with strong recent human disturbance (military training, invasive cheatgrass) than in an undisturbed counterpart area. Her findings reveal an otherwise unappreciated diversity loss. Using live-dead contrast and radiometric age dating of the colonies of dead-only corals, Roff et al. (2013) documented a previously unrecognized collapse of coral communities on the Great Barrier Reef synchronous with the late-nineteenth-century European settlement of the mainland. These results indicate that management founded on surveys conducted in the 1980s is predicated on a significantly shifted baseline [and see progressive and otherwise unrecognized simplification of metazoan reef communities driven by commercial agriculture on similar timescales by Cramer et al. (2012)].

4. CONCLUSIONS

Paleontologists have evaluated DAs for decades as keys to gauging biases in the deep-time fossil record, but DAs clearly also can be used to detect and evaluate present-day ecological changes.

Biologists are increasingly aware of the need for decadal and longer historical perspectives, particularly given intensifying pressures on today's biota, and are focusing on an array of community-level attributes that go beyond richness and the local scale. These are precisely the strengths of naturally time-averaged DAs. Thanks to our growing understanding of the nature of temporally coarse data in general, DAs are providing novel insights into the composition and structure of regional diversity, historic baselines, and the timing and pattern of range shifts, habitat use, and species turnover. As a new approach to detecting and characterizing diverse kinds of anthropogenic changes, DAs represent a valuable resource for understanding our present and future.

DISCLOSURE STATEMENT

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