

Fidelity of variation in species composition and diversity partitioning by death assemblages: time-averaging transfers diversity from beta to alpha levels

Adam Tomašových and Susan M. Kidwell

Abstract.—Despite extensive paleoecological analyses of spatial and temporal turnover in species composition, the fidelity with which time-averaged death assemblages capture variation in species composition and diversity partitioning of living communities remains unexplored. Do death assemblages vary in composition between sites to a lesser degree than do living assemblages, as would be predicted from time-averaging? And is the higher number of species observed in death relative to living assemblages reduced with increasing spatial scale? We quantify the preservation of spatial and temporal variation in species composition using 11 regional data sets based on samples of living molluscan communities and their co-occurring time-averaged death assemblages. (1) Compositional dissimilarities among living assemblages (LA) within data sets are significantly positively rank-correlated to dissimilarities among counterpart pairs of death assemblages (DA), demonstrating that *pairwise* dissimilarity within a study area has a good preservation potential in the fossil record. Dissimilarity indices that downplay the abundance of dominant species return the highest live-dead agreement of variation in species composition. (2) The *average* variation in species composition (average dissimilarity) is consistently smaller in DAs than in LAs (9 of 11 data sets). This damping of variation might arise from DAs generally having a larger sample size, but the reduction by ~10–20% mostly persists even in size-standardized analyses (4 to 7 of 11 data sets, depending on metric). Beta diversity expressed by the number of compositionally distinct communities is also significantly reduced in death assemblages in size-standardized analyses (by ~25%). This damping of variation and reduction in beta diversity is in accord with the loss of temporal resolution expected from time-averaging, without invoking taphonomic bias (from differential preservation or postmortem transportation) or sample-size effects. The loss of temporal resolution should directly reduce temporal variation, and assuming time-for-space substitution owing to random walk within one habitat and/or temporal habitat shifting, it also decreases spatial variation in species composition. (3) DAs are more diverse than LAs at the alpha scale, but the difference is reduced at gamma scales because partitioning of alpha and beta components differs significantly between LAs and DAs. This indicates that the effects of time-averaging are reduced with increasing spatial scale. Thus, overall, time-averaged molluscan DAs do capture variation among samples of the living assemblage, but they tend to damp the magnitude of variation, making them a conservative means of inferring change over time or variation among regions in species composition and diversity. Rates of temporal and spatial species turnover documented in the fossil record are thus expected to be depressed relative to the turnover rates that are predicted by models of community dynamics, which assume higher temporal resolution. Finally, the capture by DAs of underlying variation in the LA implies little variation in the *net* preservation potential of death assemblages across environments, despite the different taphonomic pathways suggested by taphofacies studies.

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Introduction

Global meta-analyses of many actualistic tests of agreement between living and death assemblages (“live-dead” studies) have shown that, in marine soft-sedimentary settings, proportional abundances of living molluscan species tend to be preserved in good rank order in death assemblages and the tax-

onomic similarity of living and death assemblages can be high (Kidwell 2001, 2007, 2008). Some of these same encouraging relationships emerge in regional live-dead studies of other metazoans, for example reef-dwelling mollusks, freshwater mollusks, reef corals, lacustrine ostracodes, fishes, and land mammals (Behrensmeyer et al. 1979, 2003; Stewart 1991;

Butler 1993; Cummins 1994; Pandolfi and Minchin 1996; Pandolfi and Greenstein 1997; Zuschin et al. 2000; Edinger et al. 2001; O'Connell and Tunnicliffe 2001; Zuschin and Oliver 2003; Alin and Cohen 2004; Sweetman and Smol 2006; Miller 2007; Reed 2007; Terry 2007; Zohar et al. 2008; and, as an introduction to the large live-dead literature on microbial eukaryotes and higher plants, see Hassan et al. 2008; Murray 1991; Jackson and Whitehead 1991; Jackson and Lyford 1999; Murray and Bowser 2000; Gavin et al. 2005; Zhao et al. 2006).

Live-dead findings for macrobenthos have encouraged the use of rank abundances, dominance, and rarity in paleoecology, especially in analyses that evaluate spatial and temporal changes in alpha diversity and rank abundance distributions (Westrop and Adrain 1998; Powell and Kowalewski 2002; Peters 2004; Bush and Bambach 2004; Olszewski and Erwin 2004; Finnegan and Droser 2005; Kowalewski et al. 2006; Wagner et al. 2006; Bulinski 2007), and that focus on spatial and temporal variation in species composition and species turnover (Miller 1986; Sepkoski 1988; Brett et al. 1996; Gardiner 2001; Olszewski and Patzkowsky 2001; Pandolfi and Jackson 2001, 2006; Cintra-Buenrostro et al. 2002; Kowalewski et al. 2002; Aronson et al. 2004, 2005; Bush et al. 2004; Webber 2005; Bonelli et al. 2006; Johnson et al. 2007; Patzkowsky and Holland 2007; Tomašových and Siblík 2007; Zuschin et al. 2007). Such variation in species composition among sites or among time intervals can be approximated by the average of between-sample dissimilarity indices or by the slopes of species-area and species-time plots (Arita and Rodríguez 2002); spatial variation in species composition is generally referred to as beta diversity (e.g., Whittaker 1960, 1972; Wilson and Shmida 1984). Quantifying temporal and spatial variation in species composition provides valuable insights into the sources of diversity variation, and makes unique predictions on the particular roles of neutral (drift), trade-off, and niche processes in community dynamics, thus distinguishing among metacommunity models (Chase et al. 2005; McGill et al. 2005; Shurin 2007; Munoz et al. 2008).

However, live-dead agreement of variation in species composition over time and/or space remains unexplored. This postmortem fidelity in spatial and temporal variation in species composition is critical, because the time-averaging that characterizes the formation of most fossil assemblages reduces their temporal resolution: alpha and beta diversity are not scale-invariant and specifically scale as a function of time (Rosenzweig 1998; McKinney and Frederick 1999; Adler and Lauenroth 2003; White et al. 2006). Thus, even in the absence of bias from inter-species differences in preservation or postmortem transportation, we would expect death assemblages (DAs) to differ from living assemblages (LAs) in the magnitude of variation in species composition that they exhibit. An empirical understanding of the scaling effects of time-averaging on spatial and/or temporal species turnover is thus of high importance in paleoecological analyses. Scale has several components, such as the grain of samples, the total extent of samples, and inter-sample distance (Palmer and White 1994). Here we mainly focus on the inherent difference in temporal resolution (grain) between LAs and DAs.

Quantitative and qualitative evidence that sites can differ in preservation pathways (e.g., for macrobenthos, the relative importance of bioerosion versus abrasion and other variables [Brett and Baird 1986; Fürsich and Flessa 1987; Meldahl and Flessa 1990; Kowalewski et al. 1994; Best and Kidwell 2000]) suggests that variation in species composition among DAs might be created entirely by taphonomic processes, and might be either greater than or less than that observed among LAs. Variation in species composition among DAs that is faithful to underlying variation among LAs thus requires that the net effect of preservation factors is relatively uniform among sites—i.e., that species preservation rates and sedimentation rates are comparable. Barring this uniformity, live-dead agreement of between-site variation in species composition might be poor, notwithstanding good *within-site* live-dead agreement in species composition.

We evaluate two hypotheses in this study. First, we test a prediction that variation in species composition will be lower among DAs

than among LAs owing to time-averaging (e.g., Johnson 1972; Behrensmeyer 1982; Fürsich and Aberhan 1990; Miller and Cummins 1990; Behrensmeyer and Chapman 1993; Kowalewski 1996; Kowalewski et al. 1998; Olszewski 1999; Martin et al. 2002; Kowalewski and Bambach 2003). Time-averaging imposes a decrease in temporal resolution: it permits mixing of skeletal remains from multiple generations of living populations characterized by temporally variable abundances arising from demographic and environmental stochasticity, and from ecological succession and environmental change (Preston 1960); it also provides a window of opportunity for post-mortem transportation to homogenize species occurrences spatially. The same mechanism predicted to reduce variation in species composition in DAs has also been assumed to underlie the excess of within-habitat alpha diversity observed in molluscan death assemblages, even after sample size-standardization (Kidwell 2002, 2007, 2008; Olszewski and Kidwell 2007). Live-dead agreement studies of coral communities indicate that DAs can indeed show lower beta diversity than LAs (Edinger et al. 2001; Pandolfi and Jackson 2006). However, the magnitude of this dampening effect on variation in species composition remains unexplored for the range of time-averaging observed in present-day level-bottom communities. In addition, during the interval of time-averaging, variation in species composition can also be affected (positively or negatively) by between-sample variance in shell preservation rates, and by the input of exotic shells from different habitats owing to postmortem transport. Second, we predict that time-averaging effects on diversity partitioning will be reduced with increasing spatial scale of sampling because rates of species accumulation in time decrease with the sampled area (Preston 1960; Adler et al. 2005). We thus expect that the magnitude of the diversity excess in DAs relative to LAs will decrease with decreasing spatial resolution from alpha to gamma scales. Therefore, empirical tests of live-dead agreement are needed to establish (1) whether in fact the variation in species composition observed in DAs is consistently damped relative to LAs, (2) the mag-

nitude of this effect, (3) whether the effects of time-averaging on diversity partitioning do decrease with increasing spatial scale, and (4) the relative importance of reduced temporal resolution, taphonomic bias, and sample-size differences.

Here, using molluscan data sets from level-bottom soft-sediment settings, we address live-dead agreement in spatial and temporal variation in species composition and beta diversity using several approaches (Fig. 1). Our general definition of beta diversity is the “effective number of elements” or “the numbers equivalents” of the beta component of any diversity index such as the Shannon entropy, Simpson concentration, or Gini-Simpson index (Hill 1973; Jost 2006)—it is thus the effective number of compositionally distinct samples in the region. Compositional dissimilarity indices such as Jaccard, Sorensen, or Horn-Morisita also approximate between-sample variation in species composition and represent monotonic transformations of such beta diversity (Jost 2007). In this study, we quantify live-dead agreement of between-sample variation in species composition with both approaches, using (1) compositional dissimilarities and (2) beta diversity defined by the numbers equivalents.

First, we assess whether between-sample dissimilarities (Vellend 2001; Ellingsen and Gray 2006) and dissimilarities between samples and their group centroid observed among LAs are captured by DAs (Anderson 2006; Anderson et al. 2006) (columns A and B in Fig. 1). We evaluate live-dead agreement in dissimilarities at two levels: (I) between individual sites (e.g., is the dissimilarity between the DA at site 1 and the DA at site 2 the same as the dissimilarity between the LAs at sites 1 and 2?), and (II) among all sites (is the average dissimilarity among DAs the same as that among LAs?). Second, we evaluate whether *variation in dissimilarities*—that is, variation in the variation in species composition among LAs (Legendre et al. 2005; Tuomisto and Ruokolainen 2006)—is preserved in DAs (level III analysis within Fig. 1). Third, we quantify live-dead agreement of *beta diversity* and of the partitioning of total diversity into alpha and beta components and their subsequent transfor-

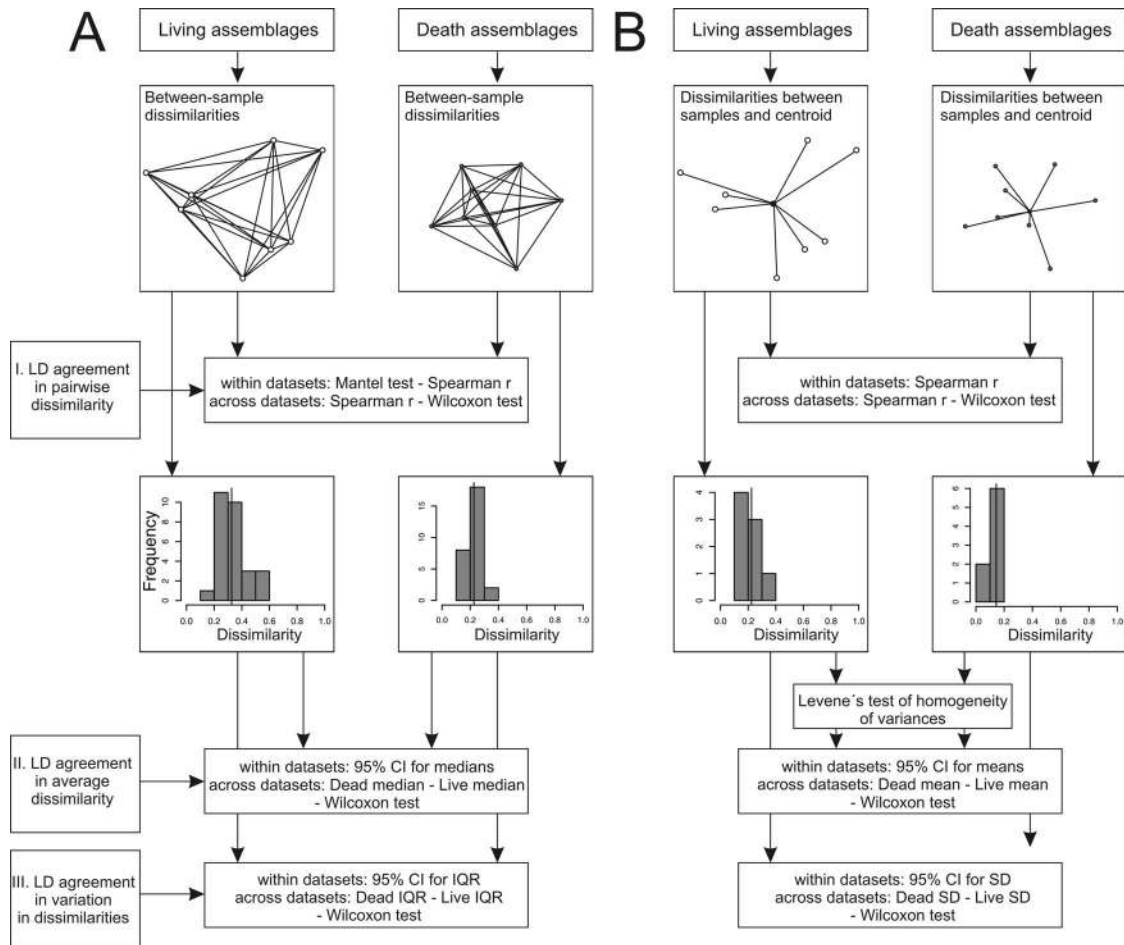


FIGURE 1. Summary of analyses of live-dead (LD) agreement in beta diversity, where variation in species composition is quantified using between-sample dissimilarities (A) and dissimilarities between samples and group centroid (B). Live-dead agreement is evaluated at three levels: (I) agreement in pairwise variation in species composition: comparisons within each of the 11 data sets, and comparison across all 11 data sets; (II) agreement in average dissimilarity, both within and across data sets; (III) agreement in average variation in dissimilarities (“variation in variation”), both within and across data sets. To evaluate the effect of data transformation, each analysis of live-dead agreement is performed with four coefficients (Manhattan, Bray-Curtis based on untransformed abundances, Bray-Curtis based on square-root-transformed abundances, and Bray-Curtis based on presence-absence data; not shown in figure).

mation into “numbers equivalents” (Hill 1973; Jost 2006, 2007). Because time-averaging also commonly increases *sample size* in DAs relative to LAs, and because dissimilarity coefficients are biased by sample size (Wolda 1981; Lande 1996; Chao et al. 2005), all of our analyses of live-dead agreement in variation in species composition take into account sample-size differences.

Methods

Data.—We quantify the live-dead agreement of variation in species composition in

nine sets of living and death assemblages that were sampled, by their original author, at different places within one biogeographic region (spatial changes in composition), and in two sets of living and death assemblages that were sampled consecutively at different times at one place (Laguna Madre) and at three sites (Corpus Christi shelf). Most regions are characterized by siliciclastic soft-bottom environments with good exchange with oceanic waters. Ten data sets are located in temperate latitudes ranging from 27° to 55°. One region is a tropical carbonate back-reef lagoon (Virgin

Islands). Six regions correspond to an open continental shelf, four regions are represented by coastal embayments and back-barrier lagoons, and one region (San Juan Channel) is a high-energy fully marine strait (Table 1). These depositional conditions are generally representative of conditions that lead to preservation of molluscan assemblages in the fossil record.

To be included, data sets had to reflect sampling from at least five samples (or sampling times) within a study area, and each sample had to include at least ten living and ten dead individuals (Table 1). All samples were quantitative (from a standardized sedimentary volume for that region) and provided counts of living and dead individuals, but sampling gear, sample volume, and mesh size varied among studies (see SOMs of Kidwell 2001 and 2007). “Living assemblage” (LA) refers to specimens collected alive; some original authors included empty shells with adhering flesh and even still-articulated empty shells in this category, which we cannot standardize post hoc. “Death assemblage” (DA) refers to specimens collected dead; with few exceptions, authors included fragments in their counts of dead individuals if unique (e.g., bivalve fragments that included the hinge, gastropods that included the apex). Finally, all data sets are from areas considered to be relatively undisturbed by human activities, in order to minimize live-dead *disagreement* that might arise from rapid recent changes in species composition rather than from natural taphonomic processes (Kidwell 2007, 2008).

Analyses of Dissimilarities.—The live-dead agreement of *pairwise dissimilarity* is evaluated using two inter-related tests: (1) a Mantel test based on the rank correlation of between-sample dissimilarities between LAs and DAs (Fig. 1A, level I). The significance of the rank correlation is evaluated by permuting rows and columns of one of the dissimilarity matrices (Legendre and Legendre 1998); and (2) the Spearman rank correlation of dissimilarities between individual assemblages and their group centroid in the multivariate space (Fig. 1B, level I; Anderson 2006; Anderson et al. 2006). Although they give similar results, we present results of both methods in detail be-

TABLE 1. Nine data sets capturing spatial variation in species composition and two data sets (TS) capturing temporal variation in species composition.

Data set	n (samples)	N (between-sample similarities)	N live species (total)	N dead species (total)	Mean sample size of		Depth range (m)	No. of facies	Spatial range (km)	Time-series (months)	Minimum spatial or temporal separation among censuses		Reference
					LA	DA							
California shelf 1975	16	120	26	50	33	154	76	4	228	0	2 km	Our unpublished data	
California shelf 2003	18	153	27	78	23	358	79	3	181	0	0.4 km	Our unpublished data	
Chihama shelf	5	10	34	75	33	99	39	1	3.7	0	0.6 km	Tsuchi (1959)	
Corpus Christi shelf	13	78	34	128	187	1698	15	3	39	0	2.7 km	White et al. (1983)	
Patagonia-Beagle Channel	5	10	58	65	495	278	117	2	247	0	2.8 km	Linse (1997, 1999)	
San Juan Channel	10	45	74	71	230	589	95	2	24	0	1.7 km	Kowalewski et al. (2003)	
Mannin Bay	54	1431	50	82	92	1849	8	5	3	0	62 m	Bosence (1979)	
Mugu Lagoon	47	1081	39	70	76	785	1	4	2	0	7 m	Warme (1971)	
Virgin Islands	18	153	20	71	26	602	2	2	0.3	0	15 m	Miller (1988)	
Corpus Christi shelf—TS	21	210	88	178	251	6596	7	1	4	14	6 weeks	Staff and Powell (1990, 1999)	
Laguna Madre—TS	14	91	31	61	32	1136	0	1	0	16	6 weeks	Staff et al. (1986)	

cause between-sample dissimilarities constitute a standard measure of spatial and temporal variation in species composition (Russell et al. 1995; Russell 1998; Harrison et al. 2006); this metric is familiar and also forms the underlying matrices for multivariate ordinations. However, using multivariate-based dissimilarities between samples and their centroid is the preferred way to test between-group (here, live-dead) differences in multivariate dispersions because between-sample dissimilarities are not independent observations (Anderson et al. 2006). We evaluate the null hypothesis that the median rank correlation between pairwise dissimilarities in LAs and DAs, averaged across 11 data sets, is greater than zero with the one-sided signed-rank Wilcoxon test.

Dissimilarity coefficients capture different components of spatial and temporal species turnover, ranging from changes in species composition related to colonization and extinction to alterations in proportional or rank-order abundance within a stable species list (Koleff et al. 2003; Anderson et al. 2006). To assess the effects of different dissimilarity coefficients and degrees of data transformation (e.g., Legendre and Gallagher 2001), we evaluate four dissimilarity indices: (1) the Manhattan distance (d_{Man} , excluding joint-absences), which stresses changes in relative abundances (Anderson et al. 2006):

$$d_{Man} = \frac{\sum_{k=1}^S w_k x_{1k} - x_{2k}}{\sum_{k=1}^S w_k},$$

where S is the number of species, x_{1k} is the abundance of species k in sampling unit 1, x_{2k} the abundance of species k in sample 2, p the number of species recorded in both samples, and w_k the weight used to provide the exclusion of joint absences by setting $w_k = 0$, when $x_{1k} = x_{2k} = 0$ and $w_k = 1$ elsewhere; (2) Bray-Curtis (BC) dissimilarity (d_{BC}) based on untransformed proportional abundance data; (3) BC dissimilarity based on square-root-transformed proportional abundances that down-weight the effects of abundant species; and (4) BC dissimilarity based on presence-absence

data, which captures only compositional changes (equivalent to Sorenson dissimilarity):

$$d_{BC} = \frac{\sum_{k=1}^S |x_{1k} - x_{2k}|}{\sum_{k=1}^S (x_{1k} + x_{2k})}.$$

Bray-Curtis dissimilarity based on untransformed abundances is standardized by the sum of species abundances in the two samples—the contribution of changes in proportional abundances is thus less distinct than it is for Manhattan distance, which is standardized by the number of species (Anderson 2006). The live-dead agreement of *average* variation in species composition is evaluated by computing (1) the median dissimilarity averaged across all between-sample comparisons, and (2) the mean dissimilarity between samples and their group centroid (Fig. 1, level II). The live-dead agreement in the variation in dissimilarities is assessed by computing (1) the interquartile range (IQR) of pairwise dissimilarities, and (2) the standard deviation of sample dissimilarities to group centroid (Fig. 1, level III).

To test the differences in average dissimilarity in LAs and DAs, we use a test for homogeneity of multivariate dispersions, where dispersions are represented by distances of samples to their group centroid in multivariate space (Anderson et al. 2006; Pélissier and Couteron 2007). We implement principal coordinate (PCO) analysis of a dissimilarity matrix (using the four dissimilarity measures described above) that places the multivariate observations (assemblages) into a Euclidean space defined by PCO axes that completely preserves the original between-sample dissimilarities (Anderson 2006). The PCO axes are split into two sets, corresponding to positive and negative eigenvalues, and the squared Euclidean distances are computed separately for the two sets because some eigenvalues are negative when Manhattan distances and BC dissimilarities are used. To compute distances between any two points in the PCO space, the two sets are recombined so that squared distances calculated from imag-

inary (negative) axes are subtracted from squared distances calculated from real (positive) axes (Anderson 2006). The test for homogeneity of multivariate dispersions is equivalent to the univariate Levene's test for homogeneity of variance. It corresponds to an ANOVA performed on distances from group centroids. A p -value is evaluated by permuting least-square residuals obtained from regression of distances to centroid on two dummy variables, and by computing the number of permuted F -values that do not exceed the observed F -value. We use 1000 permutations. The signed-rank Wilcoxon test evaluates the null hypothesis that the median difference in average dissimilarity between LAs and DAs, averaged across 11 data sets, differs from zero.

Analyses of Beta Diversity and Diversity Partitioning.—To quantify the live-dead agreement of beta diversity, we partition the total diversity of each data set (gamma; sum of all samples in study) into its alpha (within-sample) and beta (between-sample) components with Shannon entropies (e.g., Lande 1996; Loreau 2000; Veech et al. 2002; Olszewski 2004; Pélissier and Coutron 2007). We transform these components into “numbers equivalents” that correspond to the number of equally common elements (species or communities) necessary to produce the given value of the diversity index (MacArthur 1965; Hill 1973; Jost 2006). Some measures of alpha and beta diversity are not independent of each other, and in cases when alpha diversity varies, beta diversity is also forced to vary (Wilson and Shmida 1984; Jost 2006). Therefore, we decompose total diversity with the Shannon entropy (H) that can be partitioned into *independent* alpha and beta components when sample sizes are unequal (Jost 2007). We note that additive partitioning of the Gini-Simpson index and of species richness produces dependency between alpha and beta components. Although there are partitioning formulas based on the Gini-Simpson index (D) and species richness (S) that lead to independent alpha and beta components, they are not suitable for data sets with unequal sample sizes because alpha diversity can exceed gamma diversity in such cases (Jost 2007). The Shannon entropy (H) evaluates the uncertainty in predicting the

species identity of the next collected individual,

$$H = -\sum_{k=1}^S p_i \ln p_i,$$

where p_i represents the proportional abundance of species i in a sample. The alpha diversity index (H_{within}) for a data set is calculated by summing sample-level Shannon values that have been weighted for sample size (Crist et al. 2003). The gamma diversity index (H_{total}) for a data set is based on species abundances that have been summed across samples. The beta diversity index (H_{among}) is expressed by additive decomposition (Lande 1996):

$$H_{\text{among}} = H_{\text{total}} - H_{\text{within}}.$$

The exponential of Shannon entropy defines the “numbers equivalent”—the effective number of equally common species (alpha and gamma diversity) and the effective number of distinct communities (beta diversity). Dead/live ratio in the numbers equivalents of the beta component of the Shannon entropy enables us to test the first hypothesis, which predicts that beta diversity is lower in DAs than in LAs. Differences in dead/live ratio in the numbers equivalents between the alpha and gamma components of the Shannon entropy enables us to test the second hypothesis, which predicts that dead/live ratio in diversity should be higher at alpha than at gamma spatial scales.

Finally, for our 11 tests that compare LAs and DAs within data sets, we count the number of tests that were significant at uncorrected $\alpha = 0.05$ and perform a binomial test to evaluate the probability that the observed number of significant tests were obtained by chance. In tables that summarize multiple independent tests, we report in boldface p -values that are significant after sequential Bonferroni correction at $\alpha = 0.05$ for 11 tests, and in italics p -values smaller than $\alpha = 0.05$ that are insignificant after such correction. All statistical analyses were performed using the R language (R Development Core Team 2007).

Sample-Size Standardization

Community dissimilarity coefficients can be biased upward by small sample sizes be-

cause small assemblages drawn randomly from the same community will tend to be more dissimilar than large samples (Wolda 1981; Lande 1996; Chao et al. 2005). Because LAs typically have smaller sample sizes than counterpart DAs, this sample-size bias can lead to greater dissimilarity in LAs than in DAs, even in the absence of scaling to lower temporal resolution. Comparisons of diversity among LAs and DAs are in fact comparable to analyses of diversity in species-time relationships (Rosenzweig 1998). In such analyses, the null sampling model evaluates whether the change in diversity can be the consequence of random subsampling from a community (Adler and Lauenroth 2003; Adler et al. 2005), or whether the change in diversity is related to temporal heterogeneity in species abundances.

To evaluate the random sampling model, we evaluate live-dead agreement in average dissimilarity and beta diversity by equalizing sample sizes between individual pairs of living and death assemblages, but the sample sizes among LAs or among DAs can still differ (e.g., additive decomposition of the Shannon entropy allows differences in sample weights). Therefore, we resample (without replacement) DAs whose sample size exceeds that of the corresponding LAs down to the sample size of the LA within the *same* site. Resampling is repeated 100 times, generating 100 sample-size-standardized matrices with LAs and DAs. Median between-sample dissimilarity and mean dissimilarity between sample and group centroid is then computed 100 times; the means of these results represent the expected average dissimilarity without sample-size effects. Similarly, the expected beta diversity index based on the Shannon entropy is based on the mean of 100 standardized values. The test for homogeneity of multivariate dispersions is performed for one size-standardized matrix averaged over 100 size-standardized matrices. Average species abundances were rounded to integers, thus producing sample sizes comparable to standardized sample size values, and effectively eliminating rare species that on average contribute less than 0.5% to sample-size-standardized matrices.

It is important to note that size-standardi-

zation reduces the estimated effects of time-averaging on beta diversity because any decrease in temporal resolution of DAs is generally associated with an increase in sample size, assuming some positive rate of shell preservation. Therefore, any dissection of sample-size effects and scaling effects is limited by their collinearity. All LAs and DAs analyzed in this study were sampled, within a given data set, at comparable spatial scales—in fact, LAs and DAs come from the same set of bottom samples. Thus the smaller sample size in LAs thus does not correspond to lower sampling intensity. We thus report results of analyses based on both raw (unstandardized) data and sample size-standardized data.

Results

Live-Dead Agreement of Pairwise Dissimilarity.—Eight of 11 data sets show significantly positive Mantel-test rank correlations of between-sample dissimilarities between LAs and DAs ($p < 0.001$ binomial test), based on all four coefficients (Table 2); three data sets show significant correlations at $\alpha = 0.05$ only under certain data transformations. Square-root and presence-absence transformations tend to strengthen correlations (nine of 11 data sets show significant correlations at $\alpha = 0.05$, following a Bonferroni correction; Table 2).

Spearman rank correlations of dissimilarities between samples and group centroid between LAs and DAs show similar patterns. Rank correlations between Manhattan distances are significantly positive at $\alpha = 0.05$ in four data sets ($p = 0.0016$ binomial test), and correlations strengthen for BC dissimilarities based on square-root-transformed data (seven data sets with significantly positive correlations at $\alpha = 0.05$, $p < 0.001$ binomial test) and presence-absence data (eight data sets with significantly positive correlations at $\alpha = 0.05$; Table 2). Bivariate plots show that live-dead comparisons of BC dissimilarities between samples and group centroid fall either along the line of unity (i.e., dissimilarities between DAs and group centroid in a data set are equal to dissimilarities between LAs and group centroid) or, commonly, below this line (dissimilarities between DAs and group centroid are consistently smaller than dissimilarities be-

TABLE 2. Mantel-test Spearman rank correlations of between-sample dissimilarities between living and death assemblages, and the Spearman rank correlations of dissimilarities between assemblages and their group centroid. The p -values in bold represent the significant results after the sequential Bonferroni correction for 11 tests per type of data transformation, separately for living and death assemblages. The p -values in italics represent the results insignificant after the Bonferroni correction.

	Manhattan		BC untransf		BC square-root		BC pres-abs	
	(r_s)	p -value	(r_s)	p -value	(r_s)	p -value	(r_s)	p -value
Between-sample dissimilarities								
California shelf 1975	0.42	<0.001	0.42	<0.001	0.52	<0.001	0.47	<0.001
California shelf 2003	0.30	<0.001	0.44	0.002	0.59	<0.001	0.55	<0.001
Chihama shelf	0.54	<i>0.021</i>	0.73	<i>0.022</i>	0.77	0.004	0.68	0.006
Corpus Christi shelf	0.42	0.001	0.40	<0.001	0.58	<0.001	0.62	<0.001
Patagonia-Beagle Channel	0.67	<i>0.029</i>	0.27	0.25	0.70	0.063	0.83	<i>0.045</i>
San Juan Channel	0.25	0.065	0.22	0.19	0.49	0.004	0.37	0.079
Mannin Bay	0.23	<0.001	0.19	0.001	0.26	<0.001	0.22	<0.001
Mugu Lagoon	0.54	<0.001	0.68	<0.001	0.71	<0.001	0.49	<0.001
Virgin Islands	0.17	<i>0.046</i>	0.34	0.002	0.48	0.001	0.19	0.069
Corpus Christi shelf—TS	0.37	<0.001	0.79	<0.001	0.79	<0.001	0.77	<0.001
Laguna Madre—TS	-0.31	0.99	-0.15	0.85	0.11	0.26	0.42	0.005
Dissimilarities between samples and centroid								
California shelf 1975	0.3	0.23	0.51	<i>0.033</i>	0.67	0.0028	0.76	0.0004
California shelf 2003	0.33	0.21	0.29	0.28	0.48	0.06	0.61	<i>0.013</i>
Chihama shelf	0.9	0.083	0.9	0.083	0.1	0.95	-0.1	0.95
Corpus Christi shelf	0.36	0.22	0.5	0.083	0.58	<i>0.041</i>	0.72	<i>0.0072</i>
Patagonia-Beagle Channel	0.1	0.5	-0.6	0.35	0.5	0.45	1	<i>0.017</i>
San Juan Channel	0.68	<i>0.033</i>	0.61	0.0633	0.82	<i>0.0062</i>	0.5	0.14
Mannin Bay	0.1	0.46	0.22	0.11	0.28	<i>0.04</i>	0.28	<i>0.043</i>
Mugu Lagoon	0.44	0.0024	0.597	<0.0001	0.584	<0.0001	0.52	0.0002
Virgin Islands	0.49	<i>0.04</i>	0.34	0.16	0.52	<i>0.028</i>	0.197	0.43
Corpus Christi shelf—TS	-0.12	0.62	0.58	<i>0.0072</i>	0.52	<i>0.018</i>	0.65	0.0018
Laguna Madre—TS	-0.57	0.04	-0.62	<i>0.023</i>	0.02	0.95	0.65	<i>0.013</i>

tween LAs and group centroid; Fig. 2). Dissimilarity in species composition is thus generally unchanged or lower in DAs than in LAs.

The average rank correlations between LAs and DAs are generally positive for the 11 data sets, based both on between-sample dissimilarities (medians = 0.37–0.58, depending on data transformation; Fig. 3A) and on dissimilarities between samples and group centroids (medians = 0.33–0.61, Fig. 3B). All four coefficients show median correlations significantly greater than zero at $\alpha = 0.05$ in Wilcoxon signed-rank tests based on between-sample dissimilarities, and three of them do so in tests based on dissimilarities between samples and group centroids (BC dissimilarity based on untransformed data is the exception; see Supplementary Table at <http://dx.doi.org/10.1666/08024.s1>). Average correlations are higher for square-root and presence-absence transformed abundances than for untransformed data. However, 95% confidence intervals still overlap slightly among mean values, based on Pearson correlation coefficients that

have been weighted by within-sample and between-sample variance (meta-analytic averages using the random-effects model of Hedges and Vevea 1998) (Fig. 3C). Live-dead agreement in pairwise dissimilarity, when measured by rank correlation of BC dissimilarities between samples and group centroid of LAs and DAs, tends to increase with the average dissimilarity of the DAs (Fig. 3D).

Live-Dead Agreement of Average Dissimilarity.— By all four measures of species composition, DAs exhibit smaller between-sample variation than LAs, based on the average between-sample dissimilarity and the average dissimilarity between samples and their group centroids (Fig. 4; one exception is Patagonia-Beagle Channel). In unstandardized analyses, DAs in seven of 11 data sets show significantly lower average dissimilarity than LAs at $\alpha = 0.05$ regardless of data transformation ($p < 0.001$ binomial test; Table 3). In sample-size-standardized analyses, depending on data transformation, DAs in four to seven of 11 data sets show significantly lower average dissimilarity

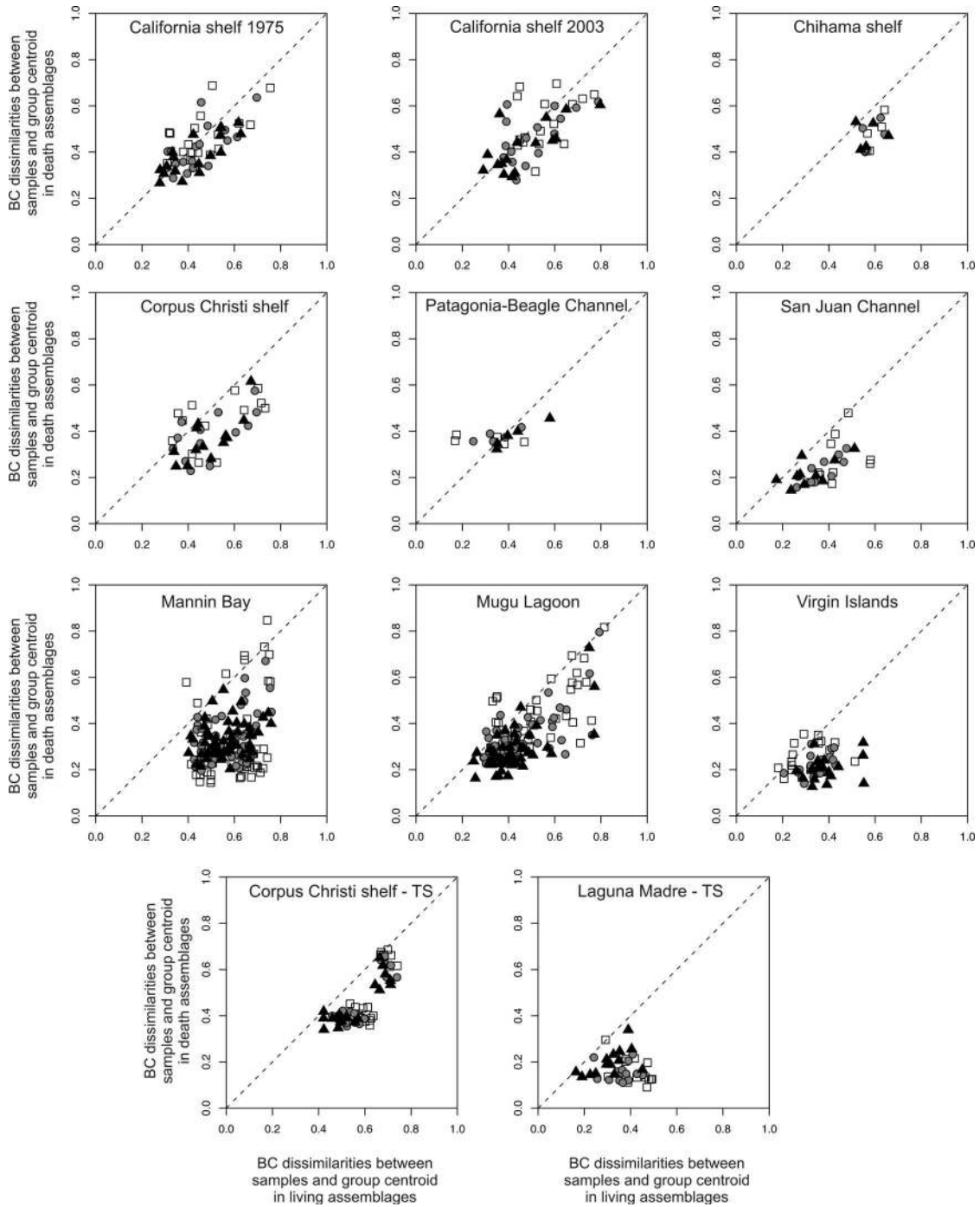


FIGURE 2. Variation in species composition between death assemblages (y-axis) and between counterpart living assemblages (x-axis), expressed as the Bray-Curtis dissimilarity between samples and their group centroid, for three levels of data transformation: untransformed abundance (white squares), square-root transformed abundance (gray circles), and presence-absence (black triangles). Between-sample variation in death assemblages is usually equal to (dashed line) or less than that observed in the living assemblage for that same pair of samples.

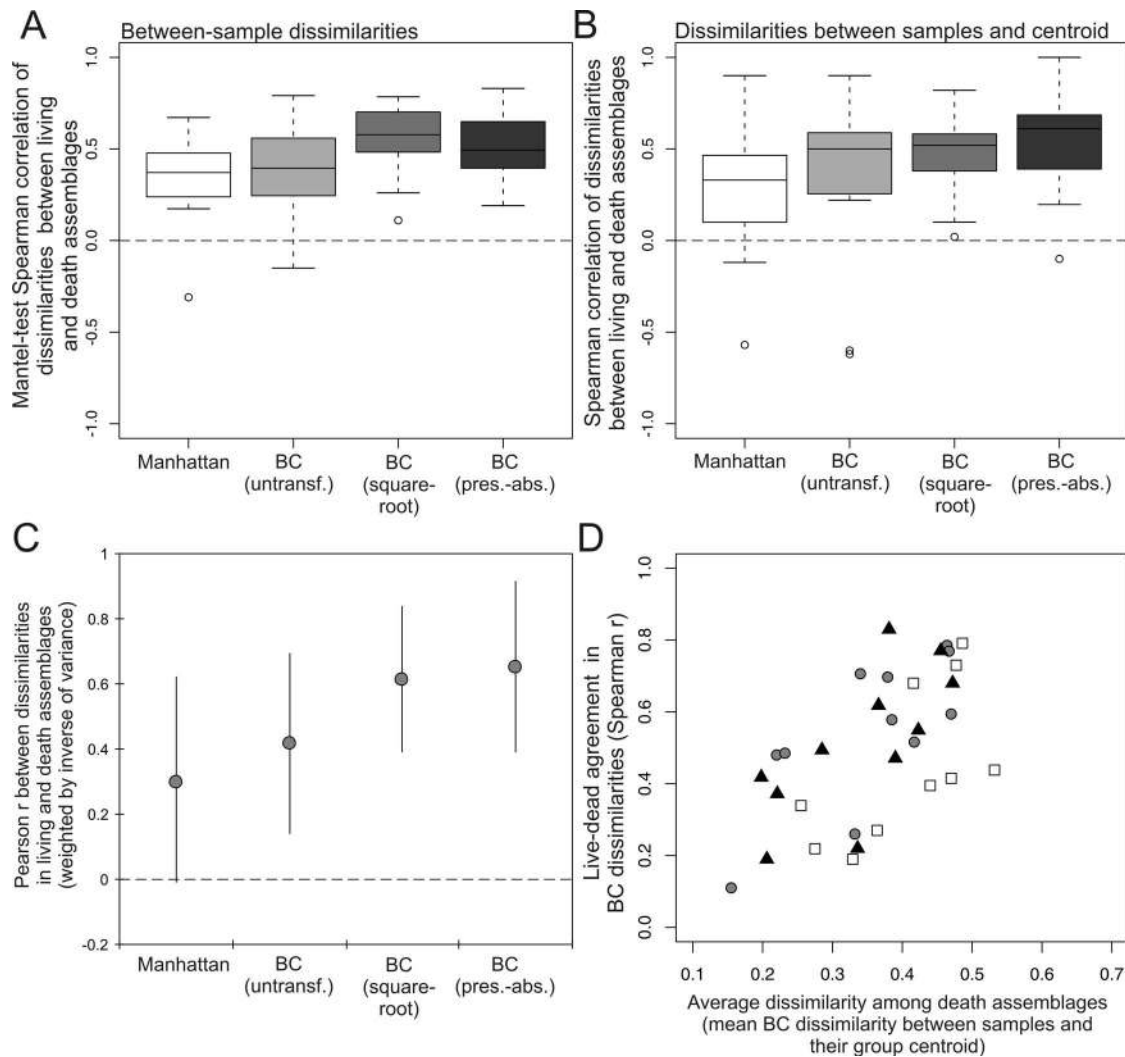


FIGURE 3. Live-dead agreement of pairwise variation in species composition is characterized by positive rank correlations when averaged across all 11 data sets, when measured both by between-sample dissimilarities (A) and by dissimilarities between assemblages and their group centroid (B). Boxplots show medians and the 25 and 75 quartiles of rank correlations, whiskers denote values 1.5 times the interquartile range, and white circles mark extreme values. C, Meta-analytical average represented by Pearson correlation coefficient with 95% confidence intervals weighted by within-sample and between-sample variance, based on random-effects model of Hedges and Vevea (1998). D, Live-dead agreement in between-sample variation in species composition (as indicated by Spearman rank correlation of BC dissimilarities between samples and their group centroid between living and death assemblages) increases significantly (Spearman r [untransf.] = 0.84, p = 0.002, Spearman r [square-root] = 0.75, p = 0.011, Spearman r [square-root] = 0.73, p = 0.014) with the degree of variability observed among death assemblages (mean BC dissimilarity between samples and their group centroid; x-axis).

than LAs, based on tests for homogeneity of multivariate dispersions (p = 0.0016 binomial test; Table 3).

The median reduction in the average dissimilarity among DAs in size-standardized analyses, relative to LAs, is 0.04–0.12 (12–29% of average dissimilarity among LAs) based on between-sample dissimilarities, and 0.03–0.06

(12–24% of average dissimilarity among LAs) based on dissimilarities between samples and group centroid (Fig. 5A,B). The average live-dead agreement in the average dissimilarity across the 11 data sets is unaffected by data transformation (Figs. 4, 5). With the exception of size-standardized analyses based on untransformed abundances, the median dead-

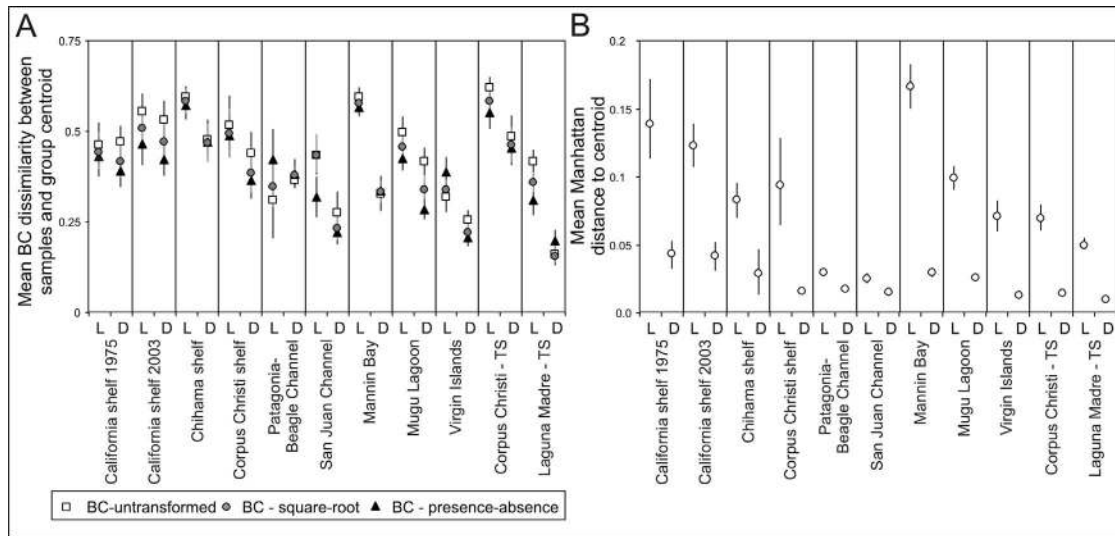


FIGURE 4. Average dissimilarity in living (L) and death assemblages (D) for each study area, measured by mean BC dissimilarity between samples and group centroid (A) and mean Manhattan distance to group centroid (B). In most data sets and by most measures of composition, death assemblages exhibit less variation among samples (i.e., compositional dissimilarities are smaller) than do living assemblages. Error bars are 95% bootstrapped confidence intervals.

live difference in the average between-sample dissimilarity and in the average dissimilarity between samples and their group centroid is significantly smaller than zero at $\alpha = 0.05$ (Wilcoxon signed-rank test; Fig. 5A,B, Supplementary Table).

Live-Dead Agreement of Variation in Dissimilarities.—The interquartile range (IQR) of BC between-sample dissimilarities is lower or equal in the DAs of nine data sets, and higher in the DAs in two data sets. Similarly, the standard deviation of BC dissimilarities between samples and their group centroid is lower in the DAs of eight data sets, and higher in two data sets (Corpus Christi shelf, and Corpus Christi shelf - TS), or varies depending on data transformation (Mannin Bay; Fig. 6A). That is, DAs generally show smaller variation in dissimilarities than do LAs. Variation in Manhattan distances is also lower in DAs than in LAs (Fig. 6B). However, averaged across the 11 data sets, the median dead-live difference in the standard deviation of BC dissimilarities of samples to their group centroid does not differ significantly from zero at $\alpha = 0.05$ (Wilcoxon signed-rank tests) in both sample size-standardized and unstandardized analyses (Fig. 7; exceptionally, the median dead-live

difference is significantly smaller than zero with presence-absence transformation). The median dead-live difference in IQR of BC between-sample dissimilarities also does not differ significantly from zero in any treatment (Supplementary Table).

Live-Dead Agreement of Beta Diversity and Diversity Partitioning.—Alpha Shannon entropy contributes more to the total Shannon entropy in DAs (median = 75%) than in LAs (median = 58%) and Shannon beta entropy correspondingly contributes more in LAs than in DAs (Table 4, Fig. 8A). The differences in median proportions of alpha and beta components between LAs and DAs are significant in both unstandardized and size-standardized analyses (Wilcoxon signed-rank test, $p = 0.0019$). Beta diversity represented by the exponential of the beta component of Shannon entropy (i.e., effective number of distinct communities sharing no species) is smaller in DAs than in LAs in both unstandardized (median dead/live ratio = 0.61, Wilcoxon signed-rank test, $p = 0.002$) and size-standardized analyses (median dead/live ratio = 0.82, Wilcoxon signed-rank test, $p = 0.003$; Table 4, Fig. 8B). Beta diversity is thus underestimated in DAs by about ~20–40%.

TABLE 3. The test of homogeneity of multivariate dispersions between living and death assemblages in unstandardized and sample size-standardized analyses. The p -values in bold represent the significant results after the sequential Bonferroni correction for 11 tests per type of data transformation, separately for living and death assemblages. The p -values in italics represent the results insignificant after the Bonferroni correction.

	Manhattan (F -value)	Permutated p -value	BC untransf (F -value)	Permutated p -value	BC square-root (F -value)	Permutated p -value	BC pres-abs (F -value)	Permutated p -value
Unstandardized analyses								
California shelf 1975	5.53	0.02	0.049	0.82	0.58	0.43	1.49	0.21
California shelf 2003	18.95	0.001	0.33	0.54	0.86	0.35	0.962	0.35
Chihama shelf	5.7	0.03	10.09	0.01	11.43	0.008	8.29	<i>0.035</i>
Corpus Christi shelf	17.23	0.001	2.34	0.14	5.94	<i>0.026</i>	9.46	0.005
Patagonia-Beagle Channel	0.05	0.78	0.84	0.37	0.667	0.47	0.75	0.43
San Juan Channel	11.58	0.006	14.3	0.005	37.05	0.001	7.17	0.023
Mannin Bay	162.5	0.001	89.86	0.001	160.6	0.001	217.6	0.001
Mugu Lagoon	74.37	0.001	8.04	0.007	21.33	0.001	38.21	0.001
Virgin Islands	75.25	0.001	6.11	<i>0.022</i>	41.27	0.001	57.37	0.001
Corpus Christi shelf—TS	36.76	0.001	19.34	0.001	14.7	0.001	12.52	0.001
Laguna Madre—TS	77.67	0.001	122.72	0.001	116.64	0.001	17.86	0.001
Size-standardized analyses								
California shelf 1975	0.31	0.56	0.22	0.66	0.025	0.87	0.17	0.66
California shelf 2003	1.09	0.31	0.05	0.82	0.001	0.97	0.001	0.99
Chihama shelf	0.37	0.55	4.37	0.064	4.75	0.04	3.94	0.09
Corpus Christi shelf	0.5	0.52	1.64	0.22	2.66	0.11	1.84	0.17
Patagonia-Beagle Channel	1.47	0.26	0.8	0.35	0.68	0.45	3.39	0.13
San Juan Channel	1.45	0.24	12.91	0.003	13.19	0.006	3.06	0.093
Mannin Bay	50.49	0.001	82.02	0.001	110.2	0.001	89.41	0.001
Mugu Lagoon	28.79	0.001	6.48	<i>0.014</i>	12.64	0.001	18.15	0.001
Virgin Islands	23.19	0.001	3.59	0.07	27.06	0.001	44.3	0.001
Corpus Christi shelf—TS	12.7	0.001	16.94	0.001	9.07	0.006	3.23	0.09
Laguna Madre—TS	2.8	0.12	114.7	0.001	87.5	0.001	16.81	0.002

A. Unstandardized analyses

B. Size-standardized analyses

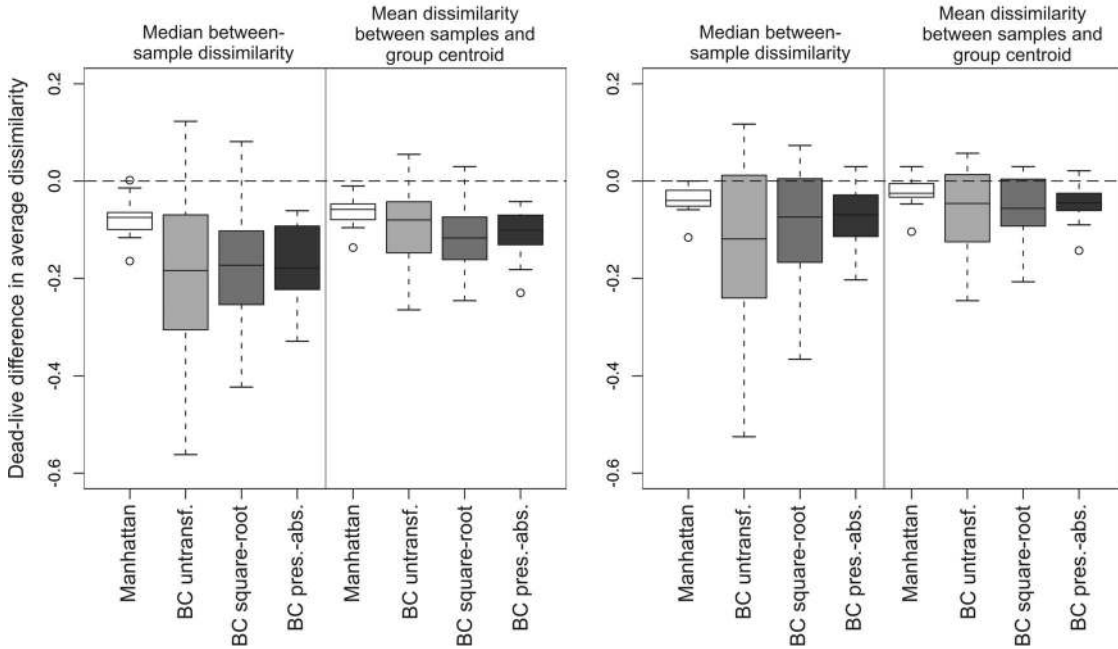


FIGURE 5. Dead-live differences in the average dissimilarity between living and death assemblages, averaged across 11 data sets, using the median of between-sample dissimilarities (left set of boxplots) and the mean of dissimilarities between samples and group centroid (right set of boxplots). Death assemblages tend to show significantly less variation than counterpart living assemblages. Live-dead agreement is better in average size-standardized analyses (B) than in unstandardized analyses (A), but in both cases the magnitude of average live-dead difference is small. Boxplot conventions as in Figure 3.

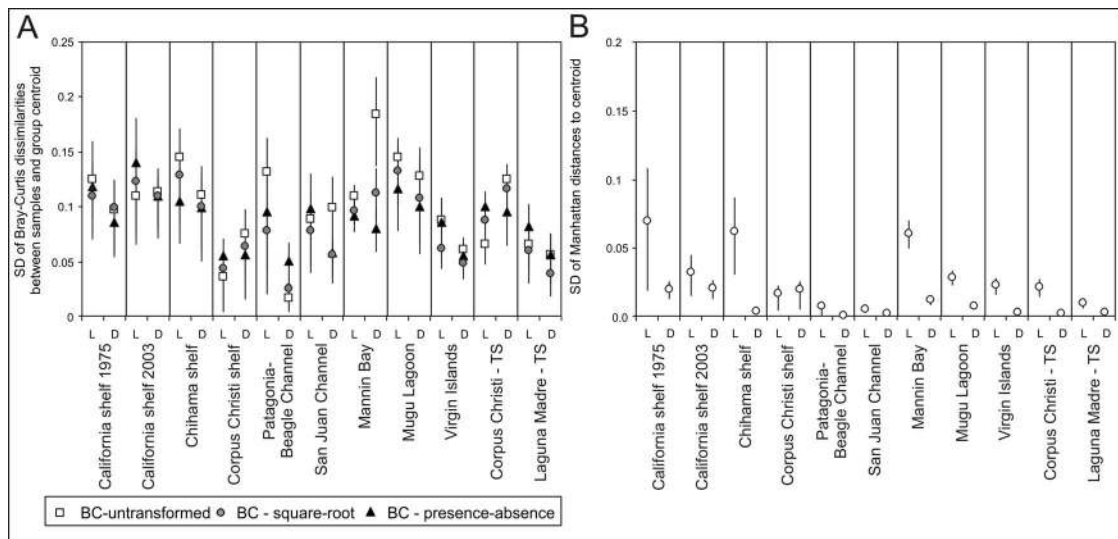


FIGURE 6. Average variation in dissimilarities between samples and their group centroid in living (L) and death (D) assemblages. A, Standard deviation of BC dissimilarities. B, Standard deviation of Manhattan distances to centroid. In most data sets and by most measures of composition, between-sample differences in death assemblages exhibit less variation (i.e., show a smaller range of values) than do living assemblages. Error bars are 95% bootstrapped confidence intervals.

A. Unstandardized analyses

B. Size-standardized analyses

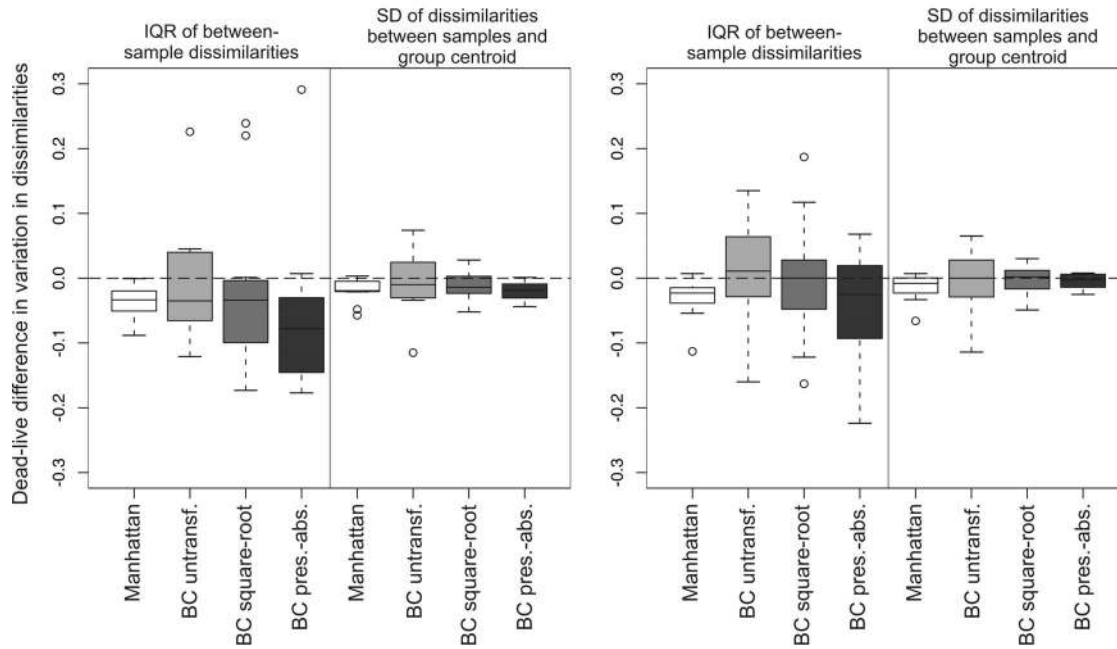


FIGURE 7. Dead-live differences in the variation in dissimilarities between samples and group centroid (standard deviation, SD) between death and living assemblages, and dead-live differences in the variation in dissimilarities (IQR) between death and living assemblages, averaged across 11 data sets. Live-dead agreement is better in sample size-standardized analyses (B) than in unstandardized analyses (A), but in both cases the magnitude of average live-dead difference is small and by most measures not significantly different from zero. Boxplot conventions as in Figure 3.

Alpha diversity represented by the exponential of the alpha component of Shannon entropy (i.e., effective number of equally common species) is on average higher in DAs than in LAs (Table 4). The median dead/live ratio is 2 in unstandardized and 1.7 in size-

standardized analyses (Wilcoxon signed-rank test, $p [H_0 = 1] = 0.003$; Fig. 8B). Gamma diversity is higher in DAs than in LAs in 8 of 11 data sets in size-standardized analyses (median dead/live ratio = 1.5 in unstandardized and 1.64 in size-standardized analyses; Wilcoxon

TABLE 4. Alpha, beta, and gamma diversity indices (Shannon entropy) in living and death assemblages, demonstrating generally lower beta diversity in death assemblages and difference in partitioning of alpha and beta components between living and death assemblages. The sample sizes of the LA and DA within the same site were resampled, without replacement, down to equal size.

Data set	Alpha diversity		Beta diversity		Gamma diversity	
	(LA)	(DA)	(LA)	(DA)	(LA)	(DA)
California shelf 1975	1.28	1.72	0.94	0.88	2.22	2.60
California shelf 2003	1.21	1.73	1.23	1.25	2.43	2.98
Chihama shelf	1.94	2.42	1.16	0.83	3.11	3.24
Corpus Christi shelf	0.76	1.91	0.57	0.43	1.33	2.34
Patagonia-Beagle Channel	1.79	2.38	0.32	0.51	2.11	2.88
San Juan Channel	2.08	2.35	0.84	0.31	2.92	2.65
Mannin Bay	0.77	1.17	1.39	0.65	2.16	1.82
Mugu Lagoon	1.19	1.84	0.99	0.85	2.19	2.68
Virgin Islands	1.33	2.24	0.47	0.61	1.79	2.85
Corpus Christi shelf—TS	0.95	2.26	1.49	0.88	2.44	3.14
Laguna Madre—TS	2.10	1.71	0.71	0.30	2.81	2.01

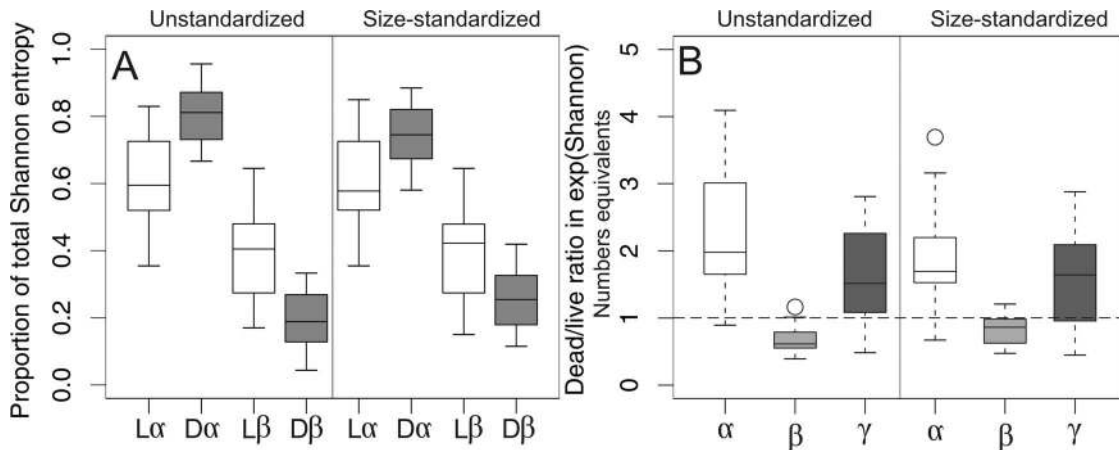


FIGURE 8. A, Proportions of alpha (within sample) and beta (among samples) diversity components contributing to gamma Shannon entropy differ between living (white boxes) and death assemblages (gray boxes), averaged across 11 data sets. B, Dead/live ratio in alpha, beta, and gamma diversity expressed by exp (Shannon) in unstandardized and size-standardized analyses. Death assemblages typically are more diverse at alpha and gamma levels even after sample-size standardization of living and death assemblages, whereas diversity is lower at the beta level (i.e., shows less variation among samples than does the living assemblage). Note that the excess of diversity at gamma level is reduced relative to alpha level. Boxplot conventions as in Figure 3.

signed-rank test, $p [H_0 = 1] = 0.004$; Fig. 8B). Alpha and gamma diversity of DAs thus generally exceeds that of LAs in these 11 data sets: such “excess” diversity is widely observed in molluscan DAs (e.g., Kidwell 2002; Olszewski and Kidwell 2007). The exceptions are the San Juan Channel and Laguna Madre where, after size-standardization, gamma diversity of the LA exceeds that of the DA (Table 4). However, the excess diversity in terms of dead/live ratio of numbers equivalents at alpha scales is still generally larger than at gamma scales (Wilcoxon signed-rank test, $p = 0.008$ for unstandardized analyses, and $p = 0.07$ for size-standardized analyses).

Discussion

Live-Dead Agreement of Pairwise Dissimilarity.—Good preservation of *pairwise dissimilarity* in 11 molluscan data sets demonstrates for the first time that pairwise between-sample variations in species composition are positively rank-correlated between living and death assemblages. Data transformation significantly affects whether pairwise dissimilarity is captured by DAs, with indices that downplay the abundance of dominant species (i.e., square-root and presence-absence transformations) finding the highest live-dead agreement of pairwise dissimilarity (Table 2, Figs.

3A–C, 4A,B). This is probably because analyses based on untransformed data are strongly affected by numerically dominant species, and those abundances tend to be more variable, owing to the mean-variance relationship: everything else being equal, higher mean abundances are generally associated with higher variance (Taylor 1961; McArdle et al. 1990; Gaston and McArdle 1994). Therefore, the lower rank correlations exhibited by Manhattan and BC coefficients based on untransformed abundances in our analyses might simply reflect the inherently higher variation of coefficients dominated by highly abundant species.

The preservation by DAs of between-sample dissimilarities and of dissimilarities between samples and group centroids is also affected by the dynamics of species turnover—that is, whether between-site variation in species composition arises predominantly from strong demographic and environmental stochasticity (leading to low live-dead correlations owing to variable dissimilarities) or from other mechanisms, e.g., species trade-offs in vital rates and/or species differences in niche preferences (trade-off and species-sorting models, leading to high live-dead correlations owing to stable dissimilarities, e.g., Chesson 2000; Chave et al. 2002). The highly

variable species compositions that arise under the neutral model with dispersal limitation (Hubbell 1997, 2001; Chave and Leigh 2002; Condit et al. 2002) should lead to low live-dead agreement of pairwise dissimilarities, relative to non-neutral models, just as communities with a higher temporal or spatial volatility of species abundances are expected to have lower live-dead agreement (Peterson 1976). We note that neutral metacommunity dynamics can lead to stable species composition under high migration rates (McGill et al. 2005; Dornelas et al. 2006). However, working with this same collection of molluscan data sets, we have found that the species composition of LAs is mainly affected by gradients in environmental conditions rather than spatial distance alone: local composition evidently arises from species sorting acting on the species niche positions, implying that dissimilarities between *living* assemblages can be relatively stable (Tomašových and Kidwell 2009).

Live-Dead Agreement of Average Dissimilarity.—Average between-sample variation in species composition, represented either by median between-sample dissimilarity or by mean dissimilarity between samples and their group centroid, is significantly lower in DAs than in LAs in both unstandardized and size-standardized analyses. This decrease in dissimilarity appears both in coefficients emphasizing abundance changes (Manhattan distance) and in those emphasizing compositional changes (BC dissimilarity on presence-absence data).

The lower average dissimilarity agrees with the hypothesis that variation decreases with time-averaging purely owing to loss of temporal resolution (e.g., Miller and Cummins 1990; Behrensmeyer and Chapman 1993; Aslan and Behrensmeyer 1996; Olszewski 1999; Martin et al. 2002). Ecological analyses also predict—and observe—that alpha diversity increases and beta diversity decreases with lower temporal resolution: (1) as theoretically expected and empirically observed, there is a positive slope between variance in species abundances and temporal resolution (Wiens 1989; Levin 1992), and (2) in species-area-time relationships, the spatial scaling exponent of the species-area relationship decreases with

decreasing temporal resolution (Adler et al. 2005).

Time-averaging can also decrease average dissimilarity by (1) increasing the size of the DA owing to the accumulation of multiple generations; dissimilarity coefficients are biased upward under small sample sizes (Lande 1996), and thus DAs will tend to be biased toward showing less dissimilarity than counterpart LAs; (2) mixing together several generations that were affected by repeated colonization, extinction and immigration events owing to demographic and environmental stochasticity, ecological succession and/or local environmental change (e.g., Preston 1960; Fürsich and Aberhan 1990; Bennington 2003); and (3) providing opportunities for mixing remains via “within-habitat” postmortem transport, which will tend to reduce average dissimilarity (Cummins et al. 1986; Miller and Cummins 1990; Tomašových 2006; Finnegan and Droser 2008). In contrast, average dissimilarity can be either increased or decreased by (4) differences in species preservation rates and (5) “out of habitat” postmortem transport. Thus, the observed decrease in average dissimilarity has several possible causes. We note that point 2 strictly applies only to the effects of time-averaging on *temporal* variation in species composition and species turnover. However, we assume that time-for-space substitution partly applies to DAs—i.e., that DAs sample species (1) from adjacent patches within one habitat owing to stochastic constrained or unconstrained random walk in community composition (Hubbell 2001; Chave et al. 2002), and (2) from different habitats owing to temporal habitat shifting over the period of time-averaging. Therefore, the reduced temporal resolution can effectively also reduce spatial variation in species composition among DAs.

In attempting to discriminate among these potential mechanisms, we find that, with sample size-standardization, the live-dead discrepancy is reduced in several data sets but mostly persists. This indicates that the lower average dissimilarity observed in DAs is not simply a product of their inherently larger sample sizes and is not explained by the random sampling model (point 1 above). Instead, the reduction in spatial (nine data sets) and

temporal variation in species composition (2 data sets) must owe to the temporal mixing of generations (point 2) and within-habitat mixing (point 3). This attribution is supported by significantly positive Spearman rank correlations between the reduction in the average dissimilarity in DAs and the ratio of dead/live individuals per data set, which should increase with time-averaging but not with differential preservation (r [BC untransformed] = -0.64 , r [BC square-root] = -0.58 , r [BC presence-absence] = -0.62). In other words, DAs with a disproportionately higher number of individuals relative to LAs are less variable in species composition than DAs with smaller excess of individuals.

Live-Dead Agreement of Variation in Dissimilarities.—The lack of consistent bias in live-dead agreement of variation in dissimilarities—that is, our observation that some DAs show greater variation rather than less variation in between-sample dissimilarity than counterpart LAs, with a net bias across the 11 data sets of close to zero—might be explained by the multiple, counteracting effects of time-averaging on DA composition. For example, an initial increment of time-averaging should damp the influence of short-term abundance fluctuations (e.g., Peterson 1976), but the DA can still reflect variations in abundance produced by environmental trends and in fact might be dominated by those trends. Time-averaging thus might actually increase variation in dissimilarities, rather than decrease it. When time-averaging is very long, for example multiple habitats and environments are being condensed, then we would expect variation in dissimilarities to consistently decrease. Our finding that the *net* bias across all data sets is close to zero indicates that, on average, variation in dissimilarities is well preserved for paleoecological analyses because the effects of time-averaging are not exclusively unidirectional. This issue is particularly relevant for analyses that evaluate variation in beta diversity by modeling dissimilarity matrices (Ferrier et al. 2007) and for analyses that assess the rate of similarity decay with distance or spatial autocorrelation (e.g., Nekola and White 1999; Sojininen et al. 2007; Tomášových and Kidwell 2009).

Live-Dead Agreement of Beta Diversity and Diversity Partitioning.—As in analyses of average dissimilarity, the lower beta diversity that we find for DAs relative to LAs in size-standardized analyses cannot be explained by the random sampling model. Total diversity is also partitioned differently between LAs and DAs, with beta diversity contributing significantly less to total diversity in DAs than in LAs. This reduction in beta diversity is consistent with the hypothesized effects of lower temporal resolution on spatial and temporal variation in species composition. We thus suggest that diversity is transferred from the beta to the alpha level during the formation of DAs.

Paleoecological analyses of beta (and alpha) diversity thus need to take into account or control for differences in time-averaging—that is, temporal resolution—among fossil assemblages: diversity is not scale-invariant (Leitner and Rosenzweig 1997; Harte et al. 1999; He and Legendre 2002; Carey et al. 2007). We stress that size-standardization alone does not reveal scaling effects caused by differences in temporal resolution, because the reduction of beta diversity and the increase in alpha diversity occur more rapidly than predicted by the random sampling model. Ignoring differences in temporal resolution among fossil assemblages—that is, building a dataset that indiscriminately mixes information from census assemblages, within-habitat time-averaged assemblages, and environmentally condensed assemblages—thus can produce trends in alpha and beta diversity at any scale. For example, as the original authors note, increases in alpha diversity over the Phanerozoic (e.g., Powell and Kowalewski 2002; Bush and Bambach 2004) might derive in part from a secular decrease in the temporal resolution of shelly DAs (e.g., owing to increasing bioturbation, increasing skeletal durability, and other factors [Thayer 1983; Kidwell and Brenchley 1994]; but see results of dating modern brachiopod DAs, which suggest that durability has perhaps not increased significantly [Carroll et al. 2003; Kidwell 2005]). Similarly, we might expect differences in beta diversity among depositional systems tracts and among different kinds of hiatal accumulations of fossils simply owing to different degrees of skel-

etal time-averaging rather than changes in ecological structure (Holland 1996; Kidwell 1991, 1997; Brett 1995; Holland and Patzkowsky 1999). Thus in testing for spatial and temporal trends in diversity, over any extent, consistency in the resolution of samples is essential: the effect of decreasing temporal resolution on diversity can be strong, and, as in the species-time relationships in ecology (Harte and Kinzig 1997; Lennon et al. 2001; Adler et al. 2005), is not simply a consequence of increasing sample size.

Controlling for shellbed type or for the degree of alteration is one means of attempting to control for variation in temporal resolution (e.g., Peters 2004; Finnegan and Droser 2005). However, current protocols for categorizing *fossil* assemblages in terms of time-averaging are quite coarse, as are our estimates of the absolute duration of time-averaging that they represent (e.g., “within-habitat time-averaged” molluscan assemblages are estimated to represent anywhere from years to a few thousand years [Kidwell and Bosence 1991], subsequently supported by dedicated direct-dating of modern assemblages [Flessa et al. 1993; Flessa and Kowalewski 1994; Martin et al. 1996; Barbour Wood et al. 2006]). The higher alpha diversity in DAs is consistent with the findings of Kidwell (2002) and Olszewski and Kidwell (2007) for the larger molluscan database that includes the data sets analyzed here, although they analyzed live-dead agreement at lower spatial resolution (at the scale of pooled multiple samples per habitat) and only within areas characterized by similar substrate type. The reduction in the excess diversity from alpha to gamma scales that we observe partly supports the hypothesis that time-averaging effects can be reduced with increasing spatial scale of sampling, because rates of temporal species turnover are expected to decrease with the sampled area (e.g., Adler et al. 2005). Therefore, time-averaging effects can be partly minimized if analyses of alpha diversity are performed at relatively large spatial scales, where the rate of species accumulation is small over the duration of “within-habitat” time-averaging. However, a substantial excess of diversity still generally persists at the gamma scale.

Sources of Variation among Data Sets and Other Caveats.—Inspection of individual results (Tables 2–4; Figs. 2, 4, 6) does not reveal any particular pattern in fidelity when data sets are sorted with respect to mesh size (ranges from 0.5 mm to 4 mm), environment (e.g., coastal embayment versus open shelf), seafloor type (e.g., sediment grain size, vegetation), species richness, or sample size. Among data sets based on temporal replicates, we find that the Corpus Christi shelf (of Staff and Powell 1990, 1999; three sites sampled 7 times over 14 months) does not differ markedly in live-dead agreement from data sets based on spatial replicates (all others listed in Table 1; all sites sampled during a single survey, which may have required only a few days or several months). In contrast the time-series from Laguna Madre (of Staff et al. 1985, 1986; single site sampled 14 times over 19 months) does show relatively low rank correlations between dissimilarity coefficients of LAs and DAs.

The data sets based on the smallest number of sampled sites and smallest number of facies types exhibit the poorest fidelity (Chihama and Patagonia-Beagle Channel shelves). However, the converse is not entirely true: low rank correlations also occur in some data sets with a relatively large number of samples and facies, such as Mannin Bay. The fact that BC dissimilarities between LAs and DAs correlate with the *average* dissimilarity (Fig. 3D) indicates that that some of the variation in the rank correlation can be explained by the average dissimilarity itself. This relationship can be expected because increasing the *range* of compositional variation may make it easier for the signal to be preserved than in cases where the range in variation is narrow. Therefore, low rank correlations (such as observed in Laguna Madre, Fig. 2) can be partly explained by low average variation in species composition.

The slightly tighter relationship found for DAs than for LAs suggests that, by virtue of time-averaging, DAs are less affected by short-term variations within a study area than are single snapshots of the living community. This suggests that the positive aspects of time-averaging—their ability to sum across stochastic and other variation in species composition—outweigh the negative aspects (the po-

tential for homogenization from postmortem transportation, the potential for live-dead mismatch from differential preservation potential of species, and the mixing of generations over periods of environmental change), at least in the data sets evaluated here.

Conclusions

Eleven regional data sets of mollusk communities show good preservation by death assemblages of compositional variation: pairwise between-sample differences in species composition are positively correlated between living and death assemblages. This positive relationship emerges using both conventional between-sample dissimilarities and multivariate dissimilarities between samples and their group centroid. Positive relationships also emerge using measures of composition that emphasize abundance changes as well as those that use only species presence/absence. However, data transformation has substantial effects: the square-root and presence-absence transformations that downweight the importance of dominant species or give equal weight to dominant and rare species capture variations in species composition and diversity consistently better than do analyses based on untransformed abundances, which are mainly affected by dominant species.

Death assemblages (DAs) consistently show lower average spatial and temporal variation in species composition, expressed by average dissimilarity and by beta diversity expressed by the Shannon entropy, than do counterpart living assemblages (LAs): the degree of variation observed in snapshot surveys of LAs is damped in DAs. The lower between-sample variation in species composition observed among DAs owes partly to the larger sample size of DAs, but in most data sets DAs continue to show lower variation in species composition even after size-standardization.

This finding of reduced spatial and temporal variation is expected from the loss of temporal resolution inherent to time-averaging because DAs can capture species from adjacent habitat patches owing to random walk in community composition and/or from different habitats owing to temporal habitat shifting. The magnitude of the damping effect, al-

though significant in many cases, is moderately high: between-sample Bray-Curtis dissimilarities values are depressed on average by 12–29% and Bray-Curtis dissimilarities between samples and centroid are depressed by 12–24%. Beta diversity expressed by the exponential of the Shannon entropy is significantly reduced in DAs relative to LAs by ~25% in size-standardized analyses. This magnitude of damping can be sufficient to diminish differences between beta diversity predicted by neutral versus niche-based meta-community dynamics (e.g., McGill et al. 2005; Dornelas et al. 2006).

Molluscan death assemblages are thus a conservative means of inferring change over time or variation among regions in species composition and diversity, at least in modern systems. Working at a similar sampling scale, and in records that include a diversity of shell sizes and types (suggesting no strong diagenetic filtering), these findings are also encouraging for the analysis of variation in much older fossil records. However, rates of temporal and spatial species turnover can be expected to be depressed in the fossil record relative to turnover rates based on unscaled models of community dynamics at higher temporal resolution.

Returning to the fundamental taphonomic issues raised in the introduction, this capture of between-sample variation in species composition implies a high degree of consistency in the *net* preservation potential of death assemblages across environments, despite the different taphonomic pathways suggested by taphofacies studies. This encouraging finding bears closer testing via dedicated actualistic experiments and modeling.

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