

## Accounting for the effects of biological variability and temporal autocorrelation in assessing the preservation of species abundance

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**Abstract.**—Quantifying the effects of taphonomic processes on species abundances in time-averaged death assemblages (DAs) is pivotal for paleoecological inference. However, fidelity estimates based on conventional “live-dead” comparisons are fundamentally ambiguous: (1) data on living assemblages (LAs) are based on a very short period of sampling and thus do not account for biological variability in the LA, (2) LAs are sampled at the same time as the DA and thus do not necessarily reflect past LAs that contributed to the DA, (3) compositions of LAs and DAs can be autocorrelated owing to shared cohorts, and (4) fidelity estimates are cross-scale estimates because DAs are time-averaged and LAs are not. Some portion of raw (total) live-dead (LD) variation in species composition thus arises from incomplete sampling of LAs and from biological temporal variation among LAs (together = premortem component of LD variation), as contrasted with *new* variation created by interspecific variation in population turnover and preservation rates and by the time-averaging of skeletal input (together = postmortem component of LD variation). To tackle these problems, we introduce a modified test for homogeneity of multivariate dispersions (HMD) in order to (1) account for temporal autocorrelation in composition between LAs and DAs and (2) decompose total LD compositional variation into premortem and postmortem components, and we use simulations to evaluate the contribution of within-habitat time-averaging on the postmortem component. Applying this approach to 31 marine molluscan data sets, each consisting of spatial replicates of LAs and DAs in a single habitat, we find that total LD variation is driven largely by variation among LAs. However, genuinely postmortem processes have significant effects on composition in 25–65% of data sets (depending on the metric) when the effects of temporal autocorrelation are taken into account using HMD. Had we ignored the effects of autocorrelation, the effects of postmortem processes would have been negligible, inflating the similarity between LAs and DAs. Simulations show that within-habitat time-averaging does not increase total LD variation to a large degree—it increases total LD variation mainly via increasing species richness, and decreases total LD variation by reducing dispersion among DAs. The postmortem component of LD variation thus arises from differential turnover and preservation and multi-habitat time-averaging. Moreover, postmortem processes have less effect on the compositions of DAs in habitats characterized by high variability among LAs than they have on DAs in temporally stable habitats, a previously unrecognized first-order factor in estimating postmortem sources of compositional variation in DAs.

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### Introduction

To untangle the effects of time-averaging and variation in rates of turnover and preservation among species on the composition of fossil assemblages, paleontologists compare modern skeletal accumulations (death assemblages, DAs) collected from terrestrial and marine landscapes with living assemblages (LAs) sampled at the same time (e.g., “live-dead” studies of Johnson 1965; Warne et al. 1976; Carthew and Bosence 1986; Greenstein and Pandolfi 1997; Jackson and Kearsley 1998; Zuschin et al. 2000; Yordanova

and Hohenegger 2002; Murray and Pudsey 2004; Lockwood and Chastant 2006; Ferguson and Miller 2007; Hassan et al. 2007; Ferguson 2008; Pike et al. 2008; Simms and Cassara 2009; Terry 2010a,b; and see meta-analysis by Kidwell 2001, 2007, 2008). However, estimating live-dead agreement in species composition using this standard approach is compromised for several reasons.

First, local DAs are almost always compared with a single survey of co-occurring living assemblages (LAs)—that is, the standing populations that exist when the DA is

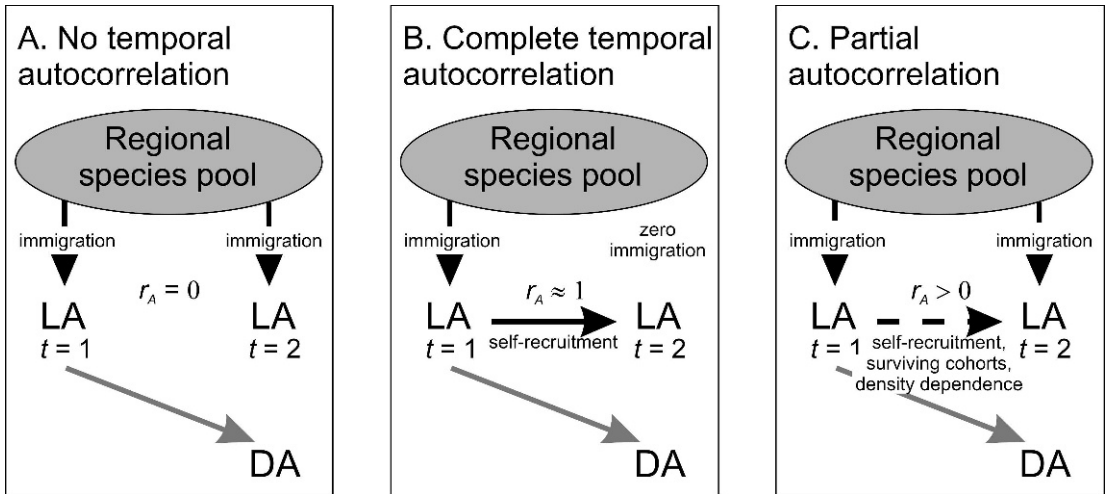


FIGURE 1. A simplified relationship showing the effect of temporal autocorrelation on analyses evaluating similarity among living and death assemblages. A, An absence of temporal autocorrelation is possible when temporally distinct and consecutive living assemblages (LAs from time 1 and time 2) are assembled by repeated species immigration from the regional species pool rather than by self-recruitment. B, Temporal autocorrelation will be high when LAs are assembled entirely or mainly by self-recruitment. C, In marine molluscan communities, dispersal frequently exceeds the spatial extent of local monitoring surveys, thus reducing the strength of self-recruitment at local scales. However, it is still likely that surviving cohorts and self-recruitment at larger spatial scales may cause LAs to be temporally autocorrelated to some degree with death assemblages (DAs) that have been collected in the same area, which reflect input from earlier LAs (gray arrows). Such autocorrelation affects comparisons of LAs and DAs extracted from *surface* (mixing zone) sediments because it violates the assumption of group independence. *Subsurface* death assemblages are also expected to differ from surface death assemblages owing to decay of autocorrelation with depth of burial. Notes:  $t$  = time step,  $r_A$  = strength of autocorrelation, LA = living assemblage, DA = death assemblage.

sampled—rather than with the LAs of previous intervals of time that are the true source LAs (Fig. 1). Even in the absence of community changes in response to environmental change or ecological succession during the interval of time-averaging, LAs that co-occur with the DA may differ from older (earlier) LAs owing to (1) demographic and environmental stochasticity that affects birth, death, and migration rates (Lande 1993; Ferson and Ginzburg 1996; Hilborn and Mangel 1997) and (2) sampling effects (e.g., Chao et al. 2005; Moore et al. 2007) (together = *premortem variation*). LAs sampled at the same moment as DAs are thus unlikely to completely match DAs in species composition even in the absence of effects from postmortem processes, within-habitat time-averaging, and time-averaging among multiple habitats.

Second, variation in species composition among consecutively sampled LAs is frequently autocorrelated at seasonal and annual scales: the same populations are being sampled to some extent. This autocorrelation among samples violates the assumption of

independence in most of the statistical tests used to estimate live-dead agreement in species composition, and can inflate the similarity between LAs and death or fossil assemblages. Finally, all DAs can be assumed to be time-averaged to some degree, and they thus represent a coarser window of sampling than provided by conventional live-collected samples of LAs. In other words, LAs and DAs are compared across temporal scales. This change in temporal scale alone can alter species composition even in the absence of interspecific differences in turnover and preservation rates (Tomašových and Kidwell 2010a,b).

Our concern with temporal autocorrelation—the second item above—is several-fold (Fig. 1). *Temporal population autocorrelation* (Lande et al. 2002) can arise (1) if there is self-recruitment, such that some living individuals are descendants of dead individuals (Fig. 1), (2) if populations consist of overlapping generations (cohorts) so that LAs and DAs contain members from the same recruitment or immigration event, and/or (3) if

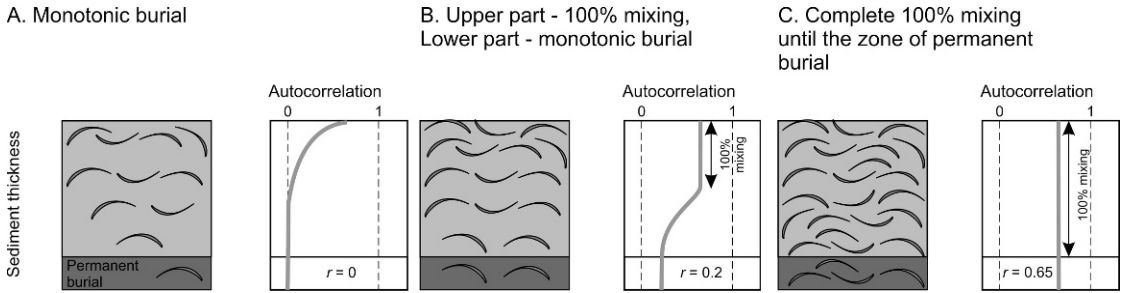


FIGURE 2. Several scenarios showing variation in the decay of temporal autocorrelation ( $r$ ) between living assemblages (LAs) and surface and subsurface death assemblages (DAs) with depth of burial. A, Continuous probabilistic burial until permanent burial. As a DA moves downward, it becomes less autocorrelated with the LA because recently dead cohorts are likely to be close to or at the sediment-water interface whereas older cohorts are present at greater sediment depths. Temporal autocorrelation will thus tend toward zero as the DA approaches the depth of permanent burial because older cohorts have a higher probability of final burial than recently dead cohorts. B, The upper portion of the sediment column is characterized by a completely homogenized mixing zone characterized by an age-homogeneous distribution of cohorts in the DA, followed by monotonic probabilistic burial to the depth of permanent burial, at which point autocorrelation begins to decay. C, The upper portion of the sediment column is completely mixed, leading to a high degree of temporal autocorrelation between the LA and the DA sampled at any depth within that mixing zone. The DA within the permanently buried zone also conserves temporal autocorrelation with its original source LA because it formed in a same way and was buried by a discrete episode of sedimentation.

population dynamics are positively density-dependent, e.g., the survivorship of juveniles of one species is higher when conspecifics are common. Temporal autocorrelation can also arise from temporally correlated environmental factors that drive population dynamics at individual stations (*environmental autocorrelation* [Halley 1996; Schwager et al. 2006]). In practical terms, both of these sources of temporal autocorrelation will be stronger factors where dispersal rates or distances are low (decreasing the probability of immigration), individual life spans are long (increasing the overlap of cohorts), spatial extent of communities is large (increasing the probability of self-recruitment), and/or temporal separation between sampling events is short. However, even in marine systems where dispersal exceeds the spatial extent of local surveys, surviving or overlapping cohorts and self-recruitment at larger spatial scales are likely to cause LAs collected from the same area as DAs to be temporally autocorrelated to some degree (McArdle and Blackwell 1989; Connell et al. 1997).

The temporal autocorrelation that exists among successive LAs can also exist between a DA and its source LAs when the DA is dominated by recently dead cohorts (e.g., Flessa et al. 1993; Meldahl et al. 1997; Kowalewski et al. 2000; Kidwell et al. 2005;

Martin 2005; Kosnik et al. 2007, 2009; Krause et al. 2010) (Fig. 2). As increments of sediment move monotonically downward to the depth of permanent burial, the temporal autocorrelation between DAs and LAs is reduced: with increasing depth, DAs become increasingly temporally separated from the input of shells from local LAs (end-member condition of continuous sedimentation; Fig. 2A). The proportion of recently dead cohorts is smaller in subsurface (buried) DAs than in surface (surficial mixed layer) DAs, resulting in a weaker or zero temporal autocorrelation of buried DAs with source LAs. Under the opposite end-member condition of strongly episodic burial events, recently dead cohorts are transferred rapidly to a depth of permanent burial, such that the buried DA partly (Fig. 2B) or completely (Fig. 2C) conserves temporal autocorrelation with its source LAs.

Here, we develop a new approach to differentiate the effects of premortem and postmortem processes on time-averaged assemblages that is appropriate for the autocorrelated samples that characterize most live-dead studies. First, we explore the effects of within-habitat time-averaging on compositional differences between LAs and DAs using neutral dispersal-limited metacommunity models that account for variation in species composition among LAs and tempo-

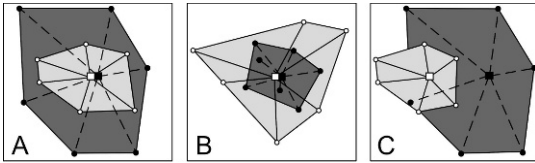


FIGURE 3. Three scenarios showing simultaneous changes in centroid location (squares) and dispersion (convex hulls defined by circles) of death assemblages (black; each DA is a replicate sample from a single small area) relative to co-occurring living assemblages (gray) in multivariate space defined by species composition. A, Variation in composition among DAs exceeds variation in composition among LAs. B, Variation in species composition among DAs is completely subsumed by variation in species composition among LAs. C, Variation in species composition among DAs only partly overlaps with variation in species composition among LAs, and the centroid of the DAs lies outside the variation among LAs.

ral autocorrelation via self-recruitment (Hubbell 2001). Within-habitat time-averaging modeled by a neutral model provides a first-order approximation that allows us to understand how much of the compositional difference (variation) between LAs and DAs can be accounted for by scale effects alone (and see Tomašových and Kidwell 2010a). Second, we use 31 molluscan data sets to evaluate (1) how much of total live-dead variation is explained by variation among LAs alone, (2) the magnitude and significance of the postmortem effects on species composition and how this compares with approaches that ignore autocorrelation, and (3) how postmortem variation correlates with methodological and environmental parameters.

### Approach

The total species composition based on multiple assemblages, using a full Euclidean multivariate space defined by principal coordinates, can be separated into two parts (Fig. 3): *the centroid location of assemblages* (mean assemblage composition) and *the dispersion of assemblages* around their centroid location (Anderson 2006; Anderson et al. 2006). When nonmetric distances are used, as here, negative eigenvalues can be produced by principal coordinate analyses. In such cases of imaginary (negative) coordinates, the squared Euclidean distances among assemblages are computed separately and are then subtracted from the squared distances

calculated on the basis of real (positive) axes (Anderson 2006). Such multivariate space completely preserves the original distances among assemblages (Anderson 2006).

Our basic approach is to decompose the amount of total live-dead (LD) variation among LAs and DAs into pre-mortem and post-mortem variation in each of our molluscan data sets. Biological and sampling variation together constitute our *pre-mortem variation*, previously referred to as “live-live variation” among spatial or temporal replicates of a habitat (to contrast with “live-dead variation”) (Kidwell 2001, 2002, 2008; Kowalewski et al. 2003). Pre-mortem variation is estimated here as the average compositional distance of spatially replicate LAs from their centroid (light gray cloud in Fig. 3A). During the formation of DAs in surficial (mixed layer) sediments, *additional (post-mortem) variation* in composition can be created (1) by interspecific differences in population turnover and preservation rates and (2) by time-averaging within one or multiple successive habitats (Johnson 1960; Van Valen 1964; Craig and Oertel 1966; Fürsich 1978; Behrensmeier and Dechant Boaz 1980; Behrensmeier 1982; Staff and Powell 1988; Bennington 2003; Kowalewski and Bambach 2003; Yanes et al. 2007; Terry 2008; Berkeley et al. 2009; Western and Behrensmeier 2009). The resulting variation in composition among spatially replicate DAs and their centroid can be larger than variation among LAs (dark gray cloud in Fig. 3A), can be subsumed within variation among LAs (Fig. 3B), can partly overlap with variation among LAs (Fig. 3C), or can occupy an entirely different portion of multivariate space. The amount of total LD variation in species composition that does *not* overlap with variation among LAs is our measure of *post-mortem* variation (see below). This variation can be expressed by sums of squared compositional distances (corrected by sample size) or by average compositional distances. When quantifying the magnitude of pre-mortem and post-mortem variation, we use averages (means) of distances because these fall within the interval [0,1], permitting comparisons among data sets that have different numbers of assemblages (different numbers of samples).

*Assumptions in Analyses of Compositional Fidelity.*—Replicate-based multivariate approaches, such as analysis of similarities, have been used to estimate the effects and significance of groups (here, effects of postmortem processes) on the composition of DAs (e.g., Pandolfi and Minchin 1996; Edinger et al. 2001; Zuschin and Oliver 2003; Tomašových and Rothfus 2005). Replicates of LAs and DAs are assumed to be exchangeable in the absence of postmortem effects, and this assumption of replicate exchangeability translates into the assumption of independent and identically distributed random errors (Clarke 1993; Anderson 2001a).

First, the presence of temporal autocorrelation between LAs and surface DAs violates exchangeability owing to the lack independence between groups of LAs and DAs (i.e., distances between LAs and DAs sampled at the same station are smaller than distances among LAs or distances among DAs) and inflates the number of degrees of freedom. This effect thus *underestimates* variation among LAs and DAs and its significance. Second, DAs frequently have lower multivariate dispersion than LAs owing to time-averaging (Tomašových and Kidwell 2009a). Inequality of dispersions also violates the assumption of exchangeability (Anderson 2001b). For example, when the dispersion of LAs exceeds the dispersion of DAs (and thus no postmortem variation exists), multivariate analyses will tend to *overestimate* the significance of variation among LAs and DAs. Finally, such approaches assume that the strength of temporal autocorrelation between surface DAs and co-occurring LAs is the same as in the relationship between LAs and subsurface assemblages that are close to the depth of permanent burial (Olszewski 2004; equivalent to the maturation zone of Sadler 1993), whereas the strength of autocorrelation is in principle most likely reduced (Fig. 2).

*Nonparametric Permutational Multivariate Analysis of Variance (NPMANOVA).*—To establish a baseline assuming full *independence* and equality of dispersions between groups of LAs and DAs assemblages, we use NPMANOVA. It is comparable to analysis of similarities but evaluates true distances rather

than rank-order distances (Anderson 2001b). The postmortem variation can be expressed as average distance between LAs and their centroid (i.e., premortem variation) subtracted from between-centroid distance (i.e., distance between centroids of LAs and DAs). This NPMANOVA approach can be adequate when the temporal separation between the cohorts that dominate LAs and DAs is relatively large so that temporal autocorrelation is negligible. In order to compute *F*-statistics, the among-group sum of squares ( $SS_A$ ) is the sum of squared distances from group centroids to the grand centroid, and the sum of squared distances from individual replicates to their group centroids correspond to within-group sum of squares ( $SS_W$ ) (Anderson 2001b).

*Homogeneity of Multivariate Dispersions (HMD).*—In order to compare compositions that are autocorrelated rather than fully independent, we introduce a modified analysis of homogeneity in multivariate dispersions (HMD). In the original approach, this analysis tests for differences in multivariate dispersions among groups (Anderson 2006). In our approach, the mean species composition of source LAs is assumed to be completely equivalent to the mean species composition of the spatially replicate LAs that exist at the time of sampling of DAs. This modification of the HMD method is possible because the relationship of LAs to DAs is directional: DAs are derived from earlier versions of LAs that are sampled at the same time as the DAs. First, rather than assuming the lack of temporal autocorrelation, non-independence between LAs and DAs sampled at the same station at local scales is removed because the location of DAs is measured with respect to centroid location of LAs, so that distances of LAs and DAs to centroid of LAs are exchangeable. Second, rather than assuming that dispersions are identical, the difference in dispersion of LAs and DAs around the centroid location of the *living* assemblages is effectively used to measure differences in species composition among LAs and DAs (Fig. 4). Therefore, in this approach (1) it is assumed that source LAs are equivalent to the sampled LAs at

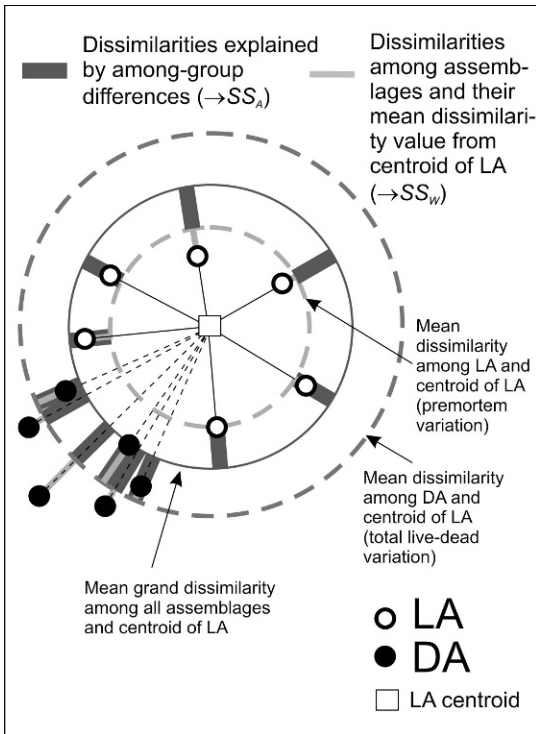


FIGURE 4. Schematic diagram showing partitioning of within-group variation (thin light gray radial lines) and among-group variation (thick dark gray radial lines) between groups of living and death assemblages in multivariate space, using a modified analysis for homogeneity of multivariate dispersions (HMD) that assumes autocorrelation between groups. The centroid of LAs represents the reference point for DAs. Total LD variation is thus the average dissimilarity among individual DAs and the centroid of LAs. Diagram depicts situation such as Figure 3C, where some postmortem variation exists.

larger spatial (habitat) scales (whereas source LAs do not need to be autocorrelated to the sampled LAs at local scales), and (2) the dispersion based on spatial replicates of LAs accounts for biological stochasticity and thus provides bounds for compositional variation that can be expected among DAs in the absence of postmortem effects. We note that applying this approach to DAs sampled in surficial sedimentary layers does not account for the possible loss of similarity between LAs and subsurface DAs.

Total LD variation is expressed as the average distance among individual death assemblages and the centroid of living assemblages. The postmortem variation unexplained by variation among LAs is expressed as the average distance between LAs and their

centroid (i.e., premortem variation) subtracted from the average distance among DAs and the centroid of LAs. The average distance among DAs and the centroid of LAs thus measures over- or under-dispersion of DAs relative to the composition of LAs (Fig. 4). *Under-dispersion* of DAs corresponds to a loss of variation compared with that of LAs, but DAs are still embedded within the multivariate space defined by those LAs. *Over-dispersion* of DAs signifies that DAs occupy portions of multivariate space outside those occupied by LAs. To compute F-statistics, the among-group sum of squared distances ( $SS_A$ ) refers to the sum of squared deviations between the grand distance (i.e., among all assemblages and the centroid of LAs) and the average group distances of LAs (i.e., among LAs and their centroid) and DAs (i.e., among DAs and centroid of LAs, Fig. 4). The within-group sum of squared distances ( $SS_W$ ) refers to the sum of squared distances between individual DAs and LAs and their average group distance from the LA centroid (Fig. 4). The F-statistic for both NPMANOVA and HMD is

$$F = \frac{SS_A / (n - 1)}{SS_W / (N - p)},$$

where  $n$  is the number of groups (i.e., two groups),  $N$  is the total number of assemblages, and  $p$  is the number of parameters. The HMD approach is implemented using the statistical programming environment R, version 2.10.1 (R Development Core Team 2009), and the code is available at [hdl.handle.net/10255/dryad.1637](http://hdl.handle.net/10255/dryad.1637).

## Methods

*Data.*—We evaluated 31 regional molluscan data sets (Table 1; also see online supplementary material at <http://dx.doi.org/10.1666/09056.s1>), each generated by sieving living and dead individuals at multiple stations distinguished by a particular depth and sediment type. A station is a sampled point on the seafloor, where sampling gear penetrates anywhere from a few centimeters up to a few decimeters of the topmost sedimentary layer. Depending upon gear and pooling of replicate samples, a single station may range from  $\sim 0.25$  m<sup>2</sup> (e.g., a

TABLE 1. Mantel tests of 31 molluscan data sets, showing that in 10 data sets on the basis of Horn-Morisita dissimilarity and in 13 data sets on the basis of Jaccard dissimilarity, LAs and DAs sampled at the same station are more similar to each other than are LAs and DAs sampled at different stations (at  $\alpha = 0.05$ , using Spearman rank correlation). Temporal autocorrelation is thus a significant factor in these data sets, despite the high dispersal capabilities of many mollusk species. *p*-values in boldface remained significant after sequential Bonferroni correction, *p*-values in italics became insignificant.

Data set	No. of sample pairs	Setting	Habitat type	Mesh size (mm)	Horn-Morisita Spearman <i>r</i>	Mantel test <i>p</i> -value	Jaccard Spearman <i>r</i>	Mantel test <i>p</i> -value	Reference
Mannin Bay 1	11	embayment	coralline algal bank	0.5	0.41	<i>0.048</i>	0.30	<i>0.015</i>	1
Mannin Bay 2	20	embayment	clean algal gravel	0.5	0	0.650	0.18	<i>0.026</i>	1
Mannin Bay 3	10	embayment	muddy algal gravel	0.5	0	0.420	0.30	0.019	1
Mannin Bay 4	10	embayment	fine sand	0.5	0.47	<i>0.011</i>	0.36	<i>0.015</i>	1
Lag La Mancha 2	4	embayment	mesohaline mud	1.5	0.78	0.087	-0.13	0.610	2
Lag La Mancha 3	6	embayment	mesohaline sandy silt	1.5	0.22	0.210	0.47	0.070	2
Tomales Bay 1	9	embayment	black mud	1.5	0.26	0.063	0.28	0.070	3
Tomales Bay 2	4	embayment	fine sand	1.5	0.14	0.500	0.26	0.340	3
Mugu Lagoon 1	14	embayment	intertidal sand	3	0.52	<b>&lt;0.001</b>	0.45	<i>0.002</i>	4
Mugu Lagoon 2	19	embayment	eelgrass	3	0.39	0.003	0.34	<i>0.008</i>	4
Mugu Lagoon 3	8	embayment	sand	3	0.83	<i>0.004</i>	0.77	<i>0.018</i>	4
Cancun 1	9	embayment	muddy shell gravel	3	0.64	<b>&lt;0.001</b>	0.067	0.067	5
Cancun 2	5	embayment	mangrove sandy mud	3	0.76	<i>0.021</i>	0.83	<i>0.026</i>	5
Contoy 1	7	embayment	mangrove sandy mud	3	0.77	<i>0.015</i>	0.06	0.410	5
Virgin Islands 1	10	embayment	dense grass	5	0.022	0.450	-0.36	0.960	6
Virgin Islands 2	8	embayment	mixed grass-sand	5	0.27	0.180	0.29	0.060	6
Patagonia shelf 1	5	shelf	mud	0.3	0.27	0.250	0.83	<i>0.038</i>	7
Amazon shelf 1	5	shelf	firm mud	0.3	0.08	0.380	0.00	0.560	8
Corpus Christi 1	6	shelf	sand	1	0.09	0.370	0.29	0.130	9
Corpus Christi 2	4	shelf	muddy sand	1	0.37	0.260	0.74	0.170	9
Chihama shelf 1	5	shelf	fine sand	1	0.73	<i>0.020</i>	0.68	<i>0.009</i>	10
S California 2003-2	8	shelf	sandy mud	1	0.24	0.180	0.30	0.120	11
S California 2003-3	7	shelf	muddy sand	1	0.27	0.170	0.87	<b>&lt;0.001</b>	11
S California 1975-2	6	shelf	sandy mud	1	0.46	0.140	0.29	0.190	11
S California 1975-3	9	shelf	muddy sand	1	0.58	<i>0.005</i>	0.63	<b>&lt;0.001</b>	11
Galveston shelf 3	7	shelf	muddy sand	1	0.31	0.097	0.48	<i>0.011</i>	11
Galveston shelf 4	8	shelf	sand	1	-0.08	0.560	0.27	0.080	12
Galveston shelf 2	4	shelf	sandy mud	1	0.66	0.250	0.09	0.670	12
Eddystone shelf 1	4	shelf	lithic gravel	1.5	0.2	0.340	-0.55	0.830	13
San Juan Channel 1	4	shelf	sand	2.3	0.2	0.520	-0.20	0.670	14
San Juan Channel 2	6	shelf	sand with boulders	2.3	0	0.510	0.61	0.090	14

References: 1 – Bosence 1979; 2 – Reguero Reza 1994; 3 – Johnson 1965; 4 – Warme 1971; 5 – Ekdale 1972, 1977; 6 – Miller 1988; 7 – Linse 1997, 1999; 8 – Aller 1995; 9 – White et al. 1983; 10 – Tsuchi 1959; 11 – Tomašových and Kidwell 2009a; 12 – White et al. 1985; 13 – Smith 1932; 14 – Kowalewski et al. 2003.

single van Veen grab) to several tens of square meters (e.g., a single dredge haul). Each station within a single habitat yields a LA and a DA, sieved from the same sedimentary volume, and an identical volume of sediment is sieved at each station from that habitat. All data sets contain at least four stations and thus four LAs and four DAs. All data sets are from subtidal, soft-sediment seafloors in coastal embayments or open shelves subject to minimal impact from human activities at the time of sampling. With the exception of four data sets from the southern California shelf (available in Data Dryad at [hdl.handle.net/10255/dryad.1225](https://hdl.handle.net/10255/dryad.1225)) and San Juan Islands (available in Data Dryad at [hdl.handle.net/10255/dryad.1637](https://hdl.handle.net/10255/dryad.1637)), these data sets are a subset of the 108 published data sets used in our previous meta-analyses (Kidwell 2001, 2008; see Supplementary Information for sources).

*Sample-Size Standardization.*—Paired LAs and DAs drawn from the same station were standardized to the same sample size  $n$  (minimum sample size observed in either the LA or the DA at each station), but that sample size generally varies among stations within individual data sets as well as among data sets. The sample size of each LA-DA pair was standardized by rarefaction, i.e., random resampling of  $n$  individuals set by the smaller assemblage, drawn without replacement from all individuals present in the larger assemblages (Hurlbert 1971; Heck et al. 1975). Each resampling run produces a slightly different species list with some differences in species identity and abundance. Resampled species abundances were averaged across 100 resampling runs and rounded to integers, eliminating rare species that on average contribute less than 0.5% to sample-size-standardized matrices. It is possible that the average diversity of the standardized assemblage will be lower than the diversity of any single resampling run, especially when the assemblage contains many rare species. In such cases, sample sizes obtained by averaging will be lower than the sample size  $n$  obtained by individual resampling runs. However, in our data sets, this procedure leads to sample sizes that are comparable to standardized sample-size values, and this effect thus should be negligible.

*Analyses.*—We use several distance measures that capture different aspects of species composition. Jaccard dissimilarity, based on presence-absence data, reflects the probability that two randomly chosen *species* from two assemblages do not belong to any of the species shared by the two assemblages. Horn-Morisita dissimilarity, based on untransformed proportional species abundances, reflects the probability that two randomly drawn *individuals* from two assemblages do not belong to the same species, relative to the probability of randomly drawing two individuals of the same species from one or another assemblage alone (Horn 1966). Both measures are independent of alpha diversity (Jost 2006), which makes them more useful here than the Bray-Curtis dissimilarities that we have used in previous analyses of similarity between LAs and DAs (Tomašových and Kidwell 2009a,b). Bray-Curtis dissimilarities have a robust and monotonic relationship with ecological distances (Faith et al. 1987; Legendre and Gallagher 2001), making them appropriate for our earlier analyses, but are sensitive to alpha diversity when based on untransformed species abundances.

In our procedure, the compositional distances (of individual assemblages to a centroid) that define total LD variation and variation among LAs are estimated independently. If these distances are constrained to have a maximum value of one—as in the case of Jaccard and Horn-Morisita indices—then a zero-sum effect applies. Namely, if variation among LAs is large and approaches the value of one, then the difference between total LD variation and variation among LAs will be negligible even when the death assemblage has experienced considerable postmortem modification (e.g., from postmortem introduction of species that are not in the pool that sources the living assemblage). To avoid a zero-sum effect and allow pre- and postmortem variation to be fully independent, we re-run some tests using a modified Gower's dissimilarity so that the upper bound of total LD variation is not constrained (Anderson et al. 2006). This index is sensitive both to changes in species composition (i.e., presence-absence data) and to order-of-magnitude



changes in species abundances (species abundances are log-transformed).

Partial Spearman rank correlation tests (i.e., evaluating correlation between two variables while controlling for a third variable [Shipley 2000; Kim and Yi 2007]) are used to evaluate the effects of mesh size (a continuous variable, ranging from 0.3 to 5 mm) and setting (categorical variable of coastal embayment versus shelf) on (1) total LD variation (measured by mean dissimilarity among DAs and the centroid of LAs), (2) premortem variation (measured by mean dissimilarity among LAs and their centroid), and (3) postmortem variation (measured by dissimilarity estimated by subtraction of premortem from total LD variation).

*Simulations.*—We use the neutral dispersal-limited metacommunity model of Hubbell (2001) as a null model that allows us to predict the species composition of LAs in the absence of per capita differences in rates of population growth (Fig. S1 in online supplementary material). The dynamic of this model accommodates both (1) biological stochasticity in LA composition over time (arising from demographic stochasticity and dispersal limitations alone) and (2) temporal autocorrelation among LAs (arising from dispersal limitation; i.e., self-recruiting local populations). To predict the species composition of the DA produced by a LA, we extend Hubbell's null model by tracking counts of dead individuals (local mortality) and assuming that per capita preservation and sampling rates do not differ among species (neutral assumption). In addition, this doubly neutral approach allows us to predict differences between groups of LAs and DAs under various degrees of within-habitat time-averaging, thus accounting for scale effects, following Tomašových and Kidwell (2010a). The details of the simulation are summarized below, but some readers may want to skip to the "Results" section. The simulation code is available at [hdl.handle.net/10255/dryad.1225](http://hdl.handle.net/10255/dryad.1225).

Variation in composition among living assemblages is predicted by taking into account community size ( $J$ ), and by estimating the fundamental biodiversity number  $\theta$  and the dispersal number ( $I$ ) (Hubbell 2001;

Etienne and Olff 2004). The biodiversity number is a dimensionless measure of metacommunity abundance structure under point mutation speciation mode (new species arise as singletons [Etienne et al. 2007]) or protracted speciation (incipient species do not need to be singletons [Rosindell et al. 2010]). The dispersal number is a measure of dispersal limitation defined as the effective number of immigrants that compete with the  $J-1$  individuals when one spot in the local assemblage becomes free (Etienne and Olff 2004). These parameters are estimated by maximum-likelihood methods from the species-abundance distributions of multiple LAs using the approach of Etienne (2007). Immigration rate  $m$  ( $m = I/[I+J-1]$ ) corresponds to the probability that a dead individual in the local community is replaced by an immigrant from the metacommunity rather than by an offspring of some original inhabitants of the local community (Hubbell 2001; Etienne and Olff 2004). This parameter is positively related to the mean dispersal distance of a species and is negatively related to the spatial extent of the station. When the ratio of sampling station size to mean dispersal distance becomes very small, the expected immigration rate is approximately equal to one (Chisholm and Lichstein 2009).

In the 31 data sets used here, immigration rates vary from 0.01 to 0.57. These values allow us to explore a relatively large portion of the total theoretical (0 to 1) parameter space. The variability of these rates probably reflects heterogeneity among data sets in the spatial extent of stations and their latitudinal position, but in general they are rather small given the potential for long dispersal by ocean currents in marine environments. We stress that *mean* dispersal distance of marine invertebrates is rather poorly known, making it difficult to assess how typical our immigration rates might be. For example, genetic and direct estimates of dispersal can differ by several orders of magnitude for a single species (Kinlan and Gaines 2003; Kinlan et al. 2005), and substantial self-recruitment can also occur even in species having a pelagic larval stage (Swearer et al. 2002). The effective dispersal can be substantially reduced by pre-

settlement mortality and by the advective and diffusive properties of water masses, so that the number of propagules can decrease rapidly away from the source population (Cowen and Sponaugle 2009).

During the formation of DAs, dead individuals are sampled from the pool of dead individuals until the count equals the mean size of LAs (sample sizes of LAs and DAs are kept equal), and correspond to the sample size  $n$  as estimated for pairs of LAs and DAs. Species abundances are then calculated for very low (five years) and very high (1000 years) durations of time-averaging. Radiocarbon and other dating indicates that this upper end-member value reflects a common maximum order-of-magnitude age for shells in molluscan death assemblages from modern coastal settings (e.g., Flessa et al. 1993; Flessa and Kowalewski 1994; Martin et al. 1996; Kowalewski et al. 1998; Rodland et al. 2006). Five years is used as the lower end-member because we find that compositions of LAs and DAs are almost identical when durations of time-averaging are less than five years, owing to temporal autocorrelation. Molluscan populations apparently do not turn over frequently enough for time-averaging effects to be distinguished from sampling effects over periods less than five years (e.g., the global median maximum life span of bivalves is nine years [Kidwell and Rothfus 2010]).

Sampling rates are defined by the size of DAs relative to the total number of dead individuals produced over the duration of time-averaging. Per capita sampling rates of individual species are equal. Although molluscan age-frequency distributions of dead individuals are commonly observed to be right-skewed, we set per capita preservation rates to one so that dead individuals are drawn from a uniform rather than an exponential age-frequency distribution (in the latter, per capita preservation rate is constant but  $<1$ ). Assuming a uniform age-frequency distribution obviously reduces the effective duration of time-averaging. This simplification is reasonable, however, because the *total* range of averaging of a uniform distribution approximates the inter-quartile range of averaging of

an exponential distribution (Tomašových and Kidwell 2010), and most empirical estimates of time-averaging adopt median or inter-quartile range values rather than the total range of age-frequency distributions as a useful characterization of temporal scale (e.g., Carroll et al. 2003; Kosnik et al. 2007).

Our simulations thus provide a prediction for total LD variation in species composition for a given level of within-habitat time-averaging in the *absence* of per capita species-specific differences in rates of turnover and preservation (Fig. S2). We focus on within-habitat time-averaging defined by the range of conditions at which the per capita vital rates of individual species remain constant. This definition of “within-habitat” is more restricted than a traditional definition, which subsumes fluctuations in species abundance related to regular seasonal or annual environmental changes (e.g., Kidwell and Bosence 1991).

## Results

*Modeled Effects of Time-Averaging on Premortem and Postmortem Variation.*—Bivariate plots of modeled assemblages display the range of relationships between variation among LAs and total LD variation arising under negligible (five years) to high (1000 years) durations of within-habitat time-averaging, in the absence of postmortem bias and multiple-habitat time-averaging (Fig. 5A,B). Such plots are a useful diagnostic tool in fidelity analyses: they show that, in the absence of postmortem bias and extensive time-averaging, an approximately isometric relationship exists between total LD variation and variation among LAs.

Total LD variation equals variation among LAs when time-averaging is negligible (five years) (Fig. 5A). With increasing within-habitat time-averaging, total LD variation can diverge from variation among LAs in ways that either create or minimize postmortem variation (this is postmortem variation arising from time-averaging alone, since per capita turnover and preservation rates are modeled as equal among all species). Total LD variation (1) can become larger than variation among LAs (a) when the *mean* DA composi-

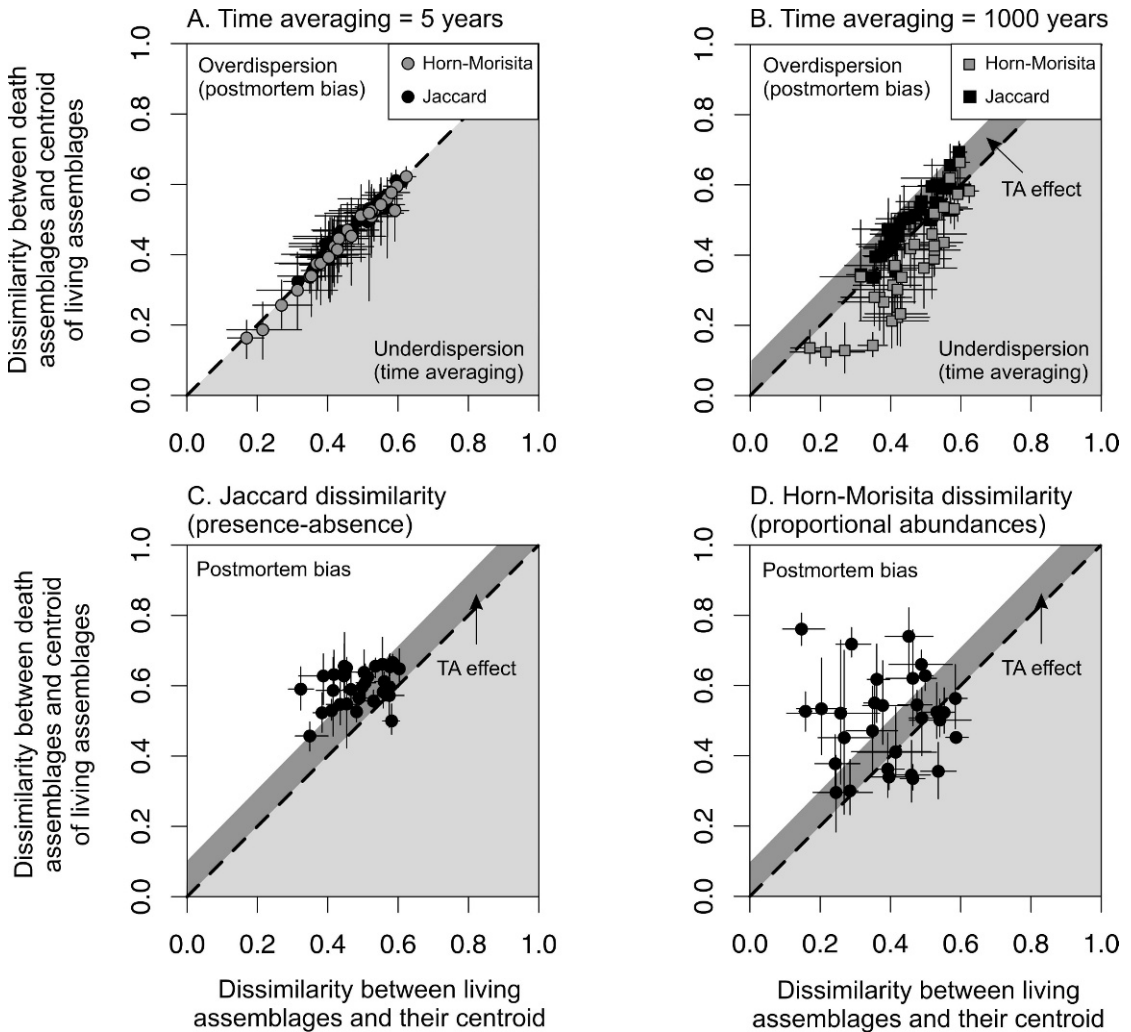


FIGURE 5. Expected relationships between premortem variation among LAs (x-axis) and total live-dead (LD) variation (y-axis) under within-habitat time-averaging (TA), simulated using neutral metacommunity dynamics and living assemblages from 31 molluscan data sets as a starting point. Each data point reflects the outcome from a different data set and the error bars are 95% bootstrapped confidence intervals. A, With negligible time-averaging (five years), data sets cluster along a positive isometric line between the average dissimilarity among LAs and their centroid on one hand (expected premortem variation) and average dissimilarity among *expected* DAs and the centroid of LAs on the other hand (expected total LD variation). B, This pattern is altered with increasing time-averaging, with the results from 1000 years of time-averaging displayed here. Using presence-absence data (black squares, Jaccard dissimilarity), millennial-scale time-averaging slightly shifts the expected centroid of DAs relative to the centroid of LAs because new species accumulate in DAs. Data sets thus move into the region of over-dispersion (that is, variation among DAs and the centroid of the LAs is greater than variation among LAs and their centroid; upper white triangle). The dark gray band in the plot thus defines the magnitude of change in composition expected from within-habitat time-averaging of LAs that is in the direction expected from postmortem bias (TA effect). Using proportional abundance data (gray squares, Horn-Morisita dissimilarity), the addition of new species has little effect but time-averaging reduces dispersion among DAs, thus reducing dissimilarity among expected DAs and the centroid of LAs and shifting data sets into the region of under-dispersion (lower light gray triangular area). *Observed* relationships among LAs and DAs from the same 31 molluscan data sets show that, when using either Jaccard (C) or Horn-Morisita (D) dissimilarity, several data sets have been affected significantly by postmortem bias and/or between-habitat time-averaging (data sets fall into the upper white triangular area). Other data sets show LD differences that can be explained entirely by within-habitat time-averaging (lower right triangular area plus narrow band of dark gray shading above the line of unity).

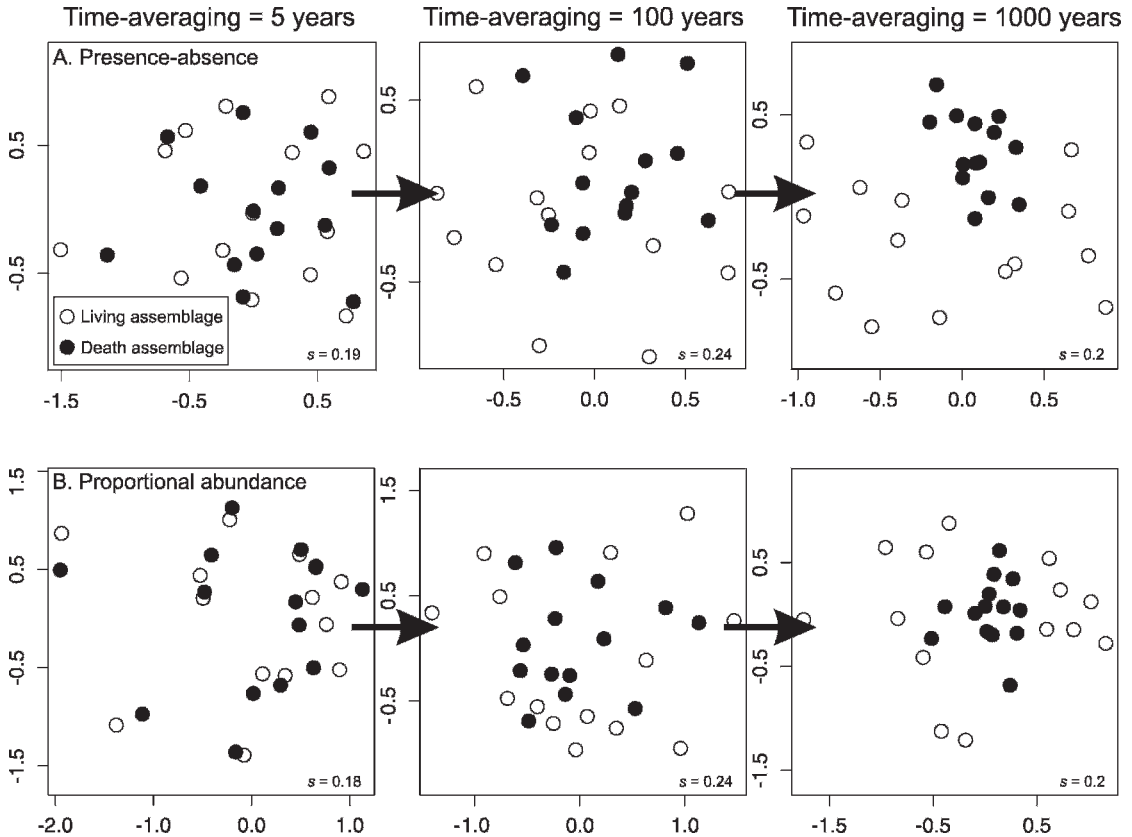


FIGURE 6. Exemplar simulation run showing how within-habitat time-averaging affects assemblage composition in multivariate space visualized by two-dimensional nonmetric multidimensional scaling. Each data point reflects the composition of a different replicate sample of either the LA (white circles) or the expected DA (black circles) collected from the same small area ( $s$  = stress value). Distances among assemblages in the plots are rescaled to raw dissimilarities so that individual ordinations have approximately comparable coordinate systems. LAs drift to some degree over time but their dispersion and centroid location are in steady state (each panel represents a successive snapshot picture of LA composition). First, when using either presence-absence data (A) or proportional abundance data (B), dispersion among DAs and their centroid is reduced in multivariate space with progressive time-averaging. This effect reduces total LD variation (defined as dissimilarity among DAs and the centroid of LAs). Second, the centroid location of DAs tends to shift away from the centroid location of LAs because autocorrelation is reduced with increasing time-averaging, which has potential to increase total LD variation (as it does in this case). A, The mean species composition of DAs shifts slightly in multivariate space using presence-absence data owing to the accumulation of rare species: the multivariate cloud defined by death assemblages is visibly not centered on the centroid location of LAs. B, This effect is negligible when using proportional abundance data: DAs remain closely centered on the centroid location of LAs. Note that DAs and co-occurring LAs sampled at the same stations are still paired after five years of time-averaging, and this autocorrelation effect is removed after 100 years of time-averaging.

tion shifts away from that of the *living* assemblages or (b) when the dispersion among DAs and *their* centroid exceeds dispersion among LAs (lower triangle in Fig. 5B, postmortem variation is created), but (2) can become larger than variation among LAs when *dispersion* among DAs and *their* centroid is reduced (upper triangle in Fig. 5B).

Simulations show that these changes reflect a variety of processes. First, as a mechanism that creates postmortem variation, DAs and

LAs become less autocorrelated with increasing time-averaging, allowing the DA centroid to move away from the LA centroid owing to true drift in the mean composition of LAs (Fig. 6). This effect increases total LD variation, thereby creating postmortem variation (black squares above the line of unity in Fig. 5B, within the dark band labeled "TA effect"). Second, acting at the same time but with an opposite effect, increasing time-averaging tends to reduce variation among

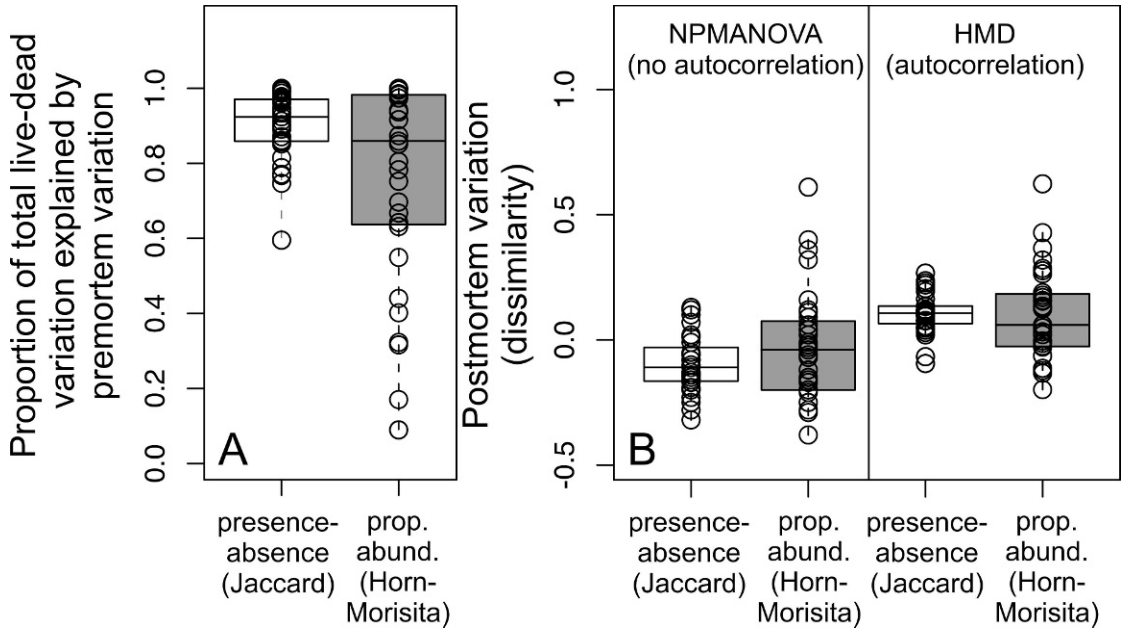


FIGURE 7. A, In the 31 molluscan data sets, premortem variation among LAs explains a large part of observed total LD variation: on average 86% of total LD variation on the basis of Jaccard dissimilarity, and 92% of total LD variation on the basis of Horn-Morisita dissimilarity. Box encloses the first to third quartiles of data around the median. Postmortem variation is defined as the component of total LD variation that is unexplained by premortem variation (schematic on left). B, Effect of analytic method on the estimated size of postmortem effects for 31 molluscan data sets. With NPMANOVA, which assumes independence among LAs and observed DAs, the average postmortem variation is negative; i.e., postmortem effects on assemblage composition do not exceed or are smaller than premortem effects. With HMD, which assumes dependence (i.e., some temporal autocorrelation) among LAs and DAs at large spatial (habitat) scales, the average dissimilarity related to postmortem effects is larger by several tenths of a dissimilarity unit and is on average positive.

DAs and their centroid because temporal fluctuations in species abundances are averaged out (Fig. 6A,B). This effect *reduces* total LD variation (i.e., the variation among DAs and the centroid of LAs, Fig. 5B) and is consistent with the reduced beta diversity that is commonly observed among time-averaged DAs (Peterson 1977; Alin and Cohen 2004; Tomašových and Kidwell 2009a). This contraction is especially notable when proportional abundance data are used (Fig. 5B): total LD variation is mostly smaller than variation among LAs because the centroid of DAs remains near that of LAs (negligible change in centroid location associated with weakening autocorrelation, Fig. 6A), whereas the dispersion of DAs around their centroid contracts strongly (gray squares in Fig. 5B, which mostly lie below the line of unity). This effect is smaller when using presence-absence data: total LD variation remains equal to or is slightly larger than variation among LAs

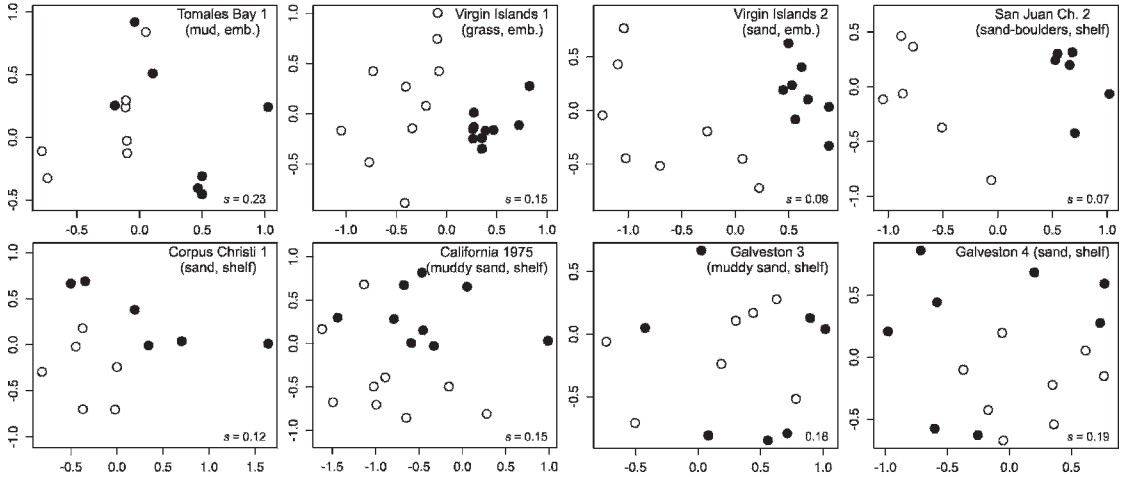
(Fig. 5B), and any shift in the DA centroid from that of the LA centroid owes to increasing species richness (black squares in Fig. 5B, Fig. 6B). The HMD approach that assumes group dependence is thus robust even when autocorrelation is negligible because within-habitat time-averaging decreases dispersion among DAs, counteracting directional changes in the mean composition of DAs.

*Observed Premortem and Postmortem Variation.*—In the 31 molluscan data sets, (premortem) variation among LAs explains a large part of total LD variation (Fig. 7A): on average 86% of total LD variation on the basis of Jaccard dissimilarity, and 92% of total LD variation on the basis of Horn-Morisita dissimilarity (Table 2). When computing this percentage, we used sums of squared dissimilarities rather than raw dissimilarities because variances are additive. NPMANOVA (assumes no autocorrelation) finds that total LD variation is significantly larger than

TABLE 2. Summary of results by data set, showing the proportion of total observed LD variation that is explained by premortem variation, the estimates of premortem and postmortem variation, and the significance values of modified tests of homogeneity in multivariate dispersions, which indicate whether variation among DAs and the centroid of LAs is larger (over-dispersion) or smaller (under-dispersion) than variation among LAs and their centroid. NS – not significant at  $\alpha = 0.05$ .

Data set	Jaccard dissimilarity				Horn-Morista dissimilarity					
	Proportion of total LD variation explained by premortem variation	Premortem variation	Postmortem variation (total LD variation)	Test of homig. in dispersions - $p$ -value	LD change in com-position	Proportion of total LD variation explained by premortem variation	Premortem variation	Postmortem variation (total LD variation)	Test of homig. in dispersions - $p$ -value	LD change in com-position
Mannin Bay 1	0.94	0.54	0.12	<0.001	over-disp.	0.86	0.46	-0.11	0.1778	NS
Mannin Bay 2	0.97	0.58	0.08	<0.001	over-disp.	0.84	0.50	0.13	0.0100	over-disp.
Mannin Bay 3	0.97	0.56	0.05	0.1079	NS	0.92	0.59	-0.13	0.0040	under-disp.
Mannin Bay 4	0.97	0.58	0.08	0.0040	over-disp.	0.95	0.55	-0.03	0.5884	NS
Lag La Mancha 2	0.97	0.58	-0.07	0.2617	NS	0.96	0.54	-0.06	0.5405	NS
Lag La Mancha 3	0.96	0.58	-0.09	0.0170	under-disp.	0.84	0.54	-0.20	0.0310	under-disp.
Tomales Bay 1	0.60	0.32	0.27	<0.001	over-disp.	0.69	0.35	0.19	0.0040	over-disp.
Tomales Bay 2	0.88	0.45	0.09	0.2647	NS	0.88	0.42	0.00	0.8921	NS
Mugu Lagoon 1	0.94	0.49	0.08	0.0210	over-disp.	0.87	0.46	-0.12	0.0190	under-disp.
Mugu Lagoon 2	0.96	0.48	0.05	0.0380	over-disp.	0.70	0.28	0.02	0.7203	NS
Mugu Lagoon 3	0.89	0.44	0.11	0.0729	NS	0.81	0.25	0.05	0.6783	NS
Cancun 2	0.98	0.56	0.05	0.0649	NS	0.92	0.49	0.03	0.6623	NS
Cancun 1	0.98	0.53	0.03	0.4775	NS	0.97	0.48	0.06	0.2438	NS
Contoy 1	0.99	0.58	0.02	0.5794	NS	0.99	0.53	-0.01	0.8432	NS
Virgin Islands 1	0.86	0.41	0.12	<0.001	over-disp.	0.17	0.16	0.37	<0.001	over-disp.
Virgin Islands 2	0.77	0.45	0.24	<0.001	over-disp.	0.09	0.15	0.62	<0.001	over-disp.
Patagonia shelf 1	0.96	0.50	0.10	0.0240	over-disp.	0.64	0.24	0.13	0.0819	NS
Amazon shelf 1	0.77	0.42	0.22	<0.001	over-disp.	0.55	0.36	0.26	<0.001	over-disp.
Corpus Christi 1	0.81	0.45	0.19	<0.001	over-disp.	0.77	0.46	0.15	0.1848	NS
Corpus Christi 2	0.75	0.39	0.23	0.0300	over-disp.	0.39	0.26	0.28	0.1029	NS
Chihama shelf 1	0.99	0.60	0.04	0.1718	NS	0.97	0.58	-0.02	0.6823	NS
S California 2003-2	0.86	0.47	0.12	0.0210	over-disp.	0.58	0.35	0.12	0.2607	NS
S California 2003-3	0.92	0.56	0.10	0.1219	NS	0.64	0.45	0.29	0.0090	over-disp.
S California 1975-2	0.79	0.45	0.21	<0.001	over-disp.	0.40	0.27	0.18	0.2997	NS
S California 1975-3	0.95	0.51	0.10	0.0440	over-disp.	0.80	0.38	0.16	0.1199	NS
Galveston shelf 3	0.93	0.51	0.11	0.0050	over-disp.	0.87	0.39	-0.03	0.7063	NS
Galveston shelf 4	0.85	0.45	0.16	<0.001	over-disp.	0.84	0.40	-0.06	0.3387	NS
Galveston shelf 2	0.91	0.50	0.14	0.0260	over-disp.	0.94	0.42	0.00	0.9351	NS
Eddystone shelf 1	0.90	0.42	0.13	0.0989	NS	0.32	0.20	0.32	0.0340	over-disp.
San Juan Channel 1	0.86	0.35	0.12	0.0310	over-disp.	0.87	0.49	0.17	0.0799	NS
San Juan Channel 2	0.87	0.38	0.13	0.0170	over-disp.	0.32	0.29	0.43	<0.001	over-disp.

## A. Jaccard dissimilarity (presence-absence)



## B. Horn-Morisita dissimilarity (proportional abundances)

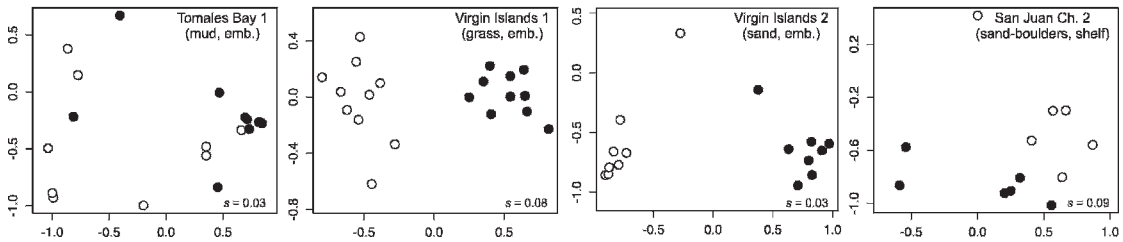


FIGURE 8. Selected data sets that show significant over-dispersion of observed death assemblages (black symbols) relative to living assemblages (white symbols) in multivariate space (here visualized by two-dimensional nonmetric multidimensional scaling), using presence-absence data (A) and proportional abundance data (B). Note:  $s$  = stress value, emb. = embayment.

premortem variation in 18 (Jaccard) and 15 (Horn-Morisita) data sets, but significance levels are enhanced by the effects of variable dispersions. The average postmortem variation is negative on the basis of Jaccard ( $-0.09$ ) and Horn-Morisita dissimilarity ( $-0.02$ ) (Fig. 7B)—that is, individual DAs are more similar in composition to the centroid of LAs than are individual LAs. In contrast, HMD (incorporating autocorrelation) finds that total LD variation is significantly larger than premortem variation in 20 (Jaccard) and 8 (Horn-Morisita) data sets (Table 2), and that the average postmortem variation is 0.11 and 0.10 respectively (Fig. 7B). Data sets where total LD variation differs significantly from premortem variation are characterized either by a complete separation of LAs and DAs in multivariate space or by an increased dispersion among DAs, even when the centroids of LAs and DAs share similar locations (Fig. 8).

Bivariate plots of our molluscan data sets show no correlation between total LD variation and variation among LAs (Fig. 5C,D, Jaccard dissimilarity: Spearman  $r = 0.3$ ,  $p = 0.1$ ; Horn-Morisita dissimilarity: Spearman  $r = 0.04$ ,  $p = 0.84$ ), in contrast to the positive isometric relationships predicted by the neutral model (Fig. 5A,B). Although some data sets fall along the expected line of correlation for good agreement, or in a band slightly above that line as expected from within-habitat time-averaging (as in Fig. 5B, especially for Jaccard dissimilarity), many data sets fall well within the upper portion of these plots (Fig. 5C,D). A small number of data sets fall into the lower portion of these plots, i.e., are significantly under-dispersed, with DAs that are more similar to the centroid of LAs than are individual LAs. In these cases, within-habitat time-averaging explains the entirety of total LD variation (as modeled in

TABLE 3. Partial Spearman rank correlations showing relationships between mesh size (partialling out the effects of environmental setting) and environmental setting (coastal embayment coded as 0, shelf coded as 1, partialling out the effects of mesh size) on (1) total live-dead variation (expressed as the average dissimilarity among death assemblages and the centroid of living assemblages), (2) premortem variation (expressed as the average dissimilarity among living assemblages), and (3) postmortem variation (expressed as the difference between total live-dead variation and premortem variation). Significant correlations are in boldface. No Bonferroni corrections applied because the multiple analyses are not strictly independent.

	Partial Spearman correlation	<i>p</i> -value
Total live-dead variation – Jaccard dissimilarity		
Mesh size	<b>−0.56</b>	<b>0.0004</b>
Coastal embayment-shelf	0.06	0.76
Total live-dead variation – HM dissimilarity		
Mesh size	0.12	0.52
Coastal embayment-shelf	0.26	0.16
Premortem variation – Jaccard dissimilarity		
Mesh size	<b>−0.4</b>	<b>0.02</b>
Coastal embayment-shelf	<b>−0.44</b>	<b>0.01</b>
Premortem variation – HM dissimilarity		
Mesh size	<b>−0.4</b>	<b>0.02</b>
Coastal embayment-shelf	<b>−0.41</b>	<b>0.016</b>
Postmortem variation – Jaccard dissimilarity		
Mesh size	0.088	0.64
Coastal embayment-shelf	<b>0.47</b>	<b>0.004</b>
Postmortem variation – HM dissimilarity		
Mesh size	<b>0.42</b>	<b>0.015</b>
Coastal embayment-shelf	<b>0.5</b>	<b>0.002</b>

Fig. 5B; e.g., Mugu Lagoon 2 [eelgrass] and Mugu Lagoon 3 [sand] data sets).

*Variation As a Function of Study Method and Setting.*—Premortem and postmortem variation behave differently as a function of mesh size (which determines the inclusion of juveniles and subadults) and study environment (coastal embayment versus open shelf) among the 31 data sets from natural settings. Mesh size and environment are collinear among these data sets—almost all shelf data sets were generated using relatively fine mesh—and thus we report only results from partial correlations (Table 3). *Premortem* variation decreases significantly with mesh size and is significantly lower in shelf than in coastal embayment habitats by both Jaccard and Horn-Morisita dissimilarity indices. *Postmortem* variation varies in the opposite way: it increases with mesh size (but only using Horn-Morisita dissimilarity) and is significantly higher in shelf than in coastal embayments (both dissimilarity metrics).

The rank correlation between premortem and postmortem variation is significantly negative (Fig. 9A, Jaccard dissimilarity: Spear-

man  $r = -0.67$ ,  $p < 0.0001$ ; Horn-Morisita dissimilarity: Spearman  $r = -0.62$ ,  $p = 0.0002$ ). Importantly, the negative correlation also characterizes the modified Gower's dissimilarity (Anderson et al. 2006) that is *not* constrained by the upper bound and thus has no zero-sum limit on the magnitude of postmortem variation (Fig. 9B, Spearman  $r = -0.87$ ,  $p < 0.0001$ ).

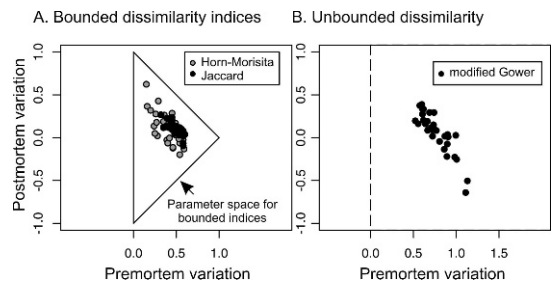


FIGURE 9. The correlation between premortem and postmortem variation is significantly negative with bounded (Jaccard and Horn-Morisita) (A) and unbounded (modified Gower; see text) (B) dissimilarities, indicating that this correlation is not an artifact of zero-sum effects. This correlation can be expected because, everything else being equal, assemblages that exhibit high spatial variation in composition occupy larger parts of multivariate space and are thus less susceptible to being shifted outside of their original space than are assemblages that occupy smaller portions of multivariate space.



Using Gower's dissimilarity, postmortem variation is also significantly larger in data sets from shelves than in those from embayments (partial Spearman  $r$  controlling for mesh size = 0.49,  $p = 0.003$ ).

### Discussion

*Finding a Good Approach.*—Evaluating the effect of variation in rates of turnover and preservation among species on the composition of assemblages and how this varies among environments requires a realistic null model for LD compositional variation that can arise from other causes, particularly from biological variability among living assemblages, from sampling, and from the effects of within-habitat time-averaging (change in temporal scale). Failure to factor out these effects can have a range of consequences. On the one hand, if the effects of biological and sampling variation are not factored out, then the raw compositional differences observed in LD studies will tend to overestimate bias because they assume that a single spatial survey provides an accurate characterization of the community. Comparing LAs and DAs of quite different temporal scales also overestimates the magnitude of taphonomic bias. For example, pooling of successive (temporally separated) LAs generally yields lower estimates of total LD variation, signifying that genuine postmortem bias is smaller when short-term fluctuations in living abundance are effectively factored out (e.g., Peterson 1976; Kidwell 2001, 2008; Hippensteel et al. 2002; Martin et al. 2002; Martin 2005; Olszewski and Kidwell 2007). On the other hand, temporal autocorrelation between LAs and surface DAs inflates their similarity and underestimates postmortem variation in standard multivariate tests because LAs and DAs are not fully independent. DAs tend to resemble LAs to some extent because a large component of the DA was so recently a part of the LA.

When multiple samples from one habitat are available, variation among these *spatially* replicate samples of the LA can be used to estimate the magnitude of biological and sampling variation and thus identify by subtraction the effects of postmortem varia-

tion, as in our approach here that uses HMD. This approach accommodates the effects of temporal autocorrelation (i.e., distances of LAs and DAs to the centroid of LAs are exchangeable) and compares the species composition of DAs with the composition that is expected to characterize source LAs. The condition for such an expectation is that LAs and DAs are temporally autocorrelated to some degree at habitat scales so that the centroids of LAs and within-habitat time-averaged DAs share locations in multivariate space (i.e., mean composition of source LAs corresponds to the mean composition of LAs sampled at the same time as DAs). We note that using spatial replicates of LAs to determine bounds for sampling and biological variation presumes a space-for-time substitution, i.e., that variation among spatially replicate samples captures temporal variability within the habitat over the duration of within-habitat time-averaging. In the 31 habitat-level molluscan data sets, a Mantel test (using Spearman correlation) shows that LAs and DAs from the same station are in fact more similar to each other than to LAs and DAs from other stations. At  $\alpha = 0.05$ , similarities among LAs and similarities among DAs are significantly rank correlated in 13 data sets on the basis of presence-absence data and in 10 data sets on the basis of proportional abundance data (Table 1). The effect of temporal autocorrelation is thus significantly present in ~30–40% of data sets even at quite local scales (binomial test,  $p < 0.0001$ ). This approach is also robust when autocorrelation effects are negligible, because within-habitat time-averaging tends to reduce dispersion among DAs.

The effects of temporal dependency between LAs and DAs on estimates of compositional similarity have rarely been explicitly mentioned in LD fidelity studies. It has, however, been incorporated implicitly into several models developed to explain the paradox of high LD compositional agreement in species or size classes that have inherently low preservation potential. Examples of such paradoxes include (1) time series where increased species abundances in LAs coincide with or are rapidly followed by increases of

the same species in DAs (Powell et al. 1986), (2) recruitment pulses in LAs that are followed by increased abundances of fragile juveniles in DAs when tracked at weekly and monthly scales (Cummins et al. 1986), and (3) size-frequency distributions of DAs that contain comparable proportions of juveniles as LAs even when multiple lines of evidence indicate that taphonomic half-lives are short and that the proportions of living juveniles vary temporally (Tomašových 2004). The implication of these observations is that DAs that are dominated by species or size classes having low preservation rates are likely dominated by recently dead cohorts of these species or size classes, and that in effect DAs are tracking changes in LAs at short time scales owing to temporal autocorrelation.

*The Variation Explained by Premortem and Postmortem Components.*—In data sets drawn from regions that are relatively unaffected by human activities and that are thus relevant analogs for paleocommunities, we find that the majority of total LD variation is on average subsumed by premortem variation among LAs, although there is considerable variation among data sets (Table 2). We nonetheless stress that the species composition of DAs is significantly different from that of LAs in 25% and 65% of data sets using HMD (cases of over-dispersion in Table 2). A small amount of this over-dispersion can arise from within-habitat time-averaging, especially when using Jaccard dissimilarity, owing to the accumulation of new species (Fig. 5B). To minimize dissimilarity arising from substantial environmental change in habitat conditions, we focused our analysis on molluscan data sets from regions that were largely unaffected by human activities (see Supplementary Information, and Kidwell 2007). The postmortem differences in species composition found here and captured by over-dispersion should thus largely be related to (1) compositional modification owing to differential turnover and preservation among species (e.g., Pandolfi and Greenstein 1997; Wright et al. 2003; James et al. 2005; Cherns et al. 2008) and (2) time-averaging of *multiple* habitats (e.g., Fürsich and Aberhan 1990).

*Methodology and Setting As Factors in Postmortem Bias.*—In previous meta-analyses using a larger but more heterogeneous version of this database and different measures, we have found that total LD differences in species composition vary significantly with mesh size and, to a lesser degree, with environmental setting and sediment type, even when mesh size is factored out (Kidwell 2001, 2002, 2007, 2008; Olszewski and Kidwell 2007). Here, we can quantitatively parse the contributions of ecological (premortem) and taphonomic (postmortem) factors to total LD differences (Table 3), although partitioning these effects is limited by the available number of data sets and by the collinearity of mesh size with environmental setting.

We find that premortem variation among LAs is largely counterbalanced by a significant trend in postmortem variation of the opposite sign in this collection of data sets from natural settings. The negative correlation found here between premortem and postmortem variation may reflect several phenomena, but it is not a simple mathematical zero-sum effect given that it persists even with the modified Gower's dissimilarity index. First, a high degree of premortem variation in LAs might make DAs immune to taphonomic biases—those LAs occupy a large portion of multivariate space, making it more difficult to create postmortem variation unless significant transport of specimens from different regions (or condensation of species from multiple habitats) occurs. The same set of taphonomic processes operating where premortem variation among LAs is low would have a higher probability of generating substantial postmortem variation in composition. It follows then that the compositions of DAs from habitats characterized by high biological variability will tend to exhibit less net modification by postmortem processes than DAs from temporally stable habitats.

Second, the higher postmortem variation that we find in data sets generated by using a larger mesh might indicate that the species composition of adult specimens in DAs is more subject to bias from variable turnover and preservation and/or to extensive time-averaging than is the species composition of

juveniles. This trend is consistent with small shells experiencing faster destruction rates (e.g., Cummins et al. 1986; Powell et al. 1986; Tomašových 2004; Kosnik et al. 2007) and showing less interspecies differences in destruction (i.e., small-bodied species might be more similar to each other in their high susceptibility to destruction than are large species). The greater inherent durability of large shells might permit significant changes in species abundances to emerge out of interspecies differences in turnover and preservation rates. Our finding here that postmortem variation is larger on continental shelves than in coastal embayments is consistent with differences in the magnitude of time-averaging (i.e., differences in the maximum ages of shells [e.g., Flessa and Kowalewski 1994]; lagoons and estuaries are also generally geologically short lived compared to open shelves, placing a shorter upper limit on time-averaging, and are natural sediment sinks, promoting higher net rates of burial). The longer the duration of time-averaging in absolute time, the more likely that temporal environmental heterogeneity will exist, thereby fostering faunal condensation, with the largest and more durable shells retaining the longest memory of associated faunal changes.

### Conclusions

Variation in composition among living assemblages (LAs) represents a null expectation for the amount of variation that can exist among LAs and death assemblages (DAs) in the *absence* of postmortem bias from differential turnover and preservation of species and in the *absence* of scaling (time-averaging). In the absence of such effects, total variation among LAs and DAs should vary positively and isometrically with variation in species composition among LAs within a habitat. Taking into account both compositional variation among LAs and temporal autocorrelation between consecutive assemblages, we find that the effects of genuinely postmortem processes are significantly positive in 25–65% of data sets, and thus should be incorporated into paleoecological inference. The effect of autocorrelation modifies the overall conjecture about the quality of the fossil record in a

given system: the effects of postmortem processes on composition are negligible if LAs and DAs are assumed to be independent.

In general, an assumption of autocorrelation at habitat scales is reasonable—it is significant in 30–40% of our data sets even at the local station scale. Our simulations using a neutral model of dispersal-limited metacommunity dynamics show that the quantitative contribution of within-habitat time-averaging to new (postmortem) variation are either minor (on proportional abundance data) or tend to increase postmortem variation slightly (on presence-absence data). Our new method, which assumes autocorrelation in mean species composition, is thus robust even where LAs and DAs are independent because within-habitat time-averaging tends to reduce compositional variation among DAs and their centroid, and thus reduces the effects of temporal drift in centroid location of DAs.

Partitioning of variation allows us to measure postmortem variation explicitly and thus use it as the response variable in estimating environmental differences in taphonomic biases. Partial rank correlations indicate that postmortem effects are larger in data sets with coarser (adult) size fractions of assemblages and on open shelf settings (Table 3). This pattern in postmortem variation contrasts with patterns in raw LD variation found in previous meta-analyses, showing the potential for premortem effects to mask underlying postmortem trends: LD differences were larger in fine-mesh data sets and in coastal embayments (e.g., Kidwell 2001, using different metrics but with data sets from largely natural settings). Here, we find that premortem and postmortem variation are negatively correlated, even when using dissimilarity indices that are not top-bounded by the value of one. The biological variability of LAs is thus a previously unrecognized first-order factor on spatial and temporal variation in the magnitude of postmortem bias: the compositions of DAs from variable habitats will tend to be less modified by postmortem processes than those from temporally stable habitats, not because postmortem processes are less severe but

because the biological variability that feeds time-averaged DAs is so large.

Finally, fidelity analyses are usually rationalized by their ability to validate or invalidate the use of paleoecological data by quantifying the magnitude or proportional impact of processes of preservation and changes in temporal scale. Although we provide such findings here, and show that several molluscan data sets analyzed here are affected by significant postmortem effects, the ultimate goal of these analyses is to inform paleoecological design so that ecological inferences directly account for preservational stochasticity and bias. For example, fidelity analyses reveal whether preservation and scaling exert directional effects on ecological attributes such as species diversity or spatial and temporal turnover in composition (they do [Tomašových and Kidwell 2009a, 2010a]), provide empirical functions that can be used to up- or downscale ecological attributes (as in analyses of alpha diversity patterns [Bush and Bambach 2004; Tomašových and Kidwell 2010b]), and show that the net effects of taphonomic processes on species composition are not independent of original community structure (largest effects where biological variability is lowest, in continental shelf settings, and among adults [this study]). Thus, just as ecological analyses try to disentangle various sources of noise and bias (e.g., detection bias) that contribute to observed patterns in living organisms, analyses in paleoecology, conservation paleobiology, and historical ecology can incorporate expected variation from preservation and temporal scaling into their inference of ecological processes from fossil and subfossil records.

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