

## Preservation of spatial and environmental gradients by death assemblages

Adam Tomašových and Susan M. Kidwell

*Abstract.*—Although only a few studies have explicitly evaluated live-dead agreement of species and community responses to environmental and spatial gradients, paleoecological analyses implicitly assume that death assemblages capture these gradients accurately. We use nine data sets from modern, relatively undisturbed coastal study areas to evaluate how the response of living molluscan assemblages to environmental gradients (water depth and seafloor type; “environmental component” of a gradient) and geographic separation (“spatial component”) is captured by their death assemblages. We find that:

1. Living assemblages vary in composition either in response to environmental gradients alone (consistent with a species-sorting model) or in response to a combination of environmental and spatial gradients (mass-effect model). None of the living assemblages support the neutral model (or the patch-dynamic model), in which variation in species abundance is related to the spatial configuration of stations alone. These findings also support assumptions that mollusk species consistently differ in responses to environmental gradients, and suggest that in the absence of post-mortem bias, environmental gradients might be accurately captured by variation in species composition among death assemblages. Death assemblages do in fact respond uniquely to environmental gradients, and show a stronger response when abundances are square-root transformed to downplay the impact of numerically abundant species and increase the effect of rare species.

2. Species’ niche positions (position of maximum abundance) along bathymetric and sedimentary gradients in death assemblages show significantly positive rank correlations to species positions in living assemblages in seven of nine data sets (both square-root-transformed and presence-absence data).

3. The proportion of compositional variation explained by environmental gradients in death assemblages is similar to that of counterpart living assemblages. Death assemblages thus show the same ability to capture environmental gradients as do living assemblages. In some instances compositional dissimilarities in death assemblages show higher rank correlation with spatial distances than with environmental gradients, but spatial structure in community composition is mainly driven by spatially structured environmental gradients.

4. Death assemblages correctly identify the dominance of niche metacommunity models in mollusk communities, as revealed by counterpart living assemblages. This analysis of the environmental resolution of death assemblages thus supports fine-scale niche and paleoenvironmental analyses using molluscan fossil records. In spite of taphonomic processes and time-averaging effects that modify community composition, death assemblages largely capture the response of living communities to environmental gradients, partly because of redundancy in community structure that is inherently associated with multispecies assemblages. The molluscan data sets show some degree of redundancy as evidenced by the presence of at least two mutually exclusive subsets of species that replicate the community structure, and simple simulations show that between-sample relationships can be preserved and remain significant even when a large proportion of species is randomly removed from data sets.

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### Introduction

Quantifying temporal changes in niche positions, breadth, and overlap is one of the major aims of evolutionary ecology (Case 1981; Holt and Gaines 1992; Holt and Gomulkiewicz 1997; Kammer et al. 1997; Tilman 2004; Schaffer and van Nes 2006; Kozak and Wiens 2006;

McPeck 2007) and paleoecology (Miller and Connolly 2001; Holland et al. 2001; Olszewski and Patzkowsky 2001; Holland and Patzkowsky 2004). In evaluating species-level (univariate) and community-level (multivariate) responses to environmental gradients, however, paleoecological and paleoenvironmental anal-

yses implicitly assume that species respond differently to environmental gradients, that species sorting consequently dominates the dynamics of community assembly from the larger metacommunity (Brett 1998; Webber 2002; Holland 2005; Holland and Patzkowsky 2007), and that death assemblages in marine and freshwater sediments accurately and confidently capture this variation in species abundances along gradients (e.g., Birks et al. 1990; Lotter et al. 1998; Kucera et al. 2005). However, other biological and taphonomic dynamics might operate. For example, species might indeed consistently differ in responses to environmental gradients as assumed in species-sorting metacommunity models (Leibold et al. 2004), but taphonomic processes might obliterate, accentuate, or shift the record of that response (e.g., Cummins et al. 1986a,b; Kowalewski 1997; Behrensmeier et al. 2005). Alternatively, under a neutral model in which species are ecologically equivalent in their per capita demographic rates and thus interchangeable (Bell 2000; Hubbell 2001; Maurer and McGill 2004; McGill et al. 2005), variation in the living community composition might be high owing to demographic stochasticity and dispersal limitation but unrelated to environmental gradients. In this case, death assemblages might not respond to environmental gradients but rather to spatial gradients alone (i.e., the geographic configuration of sampled stations, including simple distances among them) owing to dispersal limitation in living assemblages. The neutral model is an extreme end-member of community dynamics, in which community composition is determined solely by ecological drift (i.e., changes in species abundances caused by demographic and environmental stochasticity) and dispersal limitation (Holoyak and Loreau 2006; Leibold and McPeck 2006; Etienne and Alonso 2007). Nonetheless, any theoretical framework predicting the preservation potential of environmental gradients in the fossil record should have several components, including (1) a consideration of the degree to which both individual species and the multi-species composition of the living community respond to environmental gradients, (2) a consideration of the effects of taphonomic and sam-

pling biases that can skew the original patterns of species and community variation along environmental gradients, and (3) a consideration of the scaling effects that might arise from the coarse temporal resolution of death assemblages relative to the fine temporal resolution of living assemblages (this effect is analogous to the sensitivity of species-habitat relationships to the effects of spatial scale [e.g., Karl et al. 2000; Holland et al. 2004; Cushman and McGarigal 2004; Thrush et al. 2005; González-Megías et al. 2007]).

The preservation potential of environmental gradients can be evaluated at two levels: (1) the live-dead agreement of individual species responses to gradients—how a given species arrays itself along a gradient in living and death assemblages, in terms of its niche position, breadth, and carrying capacity (Whittaker 1967): this is a univariate problem; and (2) the live-dead agreement of responses of community composition to gradients—how strongly the compositional variation of a living multispecies assemblage along a gradient is preserved: this is a multivariate problem. Taphonomic processes can affect live-dead agreement in species and community responses to environmental gradients (1) by modifying the composition of death assemblages relative to the local living assemblage *within* habitats (e.g., caused by differential preservation of species, and differential generation times), and (2) by modifying compositional similarity *among* habitats along a gradient (e.g., caused by between-habitat differences in taphonomic processes, between-habitat mixing, or habitat shifting within the window of time-averaging).

The preservation of gradients is conceptualized in Figure 1. With the operation of post-mortem processes, some individuals and species might be lost or added along this gradient, reducing live-dead agreement in species composition. However, the loss of some species might not substantially change the ordination of death assemblages because, even when overlapping species responses are distributed randomly along the gradient (Fig. 1A), some species in species-rich communities will react to segments of environmental gradients in similar ways. Such species are thus

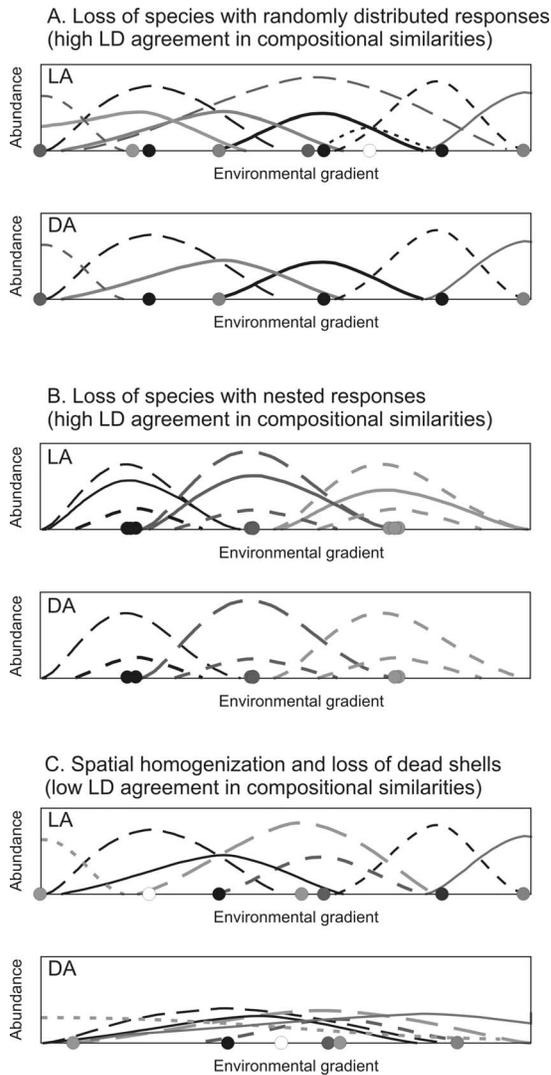


FIGURE 1. Response curves illustrating several outcomes of live-dead agreement in species and community response to an environmental gradient. A, Along a gradient with randomly overlapping species distributions, high live-dead agreement in between-site compositional dissimilarities can occur under moderate species loss because the preserved species can still discriminate among sites. B, During the transition from living to death assemblage, some species are preferentially lost owing to low durability, leading to low live-dead agreement in community composition. However, owing to their shared environmental preferences and nested community structure, community response to the environmental gradient is still captured by the death assemblages. C, During the transition from living to death assemblage, some species are destroyed, and specimens are also mixed spatially along the gradient, leading to low live-dead agreement both in community composition and in community response to the environmental gradient. LD, live-dead; LA, living assemblage; DA, death assemblage.

partly interchangeable or redundant in the way they discriminate among sites or environmental conditions. This is important because, given such redundancy, the preservation of any species does not need to be perfect to reveal community structure with reasonable fidelity. In addition, because some species can be generalists that do not vary in abundance along the gradient, their taphonomic loss does not change the resolution of environmental gradients captured by death assemblages. If species response curves are nonrandomly distributed and nested (Fig. 1B), then, although living and death assemblages might differ in community composition (because of taphonomic loss or addition of species), compositional similarities between living and death assemblages can also be preserved if a subset of species partly replicating the community structure is preserved. Finally, if postmortem loss or homogenization along the gradient is severe, or if there is little structural redundancy among species along the gradient, then both compositional similarity between living and death assemblages and live-dead agreement in the ordination of assemblages along the gradient will be low (Fig. 1C).

Structural redundancy in community composition can be defined as the presence of more than one mutually exclusive subset of species that significantly capture community structure based on the full set of species and can be explored with routines that search for such subsets (Clarke and Warwick 1998; Allen et al. 1999; Mistri et al. 2001). This redundancy does not signify or imply functional redundancy, i.e., that one subset of species is fully interchangeable with another. For example, two species can respond identically to a bathymetric gradient but can differ in substrate preference, can respond identically to only one segment of a gradient, or can differ in resource use within individual stations where they co-occur. However, structural redundancy can characterize several types of multispecies response patterns to gradients (e.g., Underwood 1978; Dale 1988; Leibold and Mikkelsen 2002; Ulrich and Gotelli 2007), and thus the preservation potential of community response by death assemblages will partly depend on the degree of redundancy in the com-

munity structure. This concept of redundancy also implies that live-dead agreement in *community response* to gradients can be decoupled from live-dead agreement in *community composition*.

Actualistic investigations of the quality of ecological information archived by death assemblages are an essential step in getting full value from paleoecological analyses in both deep and recent time. Live-dead agreement in species richness and in relative abundance is commonly studied within habitats, even permitting meta-analysis of molluscan systems (e.g., Kidwell 2001, 2007; Zuschin and Oliver 2003; Lockwood and Chastant 2007; for broader review, see Behrensmeyer et al. 2000). In contrast, the ability of death assemblages to detect environmental gradients—and in particular their ability to capture the same environmental gradient that the source living community is responding to—has been evaluated in only a few studies (e.g., Stanton 1976; Warne et al. 1976; Overpeck et al. 1985; Miller 1988; Pandolfi and Minchin 1995; Zuschin et al. 2000; Gavin et al. 2003; Aronson et al. 2005; Ferguson and Miller 2007; Hassan et al. 2008). In the three study areas where molluscan death assemblages were used to test for community-level response, their response to the environmental gradient was relatively high and comparable to that of counterpart living assemblages (Warne et al. 1976; Miller 1988; Ferguson and Miller 2007). The ability of death assemblages to accurately capture species niche positions, species breadths, and species carrying capacities (i.e., maximum abundance that can be sustained by an environment and at which the net reproductive rate equals 1) remains completely unknown.

We have several aims in this study. First, we quantify the degree to which *living* mollusk assemblages respond to environmental gradients. The origin of variation in community composition can be driven solely by environmental variation (species-sorting model; species consistently differ in niche requirements and impacts), purely by spatial variation (neutral model, or the patch-dynamic model; dispersal alone determines the geographic distribution of individuals), or by the combination of the two (mass-effect model, e.g., Lei-

bold et al. 2004; Cottenie 2005; Ellis et al. 2006). Because metacommunity dynamics are unexplored for benthic mollusks, our study on the significance of environmental variation in determining variation in species abundance is an initial step toward distinguishing the role of neutral and non-neutral processes in the assembly of present-day mollusk communities. Second, we evaluate whether individual species responses to gradients in water depth and seafloor type in living assemblages are captured by species responses in death assemblages by quantifying the degree of live-dead agreement in species niche positions, breadths, and carrying capacities. Third, we assess the degree of live-dead agreement of community response to gradients by comparing the ability of living and death community composition to capture spatial and environmental gradients when analyzed by traditional multivariate analyses. Fourth, the partition of compositional variation into environmental and spatial components allows us to distinguish whether living and death assemblages indicate the same underlying metacommunity dynamics (Legendre et al. 2005; Tuomisto and Ruokolainen 2006). Finally, we evaluate whether living molluscan assemblages exhibit structural redundancy in community composition.

#### Data Sources and Methods

We analyze nine live-dead data sets generated by quantitative sampling of molluscan communities from small but environmentally variable areas (Tsuchi 1959; Warne 1971; Bosence 1979; White et al. 1983; Miller 1988; Linse 1997, 1999; Kowalewski et al. 2003; see Supplement online at <http://dx.doi.org/10.1666/07081.s1>). To be included, a data set had to include at least five stations with at least 10 living and 10 dead individuals per station, and be comparable in spatial extent and resolution of sampling units to paleoecological data sets. Here, the maximum spatial dimension of a study area ranges from 0.3 to 247 km, and samples were standardized with respect to sediment volume (field collection methods varied among studies, but were usually van Veen or Petersen grabs on open shelves and hand-excavated cores in bays and lagoons).

Data sets almost always include larger numbers of dead than living specimens. This asymmetry may reduce dead-live agreement because community dissimilarity indices are sample-size biased (Wolda 1981; Lande 1996).

To avoid instances where the death assemblage might be in disequilibrium with the living assemblage owing to recent anthropogenic impacts (Kidwell 2007, 2008), we focus on data sets from relatively undisturbed areas. In the southern California Bight, whose shelf has a long history of point-source pollution, stations located within wastewater-outfall zones were excluded from analyses. On the Texas shelf (Corpus Christi), the seafloor has been subject to intense bottom-trawling for decades; this disturbance has not reduced live-dead agreement in other metrics (Kidwell 2007, 2008), and so we include this data set in our analysis.

For eight data sets, the author’s original sampling design encompasses environmental variation both in water depth and in “facies” (seafloor type, for example variation in sediment grain size, sorting, and/or extent of vegetation), but for one data set (Chihama shelf) only water depth varies among stations (Supplement Table 1). To quantify facies variation, we established six categories, using data from the original authors: mud (<10 wt% sand), sandy mud (10–49 wt% sand), muddy sand (50–90 wt% sand), sand (<10 wt% mud), gravel or gravelly sediments (>10 wt% gravel-sized particles; may be lithic or shell gravel), and grass (sufficient abundance at least seasonally to be mentioned by original author [per Kidwell 2007]). Data sets are from exclusively subtidal areas of lagoons, estuaries, or open continental shelves, with one exception (Supplement Table 1; Mugu Lagoon data set includes intertidal as well as subtidal stations). Each data set thus also encompasses variation in additional environmental variables such as temperature and salinity, but these are not investigated here. The spatial gradient is the geographic spacing of stations represented by UTM (Universal Transverse Mercator) coordinates (measured from the station maps of the original authors). These data sets are a subset of those used in earlier global meta-analyses (e.g., Kidwell 2001,

TABLE 1. Summary of analyses that evaluate live-dead agreement of species and community responses to environmental and spatial gradients. Live-dead agreement of individual species responses is assessed with the Spearman rank correlation between three species-level traits in living and death assemblages (i.e., species niche positions, species niche breadth, and species carrying capacities predicted by generalized linear models, GAM). The agreement of community responses is defined as the dead-live difference in (1) the proportion of compositional variation explained by environmental factors in distance-based redundancy analysis of principal coordinates (CAP), (2) the proportion of compositional variation uniquely explained by environmental and spatial components in redundancy analysis, and (3) rank correlation and ANOSIM R statistic, which measure relationships between depth differences, facies differences, and spatial distances on one hand, and compositional dissimilarities on the other hand. BC, Bray-Curtis.

Variable measured	Statistical analysis	Analysis of live-dead agreement
Species position (preferred environment)	Mean score along CAP 1 axis weighted by abundance	Spearman rank correlation
Species niche breadth	Weighted standard deviation along CAP 1 axis	Spearman rank correlation
Species carrying capacity	Abundance predicted by GAM along CAP 1 axis	Spearman rank correlation
Variation explained by environment	Distance-based RDA of principal coordinates (CAP)	Dead-live difference in variation explained
Variation uniquely explained by environment	Variance partitioning—Redundancy analysis	Dead-live difference in variation explained
Variation uniquely explained by space	Variance partitioning—Redundancy analysis	Dead-live difference in variation explained
Spatial distance-BC dissimilarity relationship	Mantel test (Spearman rank correlation)	Dead-live difference in correlation
Depth difference-BC dissimilarity relationship	Mantel test (Spearman rank correlation)	Dead-live difference in correlation
Facies difference-BC dissimilarity relationship	Analysis of similarities	Dead-live difference in R statistic

2007), where live-dead agreement was assessed *within* habitats, on the basis of pooled counts of living and dead individuals from multiple stations of a single seafloor type. Data sets are examined here at a much finer spatial resolution: we compare variation among stations (assemblages) along gradients that cross multiple habitats, without pooling.

Dissimilarity coefficients based on presence-absence data (e.g., Sorenson index) differ from those based on untransformed proportional abundance (e.g., Manhattan distance; Anderson et al. 2006) because they capture different aspects of community turnover. Presence-absence indices reveal information about extinction-colonization dynamics that happen at larger spatial and temporal scales than small-scale processes of birth-death dynamics revealed by abundance indices (e.g., Warwick 1988; Sale 1998; Legendre and Gallagher 2001; Pandolfi 2001; Lasiak 2003; Anderson et al. 2006). To evaluate these effects of data transformation on the detection of gradients, we evaluate live-dead agreement at three levels of transformation: (1) Bray-Curtis (BC) dissimilarity based on untransformed proportional abundances, which will be most sensitive to changes in dominant species; (2) BC dissimilarity based on square-root-transformed proportional abundances, which reduces the effect of dominant species; and (3) BC dissimilarity based on presence-absence data, which gives equal weights to abundant and rare species (same as the Sorenson dissimilarity; e.g., Rahel 1990; Olsgard et al. 1997; Clarke et al. 2006).

We analyze compositional variation among living and among death assemblages along environmental gradients by using distance-based redundancy analysis of principal coordinates (CAP) (Legendre and Anderson 1999; Oksanen et al. 2005). CAP can be used with any dissimilarity measure, and is performed on the axes obtained from a principal coordinate analysis (PCO) that maximize compositional differences among sites, and is followed by redundancy analysis (RDA) of principal coordinates (Oksanen et al. 2005). This method is conceptually allied with canonical analysis of principal coordinates that uses canonical correlation analysis of principal coordi-

nates rather than redundancy analysis (Anderson and Willis 2003). Canonical correlation analysis evaluates relationship between two sets of variables, whereas redundancy analysis evaluates how much of the variation in one set of (biotic) variables can be explained by the other set of (environmental) variables. The relationship between species abundance and CAP axes is not constrained to be linear (Legendre and Anderson 1999). We found that canonical correspondence analysis (CCA) (ter Braak and Prentice 1988; ter Braak and Verdonschot 1995) and outlying mean index analysis (OMI) (Dolédec et al. 2000) yield generally similar results (see Supplement).

We use several approaches to address live-dead agreement in species and community responses to environmental and spatial gradients (Table 1). First, we assess live-dead agreement in species niche positions, species niche breadths, and maximum species carrying capacity using the Spearman rank correlation coefficient. The niche position of a species along the first axis of CAP (i.e., environmental gradient extracted using the depth and facies variables) is represented by the mean of occupied station scores weighted by species abundances (e.g., Thioulouse and Chessel 1992). Species niche breadth is measured as the weighted standard deviation of occupied site scores along the environmental gradient, where species proportional abundance within occupied sites is the weighting factor (e.g., Green 1971; Dolédec et al. 2000; Holland et al. 2001; Thuiller et al. 2004; Pither and Aarssen 2005).

Although species responses can also be evaluated with respect to raw environmental gradients, gradient scores extracted by CAP axes take into account potential interaction effects of depth and substrate on community composition. We also extract environmental gradients separately for depth and facies, but these analyses give the same results as those based on the combined depth and facies gradients (see Supplement). To estimate the shapes of response curves along CAP axis 1 (Fig. 2), we use generalized additive models (GAM), a method that is comparable to generalized linear models (Yee and Mitchell 1991; Austin 2002; Oksanen and Minchin 2002;

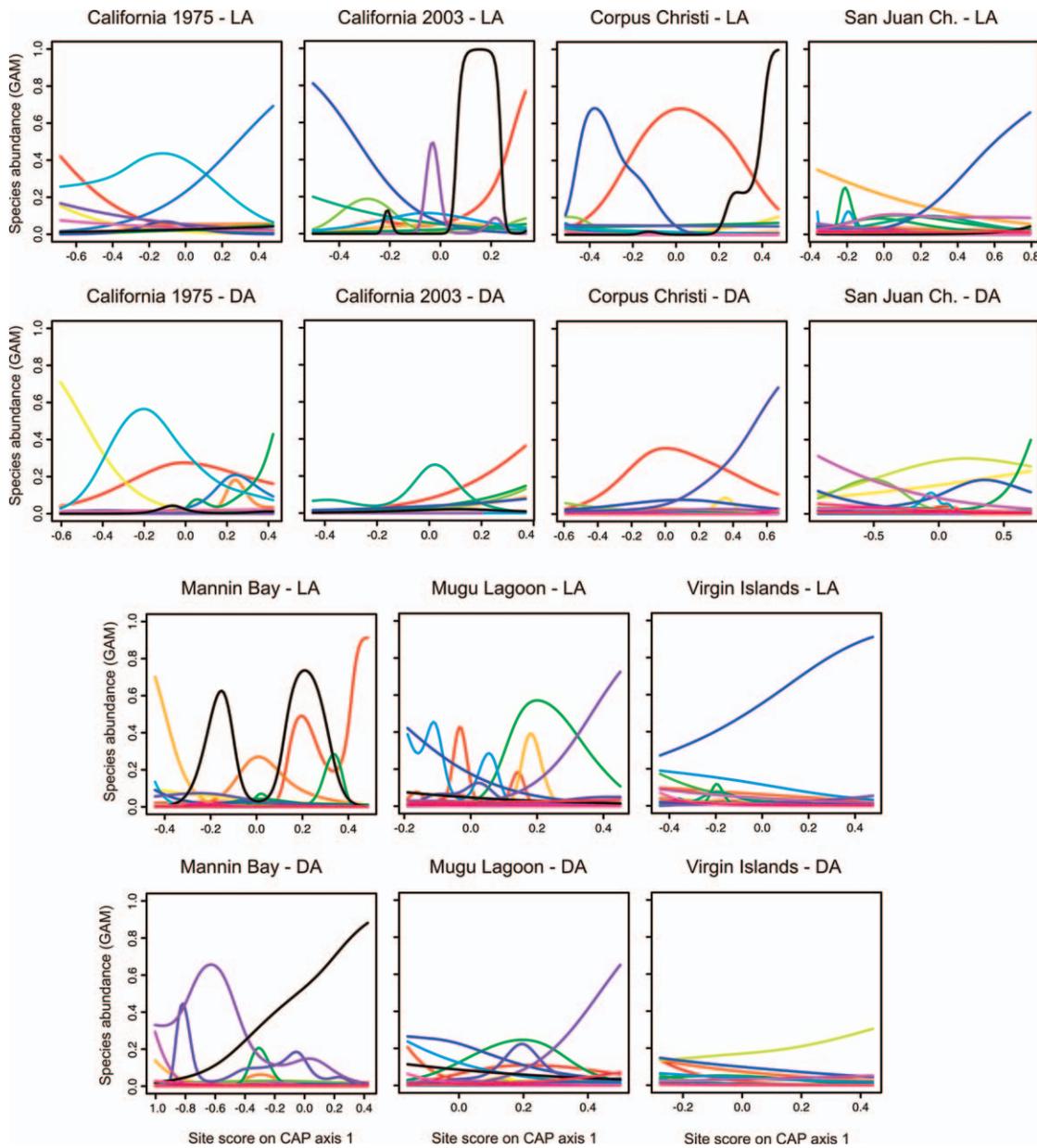


FIGURE 2. Differences in species response curves between living and death assemblages of seven data sets along a combined depth+facies gradient (x-axis; based on the first axis derived from distance-based RDA of principal coordinates). Response curves reflect variation in abundance as smoothed by a generalized additive model (GAM). We use the logit function as the link function to ensure that the predicted abundances range between zero and unity, and the quasi-binomial variance function, which is appropriate for proportional data and allows aggregation of individuals in space. The link function determines how the mean of proportional abundances depends on environmental variables, and the variance function determines how the variance of the proportional abundances depends on its mean. Species that occur in only one or two stations were excluded from analyses. Responses were not analyzed for the Chihama data set because only one species occurs in more than two stations. The same species in living and death assemblages are coded by the same color.

Kindt and Coe 2005) (see Supplement). To determine species carrying capacity, we use the maximum value of proportional abundance that is predicted by the GAM curve at its niche position. A one-sided signed-rank Wilcoxon test evaluates the null hypothesis that the median rank correlation in individual species' responses between living and death assemblages, averaged across nine data sets, is significantly greater than zero.

Second, we analyze community responses to environmental gradients using distance-based redundancy analysis of principal coordinates (CAP), Mantel tests, and variance partitioning into environmental and spatial components. In CAP, the proportion of compositional variation explained by the environmental variable corresponds to the sum of eigenvalues explained by the environmental factor (extracted by RDA) relative to the sum of all eigenvalues (Legendre and Anderson 1999), although negative eigenvalues are ignored. The proportion of compositional variation explained by environmental factors thus quantifies their influence on the community composition. Dead-live difference in the proportional variation that is explained by environmental variables measures the agreement with which the living and death assemblages capture the environmental gradient.

A Mantel test based on Spearman rank correlation can be used to evaluate whether community composition differs as a function of spatial proximity by testing whether rank-order BC dissimilarities of living and death assemblages are nonrandomly related to spatial distances. By computing a correlation between BC dissimilarities and spatial distances, the Mantel test evaluates whether compositional dissimilarities decrease as the sampled stations become geographically closer (Legendre and Fortin 1989), and thus whether community composition is more spatially autocorrelated than expected under a random arrangement of station-pairs in space (Legendre 1993). We also correlate compositional dissimilarities with depth and facies differences in Mantel tests, but these analyses corroborate the results based on CAP (see Supplement).

To evaluate the roles of spatial and environmental components in determining variation

in the community composition of living and death assemblages, we use redundancy analysis (RDA) to decompose the total variation in the matrix of species abundances into unique spatial and environmental components (Borcard et al. 1992; Méot et al. 1998; Cottenie et al. 2003; Vanschoenwinkel et al. 2007). Note that this redundancy analysis is not equivalent to the concept of structural redundancy. The redundancy analysis is similar to CAP—it evaluates similarity using strictly Euclidean correlations or covariances, whereas CAP allows non-Euclidean dissimilarities like the Bray-Curtis index. We use RDA for multivariate partitioning of the community matrix because the partitioning of CAP remains unexplored (Peres-Neto et al. 2006). We use the function `varpart()` from the `vegan` package (Oksanen et al. 2005) to partition variation within the community matrix with respect to two explanatory tables—one with spatial coordinates and another with depth and facies variables.  $R^2$  measures the amount of variation in the community matrix that is explained exclusively by environmental (E) or spatial (S) variables. Five different components of the variation in the community matrix are measured, including the total explained variation [E + S], environmental variation [E], spatial variation [S], environmental variation without a spatial component [E|S, “unique environmental component”], and spatial variation without the environmental component [S|E, “unique spatial component”].  $R^2$  is adjusted to represent unbiased estimates of the partitioning according to Peres-Neto et al. (2006). The significance of these components is evaluated with a permutation test (`permutest.cca()` in the `vegan` package), with 1000 permutations. According to Cottenie (2005), assemblages showing a significant unique environmental component can be assigned to the species-sorting model; assemblages showing a significant unique spatial component are assigned to the neutral model (or the patch-dynamic model, which cannot be distinguished from the neutral model with such analysis); and assemblages showing both significant environmental and spatial components are assigned to the mass-effect model. Assemblages that do not show significantly high unique

components remain undetermined with respect to the metacommunity model. Because our analysis includes two environmental variables only, it will thus be conservative if it supports the species-sorting and mass-effect models.

In all analyses, continuous (depth) and categorical (facies) variables were standardized into zero mean and unit variance. Facies variables are ordered according to grain size and presence of vegetation (except Mugu Lagoon; see Supplement). The spatial variables are represented by UTM coordinates. For every live-dead comparison, the number of stations was equal (within each study area, a single set of stations was used to generate both the living and death assemblage information), thus avoiding problems of comparing patterns based on unequal numbers of assemblages (Cottenie 2005). To evaluate average live-dead agreement in community response to environmental gradients, we use the two-sided signed-rank Wilcoxon test to assess the null hypothesis that the median difference in the proportion of variation explained by environmental and spatial components, averaged across data sets, between death and living assemblages differs significantly from zero.

We also explore the relationship between live-dead agreement in community composition and live-dead agreement in the position of living and death assemblages along a compositional gradient extracted by PCO axis 1. First, we evaluate compositional overlap between living and death assemblages with the ANOSIM  $R$  statistic. Analysis of similarities (ANOSIM), which is a categorical test comparable to the Mantel test (Legendre and Legendre 1998; Somerfield et al. 2002), evaluates whether rank-order dissimilarities within living and within death assemblages are smaller than rank-order dissimilarities between living and death assemblages. It computes an  $R$  statistic that measures the average difference in rank-order Bray-Curtis dissimilarity between living and death assemblages (Clarke and Green 1988). For  $R = 1$ , living and death assemblages are completely different in composition. For  $R = 0$ , the within-habitat average rank dissimilarity within living and within death assemblages is not smaller than the av-

erage rank dissimilarity between living and death assemblages. We note that this statistic is affected by changes in both location (i.e., mean composition) and dispersion (i.e., average distance between assemblages and their centroid) of assemblages in multivariate space (Clarke 1993; Anderson 2001). Second, we ordinate the assemblages in terms of their composition with PCO; the first PCO axis, which extracts the maximum amount of compositional variation, is used as a measure of assemblage ordination along the compositional gradient. The Spearman rank coefficient then quantifies live-dead agreement in the ordination of living and death assemblages along the first PCO axis.

To explore the structural redundancy within living communities, we use the stepwise procedure BVSTEP (Clarke and Warwick 1998). This procedure tests for the presence of structural redundancy in molluscan assemblages, i.e., whether there is more than one mutually exclusive subset of species that can replicate the community structure based on the full set of species. The number of such species subsets quantifies the extent of structural redundancy. First, an iterative procedure finds a minimal subset of species that significantly capture between-sample compositional dissimilarities based on the full set of species (see details in Clarke and Warwick 1998). Our criterion for the replication of the community structure is that the Spearman rank correlation ( $r$ ) between dissimilarity matrices based on the full species list and the minimal subset of species has to be larger than some specified threshold value of  $r$ . Clarke and Warwick (1998) used the  $r = 0.95$  threshold in a data set with 125 species from several phyla, but the total species richness in the molluscan living assemblages is lower (20–74 species) and we thus use the more relaxed threshold value  $r = 0.75$ . Second, after elimination of the first minimal subset of species, the iterative procedure searches for the second minimal subset of species that can significantly capture compositional dissimilarities of the full species matrix. The significance of rank correlation is estimated with a permutation test.

## Results

*Response of Living and Death Assemblages to Environmental and Spatial Gradients.*—Both living and death assemblages consistently vary in composition either in response to environmental gradients alone (species-sorting model) or in response to both environmental and spatial gradients (mass-effect model; Table 2). The unique environmental component explains a significant proportion of compositional variation in six living assemblages and four death assemblages when we use square-root-transformed data ( $p = 0.002$  and  $p < 0.0001$  binomial test, respectively). Analyses based on untransformed abundances and presence-absence data give similar results (Table 2). Only one data set—the living assemblage from the Virgin Islands—remains undetermined regardless of the level of data transformation. Regardless of data transformation, none of the living assemblages support the neutral model (or the patch-dynamic model).

*Live-Dead Agreement in Species Responses to Environmental Gradients.*—Species response curves are highly variable in skewness and kurtosis among species within living and death assemblages, and also differ between paired living and death assemblages (Fig. 2). Many rare species show a relatively uniform response with respect to the first CAP axis. However, species niche positions along both bathymetric and facies gradients in death assemblages show relatively high agreement to their positions in counterpart living assemblages (Fig. 3, Table 3, see summary in Table 4). Rank correlations in species positions between living and death assemblages are significantly positive in four data sets when we use square-root transformation ( $p = 0.0004$  binomial test) and in six data sets when we use presence-absence transformation ( $p < 0.0001$  binomial test). Live-dead agreement is invariably significantly positive ( $\alpha = 0.05$ ) in Wilcoxon signed-rank tests, according to the median rank correlation averaged across data sets, and generally improves with the degree of data transformation (Fig. 4, Table 3). Live-dead agreement of species breadths varies among data sets (Table 3). Regardless of data

transformation, the median rank correlation between species breadths in living and death assemblages is significantly positive at  $\alpha = 0.05$  in Wilcoxon signed-rank tests (Fig. 4). In terms of live-dead agreement in species carrying capacities, three of seven data sets exhibit moderately high and significant relationships under presence-absence transformation ( $p = 0.004$  binomial test), and two of seven data sets show significance for  $\alpha = 0.05$  under no and square-root transformation ( $p = 0.044$  binomial test, Table 3). The median rank correlation between species carrying capacities in living and death assemblages is significantly positive at  $\alpha = 0.05$  in Wilcoxon signed-rank tests under all three levels of data transformation (Fig. 4). For all three measures of species response, average live-dead agreement is generally higher in strength and significance when square-root-transformed abundance and presence-absence data are used relative to untransformed data (Table 3, Fig. 4).

*Live-Dead Agreement in Community Responses to Environmental Gradients.*—Depth and facies gradients have similar effects on the community composition of living and death assemblages in terms of the proportion of compositional variation explained by environmental gradient with respect to the first CAP axis and its significance (Table 3, Figs. 5, 6). Depth and facies explain a significant proportion of compositional variation in death assemblages when a significant proportion of compositional variation is also explained by the counterpart living assemblage (see summary in Table 4). The proportions of variation explained by the environmental gradients are similar between living and death assemblages (Table 3). The proportion of variation explained can either increase or decrease as the severity of transformation increases. The plots in Figure 5 and 6 show that coding by facies segregates stations about the same way in both living and death assemblages, especially using square-root-transformed data. These plots also show that (1) the direction of depth and facies gradients, representing the most rapid change in the environmental variable with respect to the first and the second CAP axis, and (2) their lengths, corresponding to the proportion of compositional variation explained by both

TABLE 2. Variation in community structure of living and death assemblages explained by unique environmental and spatial variables. The components are environment independent of space [E|S], and space independent of environment [S|E]. Metacommunity types: SS, species-sorting model; SS+ME, mass-effect model; NM/PD, neutral model/patch-dynamic model; UN, undetermined. The *p*-values in boldface are results that are significant after sequential Bonferroni correction for seven tests per type of data transformation, separately for living and death assemblages; *p*-values in italics are results that became insignificant after Bonferroni correction. However, note that the Bonferroni correction inflates the type II error (Moran 2003). Partitioning of the community matrices into environmental and spatial components was not possible for the Chihama and Patagonia data sets, which have five stations only.

Data set	L/D	Meta-community (untransformed)				Meta-community (square-root)				Meta-community (PA)						
		E S	<i>p</i>	S E	<i>p</i>	E S	<i>p</i>	S E	<i>p</i>	E S	<i>p</i>	S E	<i>p</i>			
California 1975 shelf	Dead	0.022	0.34	0.07	0.13	UN	0.11	0.019	0.1	0.025	SS+ME	0.13	<b>0.001</b>	0.07	0.023	SS+ME
	Live	0.05	0.16	0.05	0.15	UN	0.07	0.05	0.05	0.1	SS	0.06	0.059	0	0.47	(SS)
California 2003 shelf	Dead	0.23	< <b>0.001</b>	0.02	0.26	SS	0.2	< <b>0.001</b>	0.07	0.041	SS+ME	0.09	0.026	0.05	0.099	SS
	Live	0.22	< <b>0.001</b>	0.16	<b>0.001</b>	SS+ME	0.19	< <b>0.001</b>	0.11	<b>0.003</b>	SS+ME	0.1	<b>0.006</b>	0.04	0.11	SS
Corpus Christi shelf	Dead	0.028	0.53	-0.1	0.82	UN	0.04	0.29	-0.02	0.51	UN	0.095	<b>0.006</b>	0.088	<b>0.005</b>	SS+ME
	Live	0.12	0.13	0.016	0.43	UN	0.17	0.022	0.11	0.07	SS	0.22	< <b>0.001</b>	0.14	<b>0.006</b>	SS+ME
San Juan Channel	Dead	0.18	0.082	0.13	0.168	UN	0.17	0.028	0.16	0.021	SS+ME	0.1	0.017	0.11	<b>0.008</b>	SS+ME
	Live	0.2	0.274	0.06	0.087	UN	0.31	< <b>0.001</b>	0.11	0.056	SS	0.18	<b>0.005</b>	0.06	0.18	SS
Mannin Bay	Dead	0	0.53	0.002	0.36	UN	0.025	0.07	0.026	0.063	UN	0.049	< <b>0.001</b>	0.062	< <b>0.001</b>	SS+ME
	Live	0.08	< <b>0.001</b>	0.06	<b>0.008</b>	SS+ME	0.064	<b>0.001</b>	0.06	<b>0.002</b>	SS+ME	0.024	<b>0.007</b>	0.056	< <b>0.001</b>	SS+ME
Mugu Lagoon	Dead	0.06	<b>0.006</b>	0.1	< <b>0.001</b>	SS+ME	0.029	0.038	0.14	< <b>0.001</b>	SS+ME	0.01	0.095	0.095	< <b>0.001</b>	NM/PD
	Live	0.05	<b>0.006</b>	0.09	< <b>0.001</b>	SS+ME	0.05	<b>0.005</b>	0.12	< <b>0.001</b>	SS+ME	0.027	0.019	0.068	< <b>0.001</b>	SS+ME
Virgin Islands	Dead	0.14	<b>0.005</b>	0.07	0.015	SS+ME	0.076	0.05	0.039	0.075	SS	0	0.44	0	0.46	UN
	Live	-0.05	0.72	0.015	0.25	UN	0.018	0.3	0.039	0.12	UN	0.028	0.195	0.023	0.155	UN

TABLE 3. Summary of live-dead agreement in (1) species niche positions (weighted mean of site scores occupied by species), (2) species niche breadths (weighted standard deviations of sites scores occupied by species), (3) species carrying capacities (maximum abundance at species position predicted by GAM), (4) the proportion of variation explained by environmental variables (ratio of constrained inertia to total inertia) based on distance-based RDA of principal coordinates, (5) the relationship between spatial distance and compositional dissimilarity based on the Mantel test, and (6) ordination of stations along PCO axis 1. Boldface and italicized *p*-values as in Table 2. Live-dead agreement was tested separately for three levels of data transformation. Carrying capacities were not predicted for the Patagonia data set because the number of unique site scores on environmental gradients predicted by CAP was too small and the number of unique covariate combinations was smaller than the maximum degrees of freedom in GAM. Explanations: *r*, Spearman rank correlation; CI, variation explained by depth and facies; UNCI, variation unexplained.

	Positions		Breadth		Capacity		CAP-live (depth + facies)			
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	CI	UNCI	exp	<i>P</i>
Untransformed										
California 1975 shelf	0.48	0.12	0.02	0.95	0.34	0.28	13.06	59.05	0.18	0.05
California 2003 shelf	0.43	0.25	0.37	0.34	-0.24	0.58	29.2	48.5	0.38	<0.005
Corpus Christi shelf	0.47	0.09	-0.59	0.029	0.05	0.88	11.72	34	0.26	0.073
Patagonia shelf	0.68	<b>0.0072</b>	0.704	<b>0.0049</b>	NA	NA	1.38	0.81	0.63	0.37
San Juan Channel	0.16	0.42	0.225	0.258	0.024	0.91	7.16	10.48	0.41	<0.005
Mannin Bay	0.236	0.24	0.267	0.19	0.48	0.015	77.28	1052.5	0.07	0.033
Mugu Lagoon	0.691	<b>0.0002</b>	0.685	<b>0.0002</b>	0.77	<0.0001	119.6	510.9	0.19	<0.005
Virgin Islands	0.54	0.033	0.37	0.15	0.36	0.16	9.13	26.11	0.26	0.022
Square-root transformed										
California 1975	0.54	0.07	0.43	0.17	0.1	0.74	12.59	55.07	0.19	0.04
California 2003	-0.08	0.84	0.57	0.12	-0.24	0.58	23.29	44.28	0.34	<0.005
Corpus Christi	0.58	0.031	0.11	0.71	0.5	0.08	11.89	29.74	0.29	0.024
Patagonia	0.78	<b>0.001</b>	0.61	0.02	NA	NA	1.86	0.67	0.74	0.12
San Juan Channel	0.37	0.059	0.23	0.25	0.28	0.16	5.77	7.01	0.45	<0.005
Mannin	0.5	0.0097	0.17	0.39	0.28	0.18	81.75	1042.5	0.08	<b>0.005</b>
Mugu Lagoon	0.82	<0.0001	0.72	<0.0001	0.47	0.018	99.3	458.1	0.18	<0.005
Virgin Islands	0.45	0.081	0.38	0.15	0.59	0.02	11.97	28.46	0.30	<b>0.01</b>
Presence-absence										
California 1975	0.57	0.05	0.27	0.38	0.15	0.64	12.39	57.59	0.18	0.07
California 2003	0.16	0.68	0.42	0.26	0.32	0.44	16.66	44.43	0.27	<0.005
Corpus Christi	0.58	0.029	0.32	0.26	0.18	0.59	12.21	28.15	0.30	0.041
Patagonia	0.79	<b>0.0009</b>	0.65	0.01	NA	NA	2.46	1.27	0.66	0.18

variables, are very similar *between* living and death assemblages. Correlations captured by living assemblages between depth and facies differences on one hand and compositional dissimilarities on the other hand are also relatively well preserved by death assemblages (see Supplement). Regardless of data transformation, the median dead-live difference in the compositional variation explained by the effects of depth and facies, averaged across data sets, does not differ significantly from zero at  $\alpha = 0.05$  in Wilcoxon signed-rank tests (Fig. 7A).

*Live-Dead Agreement in Community Responses to Spatial Gradients.*—Mantel tests demonstrate that, in terms of rank correlations among spatial distances and compositional dissimilarities and their significance, the community compositions of living and death assemblages re-

spond similarly to spatial gradients (Table 3). Living and death assemblages of three data sets exhibit similarly high and positive spatial structure in community composition, expressed by positive rank correlations between pairwise BC dissimilarities and spatial distances (significant or of borderline significance for  $\alpha = 0.05$ , Table 3; regardless of data transformation). The median difference in the Mantel-test rank correlation between death and living assemblages does not significantly differ from zero at  $\alpha = 0.05$  in two-sided Wilcoxon signed-rank tests (Fig. 7B). In six of nine data sets, depth and/or facies gradients are themselves spatially structured (Supplement), and thus observed responses (correlations) of community structure (and of species abundance) to space can be epiphenomena of underlying responses to environmental gradients.

TABLE 3. Extended.

CAP-dead (depth + facies)				Mantel test-live (space)		Mantel test-dead (space)		PCO axis 1	
CI	UNCI	exp	<i>P</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
17.05	55.81	0.23	0.015	0.1	0.14	0.27	<b>0.005</b>	0.27	0.2800
24.56	46.82	0.34	< <b>0.005</b>	0.21	0.033	0.05	0.28	0.75	0.0011
9	23.28	0.28	0.11	-0.077	0.69	-0.074	0.7	0.65	0.0200
1.6	1.04	0.61	0.15	0.042	0.4	0.6	0.021	0.9	0.0830
2.05	5.57	0.27	0.16	0.43	0.023	-0.03	0.54	0.55	0.1000
23.77	409.2	0.05	0.18	0.077	0.051	0.006	0.46	0.25	0.0700
86.98	350.6	0.20	< <b>0.005</b>	0.33	< <b>0.001</b>	0.426	< <b>0.001</b>	0.74	< <b>0.0001</b>
12.66	8.55	0.60	< <b>0.005</b>	0.335	<b>0.003</b>	0.743	< <b>0.001</b>	0.56	0.0160
14.97	42.61	0.26	< <b>0.005</b>	0.11	0.13	0.26	0.016	0.32	0.1900
19.96	35.91	0.36	< <b>0.005</b>	0.2	0.035	0.13	0.11	0.61	0.014
6.76	17.77	0.28	0.05	-0.04	0.59	-0.06	0.74	0.79	0.002
1.92	0.96	0.67	<b>0.017</b>	0.534	0.12	0.77	0.042	0.9	0.0830
1.55	3.57	0.31	0.042	0.246	0.1	0.012	0.46	0.72	0.0240
30.70	355.3	0.08	<b>0.005</b>	0.09	0.037	0.16	<b>0.006</b>	0.38	0.004
58.04	233.9	0.20	< <b>0.005</b>	0.35	< <b>0.001</b>	0.449	< <b>0.001</b>	0.72	< <b>0.0001</b>
8.21	7.53	0.52	< <b>0.005</b>	0.54	< <b>0.001</b>	0.75	< <b>0.001</b>	0.56	0.0170
15.35	36.74	0.29	< <b>0.005</b>	0.03	0.35	0.14	0.058	0.25	0.3100
13.53	33.35	0.29	< <b>0.005</b>	0.11	0.14	0.24	0.013	0.44	0.0860
5.44	16.86	0.24	0.045	-0.02	0.52	-0.09	0.73	0.75	<b>0.0046</b>
1.92	1.03	0.65	0.02	0.58	0.092	0.75	0.058	0.7	0.2300

*Live-Dead Agreement in Metacommunity Structure.*—As in living assemblages, the variation in community composition displayed by death assemblages is dominated by the unique environmental component alone [E|S], by both unique environmental [E|S] and unique spatial components [S|E], or by neither of the unique components (neither explains a significant part of the variance; Table 2). Death assemblages thus indicate species-sorting models, mass-effect models, or undetermined metacommunity models. Only in one case (Mugu Lagoon under presence-absence transformation) is the variation in death assemblages explained exclusively by the unique spatial component, which is consistent with the neutral or patch-dynamic model. The degree of transformation substantially affects the outcome of these tests as well as the degree

of agreement between living and death assemblages (Table 2). However, data transformation does not change the signal of the metacommunity structure toward the opposite (neutral) models that predict that variation in community composition is mainly explained by the spatial component. Square-root-transformed abundances and presence-absence data return the largest number of conclusive results regarding the determination of the metacommunity model. The median differences in the compositional variation explained by spatial and environmental components between death and living assemblages, averaged across seven data sets, approximate zero and do not differ significantly from zero at  $\alpha = 0.05$  in Wilcoxon signed-rank tests (Fig. 7C).

*Live-Dead Agreement in Community Composition and in Compositional Relationships among*

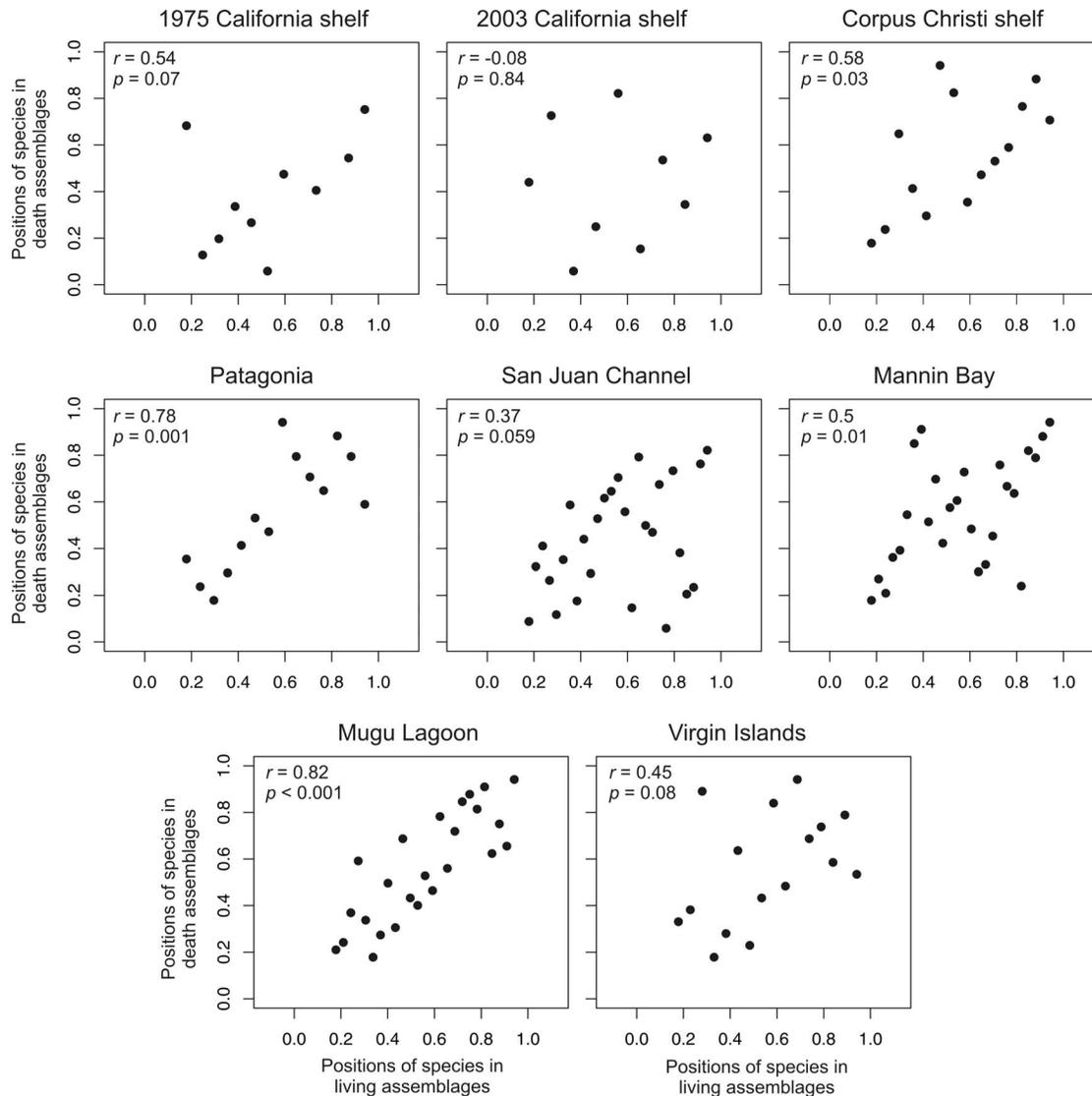


FIGURE 3. Live-dead agreement in species niche positions displayed as bivariate scatterplots with Spearman rank correlations ( $r$ ). Species that occur in one or two stations only were excluded from analyses. Niche positions are based on square-root-transformed abundances. In seven of eight data sets, species positions are positively correlated, and significantly so in half of these data sets.

*Assemblages.*—With the exception of the Chihama shelf and Patagonia shelf data sets, which both have small numbers of stations, death assemblages of all data sets differ significantly in composition from their counterpart living assemblages, regardless of data transformation (ANOSIM, Supplement). These significant live-dead differences in community composition as measured by ANOSIM are not mutually exclusive with the finding of global meta-analyses that species abundances

are generally significantly positively rank correlated when samples (assemblages) are *pooled* within habitats (Kidwell 2001). Indeed, in all nine data sets analyzed here, the Spearman rank correlation in species abundances between living and death assemblages pooled across an entire study area are invariably significantly positive at  $\alpha = 0.05$  (Supplement). In addition, compositional differences between living and death assemblages can also be partly affected by the lower dispersion of

TABLE 4. Summary of live-dead agreement in both species- and community-level response to environmental and spatial gradients for nine data sets. Abbreviations: [E]S, environment independent of space; [S]E, space independent of environment; BC, Bray-Curtis; S, good live-dead agreement, i.e., congruence in response signal at least under one type of data transformation; NS, poor live-dead agreement, i.e., incongruence in response signal; NA, small sample size or undetermined response signal.

	Niche positions	Niche breadth	Carrying capacity	Variation explained by environment	Variance partitioning [E S]	Variance partitioning [S E]	Spatial distance-BC dissimilarity	Depth difference-BC dissimilarity	Facies difference-BC dissimilarity
California 1975 shelf	S	NS	NS	S	S	NS	NS	NS	NA
California 2003 shelf	NS	NS	NS	S	S	S	NS	S	S
Chihama shelf	NA	NA	NA	S	NA	NA	S	S	NA
Corpus Christi shelf	S	S	NS	S	S	S	NA	S	S
Patagonia shelf	S	S	NA	NS	NA	NA	NS	NA	S
San Juan Channel	S	S	NS	S	S	NS	NS	S	NS
Mannin Bay	S	NS	S	S	S	S	S	S	S
Mugu Lagoon	S	S	S	S	S	S	S	NS	S
Virgin Islands	S	NS	S	S	NS	NS	S	S	S

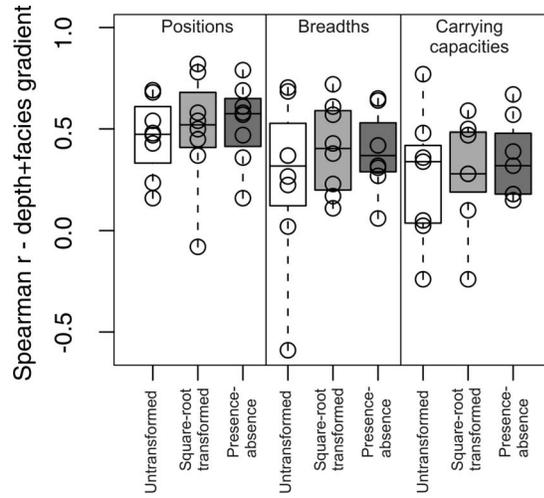


FIGURE 4. Live-dead agreement in species responses to the combined depth+facies gradient, averaged across all data sets. Boxplots display median and 25 and 75 quartile values. Species responses captured by death assemblages are positively correlated with these in living assemblages.

death assemblages in multivariate space, which can be caused by time-averaging effects alone (Tomašových and Kidwell 2009).

Rank correlations that compare the ordination of living and death assemblages (at station spatial scales) along a compositional gradient (represented by the first PCO axis) are significantly positive in four to six of nine data sets, depending on data transformation (Table 3), indicating that live-dead differences in composition are not so strong as to lose the underlying biological pattern in the compositional variation among assemblages. With the exception of the Chihama data set and regardless of data transformation, all other data sets invariably show that at least two different subsets of species significantly replicate the community structure displayed by the full species list, in terms of significant rank correlation between dissimilarities based on the full set of species and dissimilarities based on the subset of species (using the threshold rank correlation of 0.75). It is notable that these minimal subsets can consist of one to four species only (see Supplement).

Simple simulations that incorporate random loss of an increasing number of individual species from a data set show that, for all nine molluscan data sets, the rate of degr-

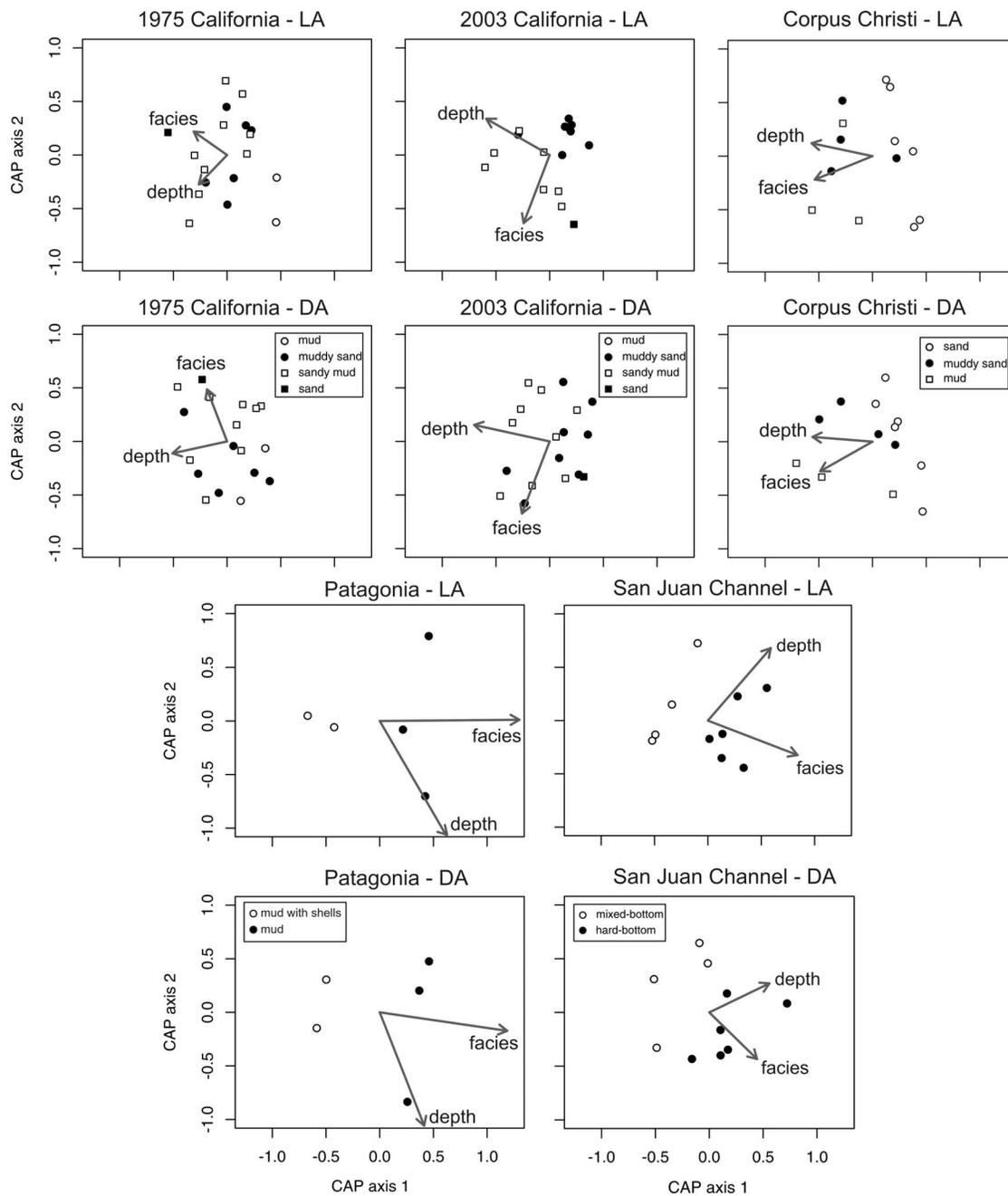


FIGURE 5. Comparison of the proportion of compositional variation explained by two environmental factors (depth and facies) between living (LA) and death assemblages (DA) in open shelf environments (scaled by the length of the arrows), based on distance-based RDA of principal coordinates using square-root-transformed abundances. Vectors originate at the centroid of the multivariate space. The arrows point to the direction of the gradient represented by the environmental variable. They show that the segregation among the coded facies groups, as well as the direction of depth and facies gradients (representing the most rapid change in the environmental variable with respect to the first and the second CAP axis), is highly comparable between living and death assemblages. However, note that (1) although the direction of arrows in the left-right or top-down direction is arbitrary, it is fixed with respect to the position of axes, and (2) the length of the environmental vectors is fixed to be equal within living and within death assemblages (corresponding to the total proportion of compositional variation explained simultaneously by both variables). Their lengths thus can be compared between living and death assemblages.

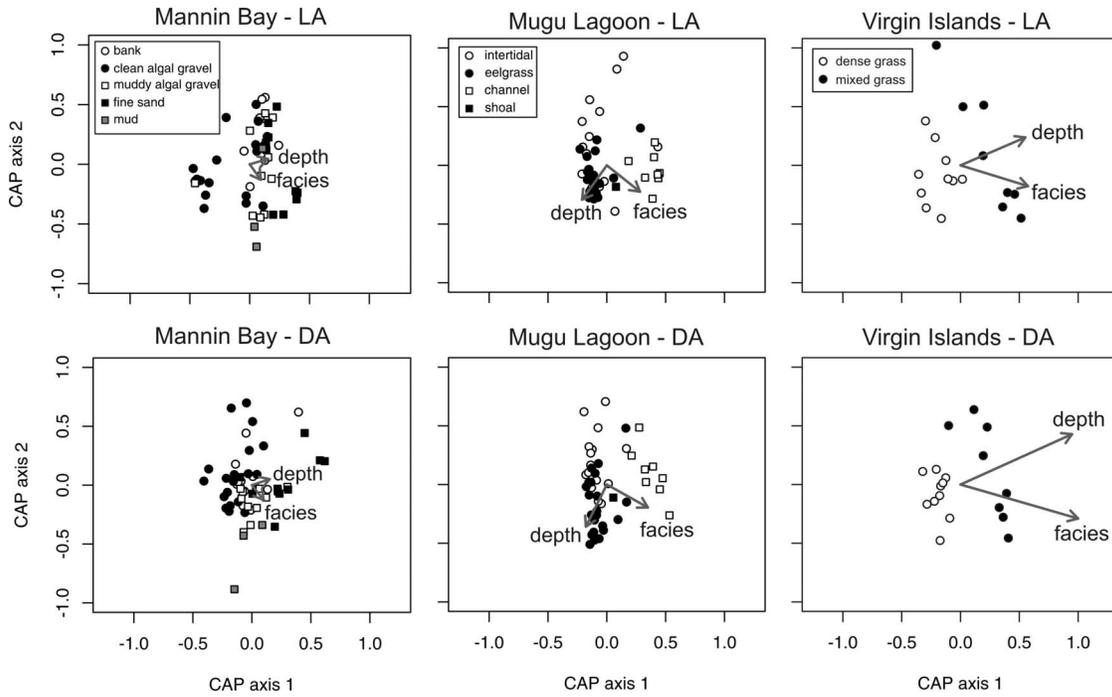


FIGURE 6. Comparison of the proportion of compositional variation explained by two environmental (depth and facies) factors (scaled by the length of the arrows) between living (LA) and death assemblages (DA) of lagoonal and bay environments, based on distance-based RDA of principal coordinates using square-root-transformed abundances. The arrows point to the direction of the gradient represented by the environmental variable. The segregation among the coded facies groups and the direction of the depth and facies gradients, representing the most rapid change in the environmental variable with respect to the first and the second CAP axis, are comparable between living and death assemblages.

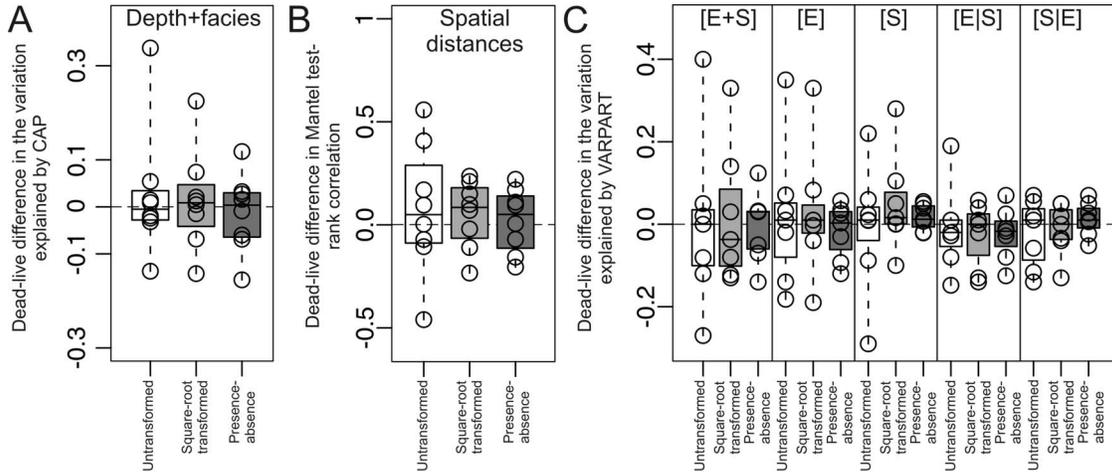


FIGURE 7. Living and death assemblages show strong agreement in the degree to which the tested factors influence community response. A, Community responses to environmental gradients measured by the proportion of variation explained by distance-based RDA of principal coordinates (CAP). B, Community responses to spatial gradients measured by Mantel tests. C, Live-dead agreement in the metacommunity structure measured by partitioning the proportion of variance into environmental and spatial components. The five different components of the variation in the community matrix are total explained variation [E + S], environmental variation [E], spatial variation [S], environmental variation without a spatial component [E|S], and spatial variation without the environmental component [S|E]. Display as in Figure 4.

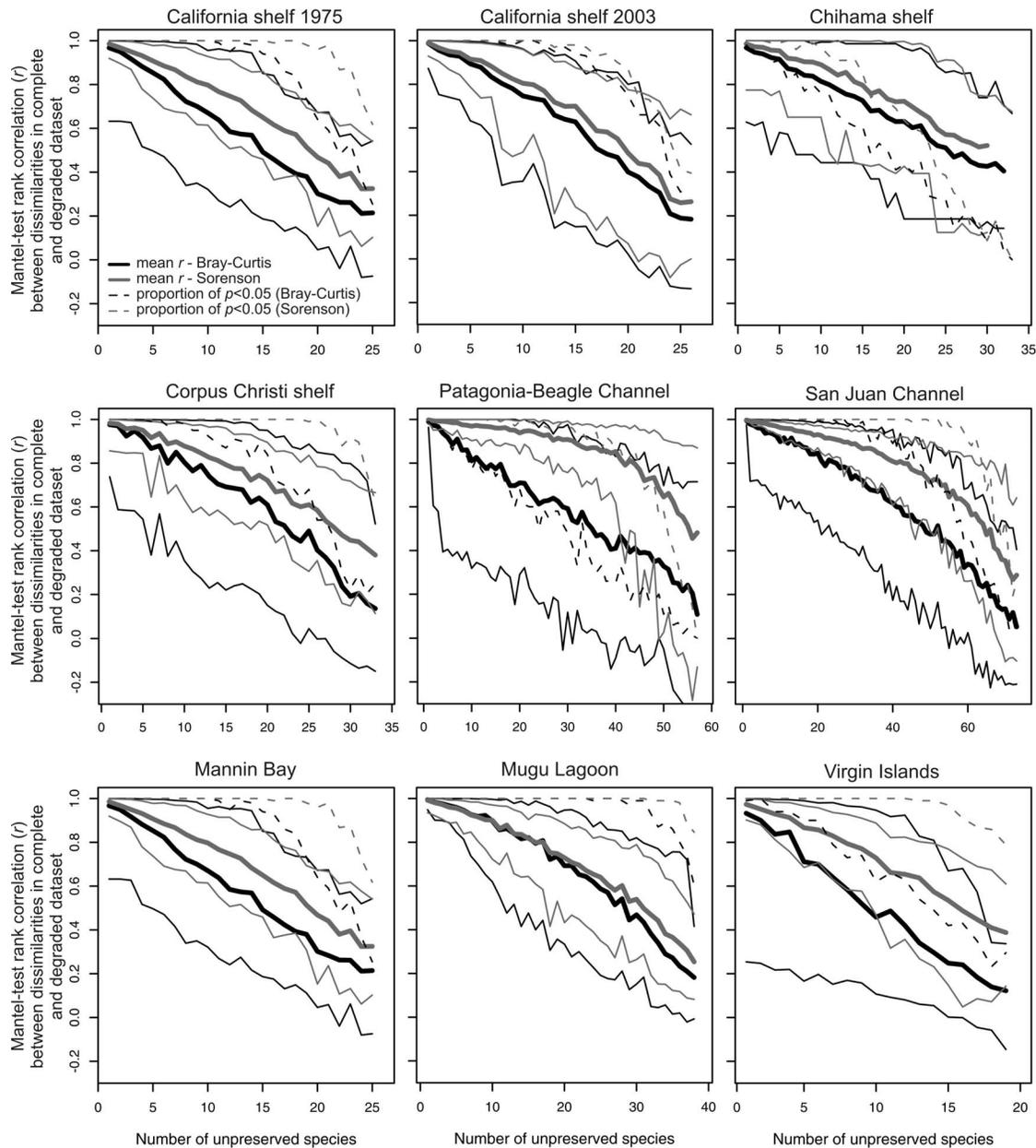


FIGURE 8. Effects of random species loss on the Mantel-test Spearman rank correlation between dissimilarities based on the full set of species and dissimilarities based on the degraded set of species in living assemblages of nine molluscan data sets. Random removal of species, without replacement, is repeated 100 times for one to the total number of species minus one. On average, a relatively high rank correlation persists and the proportion of tests with permuted  $p < 0.05$  remains fairly high even when a large proportion of species is lost. The rate of degradation is higher in BC similarity based on untransformed proportional abundances than in BC (Sorensen) similarity based on presence-absence data. Thick lines display average rank correlation (based on 100 simulations), thin lines represent 95<sup>th</sup> quantiles, and dashed lines represent the proportion of permuted  $p < 0.05$ .

dation in community structure is indeed rather slow and a large proportion of species can be removed before the community structure is lost (Fig. 8). After a given number of species

is removed, without replacement, from a data set formed by living assemblages, a Mantel-test Spearman rank correlation between original dissimilarities based on the full data set

and dissimilarities based on the degraded data set is computed, and this routine is repeated 100 times for one species up to the total number of species (Fig. 8). These simulations demonstrate that, on average, (1) the Mantel-test rank correlation in dissimilarities between the full and degraded data sets can remain quite high and significant even when a substantial number of species is lost, and (2) the proportion of tests with permuted  $p < 0.05$  remains quite high and the average rank correlations remain positive even when most of the species are removed from the data sets. Finally, the rate of degradation is higher in BC similarity based on untransformed proportional abundances than in BC (Sorenson) similarity based on presence-absence data.

### Discussion

*Responses of Living Assemblages to Environmental Gradients—Neutral or Niche Dynamics?.*—Live-dead agreement in species and community responses to environmental gradients depends not only on possible taphonomic effects—e.g., homogenization by postmortem transportation, or modification of species abundances owing to differential life spans—but on the underlying dynamics of living communities. Species responses to environmental gradients might diverge significantly between living and death assemblages even without any taphonomic and sampling biases, if, for example, the living assemblage follows neutral dynamics, whereby species are interchangeable in terms of their per capita demographic rates (e.g., Hubbell 2005; Gravel et al. 2006; Adler et al. 2007), and time-averaging is long enough to allow the mixing of several non-contemporaneous generations in the death assemblage. If on the other hand, community dynamics are mainly governed by a species-sorting model, in which species differ in niche requirements and impacts, then live-dead agreement would be expected to be generally higher, assuming an absence of taphonomic bias and absence of environmental change during time-averaging.

Our results thus support the prevailing working assumption of molluscan paleoecological analyses, namely that death assemblages are able to capture environmental gra-

dients in community composition, and that they can do this because living assemblages vary along environmental gradients owing to differences in species' niche requirements and impacts (i.e., species-sorting or mass-effect models of community assembly). The dominance of niche models is also supported by multivariate tests, which show significant effects of environmental variables on the community composition of living assemblages in all nine study areas. The dominance of species-sorting and mass-effect models in the origin of variation in community composition in living mollusk communities thus forecasts that live-dead agreement in responses of mollusk death assemblages to environmental gradients can be high in the absence of both taphonomic biases and environmental variability.

*Live-Dead Agreement in Species Responses to Environmental Gradients.*—Evaluating whether relationships between species niche positions and environmental gradients are shared by two or more independent regions with similar species pools is a test of nonrandom niche requirements (Karst et al. 2005; McGill et al. 2006; Azeria and Kolasa 2008). Extending this concept to the comparison of niche requirements between living and death assemblages corresponds to some degree, in the absence of taphonomic bias, to testing whether species possess time-invariant and unique responses to the ambient environment, i.e., whether species requirements and impacts are invariant in time or whether they changed through time on ecological time scales.

Species-sorting metacommunity models cannot be rejected in cases where this live-dead agreement is weak (because taphonomic biases can degrade agreement in responses to environmental gradients), and living and death assemblages might be also temporally autocorrelated to some degree (McGill 2003), but the presence of high live-dead agreement provides some support for niche models. The significantly positive rank correlations of species niche positions and niche breadths between living and death assemblages imply that postmortem taphonomic biases did not strongly degrade the environmental responses of species preserved in the death assemblages.

Previous estimates of agreement in species relative abundances (Kidwell 2001, 2007) were based on the Spearman rank correlation between the abundances of living and dead species pooled across two or more stations within a relatively homogeneous habitat (facies); owing to pooling, these estimates are for a coarser spatial (habitat-level) scale than the local, station-by-station comparisons evaluated here. The estimates of live-dead agreement in carrying capacities in our study, approximated by maximum abundances predicted by GAM at species niche position, are computed for sets of stations arrayed across a *series* of habitats, and thus maximum abundances (and live-dead agreement in maximum abundances) correspond to a finer, local community (patch) scale.

*Live-Dead Agreement in Community Responses to Environmental Gradients.*—Compositional separation of assemblages along depth and facies gradients—i.e., the proportion of compositional variation accounted for by environmental factors, and relationships between environmental differences and compositional dissimilarities—are quite well preserved in death assemblages. This agreement implies that environmental assessments based on fossil assemblages can be as powerful as those based on living assemblages. In some cases, death assemblages capture environmental gradients better than living assemblages, possibly because demographic and environmental stochasticity in vital rates (e.g., Lande 1993), which can blur composition of living assemblages over short durations, is homogenized in death assemblages, which capture community composition over longer temporal durations (e.g., Peterson 1976; Kowalewski et al. 1998; Olszewski 1999; Martin et al. 2002).

However, we also note that even where living assemblages do not change in composition along an environmental gradient, death assemblages might still capture that environmental gradient owing to environment-specific taphonomic processes, such as between-habitat differences in destruction rates and susceptibility to transportation (e.g., Fürsich and Flessa 1987; Powell et al. 2008). Therefore, in some cases, taphonomic biases might enhance or engender environmental signals in

death assemblages. However, in our study here, the tests of individual species responses indicate that molluscan death assemblages are capturing ecological rather than taphonomic signals. Our findings indicate that *net* taphonomic bias can be fairly constant along environmental gradients, although it is possible that some taphonomic processes accentuate community response. The apparent lack of variation in bias among facies is also consistent with previous meta-analyses, where variation in live-dead agreement with sediment grain size is either weak or zero, contrary to expectations (Kidwell 2001, 2002a, 2008; Olszewski and Kidwell 2007).

Bray-Curtis dissimilarity based on square-root-transformed species abundances generally performs better than other indices; i.e., it resolves environmental gradients more strongly than either untransformed abundances or presence-absence data, either in terms of the variation explained by environmental variables, or in terms of their significance levels. The effectiveness of square-root transformation has also been emphasized in other marine community studies (e.g., Warwick 1988; Olsgard et al. 1997), and probably reflects the degree to which it dampens the effect of numerically abundant species without filtering all abundance information from the analysis as in presence-absence transformation, which gives equal weights to abundant and rare species. On one hand, changes in untransformed abundances might be responses to fine-scale environmental gradients not captured by bathymetric and substrate differences. On the other hand, presence-absence data can reflect only rather coarse grained environmental differences. Differences between standing species abundances in living assemblages and abundances of dead individuals in death assemblages owing to differences in population turnover rates (Van Valen 1964; Kranz 1977) can also be partly alleviated by square-root transformation if highly abundant species in the death assemblage arise by short life spans, rather than by high standing abundance.

*Live-Dead Agreement in Community Responses to Spatial Gradients.*—Spatial structure in community composition can arise by population

dynamics alone (Halley 1996; Akcakaya et al. 2003; e.g., patchiness within environmentally homogeneous areas). Neutral (and patch-dynamic) models predict that when dispersal is limited, community composition will be spatially structured because compositional dissimilarity among communities is expected to increase with increasing spatial distance (e.g., Legendre et al. 2005; Tuomisto and Ruokolainen 2006; Jones et al. 2008). However, the spatial structure in community composition revealed by a Mantel test does not in itself support the neutral (or patch-dynamic) model because environmental gradients that can influence species distribution are commonly spatially structured (Bell et al. 1993; Gilbert and Lechowicz 2004). The high live-dead agreement that we find in spatial structure probably mainly reflects the high agreement in responses to environmental gradients, both because environmental gradients are in fact strongly spatially structured and because the absolute spatial extents of the study areas are mostly small compared to likely larval-dispersal capabilities.

*Live-Dead Agreement in Metacommunity Structure.*—The variation in community composition in our nine data sets is generally dominated either by a pure environmental component (species-sorting model) or by both environmental and spatial components (mass-effect model) in both living and death assemblages, thus showing the high agreement between living and death assemblages in capturing the general type of metacommunity models. Scaling effects owing to the decrease in temporal resolution of death assemblages (relative to snapshot samples of the living assemblages) might affect live-dead agreement in metacommunity structure in several different ways. First, time-averaging can be expected to enhance the signal of species and community response to *environmental* gradients because short-term stochasticity in birth, death, and immigration rates can be averaged over longer temporal scales and thus homogenized in death assemblages (Behrensmeier et al. 1979; Behrensmeier 1982; Fürsich and Aberhan 1990; Kowalewski 1996; Olszewski 1999; Kidwell 2002b; Kosnik et al. 2007). Therefore, the role of the environmental com-

ponent in driving metacommunity dynamics might be partly overestimated in the fossil record, and in turn, the role of demographic and environmental stochasticity in governing species abundances underestimated. (This scenario of course is contingent upon environmental stability over the period of time-averaging.) Second, time-averaging can be expected to reduce the signal of *spatial* structure in community composition. On one hand, the composition of the local living assemblage changes in space owing to dispersal limitation (unrelated to environmental gradients) and dispersal limitation thus leads to a spatial decrease in community similarity (Chave and Leigh 2002). On the other hand, with increasing time, community similarities among sites also change owing to stochasticity effects, and between-site variations in composition can also be mimicked by temporal changes within individual sites (McKinney and Allmon 1995). Therefore, the homogenizing effect of time-averaging can erase short-term spatial dependency among local living assemblages (but see Bennington 2003 for preservation of small-scale spatial patchiness by fossil assemblages).

Contrary to this expectation, the variance decomposition analyses show that in four of the nine data sets, species-sorting models apply in living assemblages but mass-effect models apply in death assemblages, implying a greater importance of spatial components in death assemblages. It can be argued, however, that this signal simply reflects capture by death assemblages of spatially structured environmental variables that were unmeasured, for example intensity of sediment winnowing (promoting loss via postmortem transport) or change in sediment organic content (affecting porewater saturation). Owing to some of the same ambiguities that plague its recognition in living communities (e.g., Tuomisto and Ruokolainen 2006; Jabot et al. 2008), the question of whether the metacommunity signal of the neutral model, driven by spatial or temporal autocorrelated population dynamics, can be preserved in the fossil record thus remains open.

*Factors Influencing the Capture by Death Assemblages of Species and Community Response.*—Our results constitute positive outcomes for

both working assumptions of paleoecology, namely (1) the importance of niche assembly in the living assemblages, so that species abundances vary predictably along environmental gradients, and (2) a lack of substantial degradation of those patterns by postmortem processes. These data sets were selected on the basis of sample size and lack of strong anthropogenic influence, and not for their likelihood to exhibit a particular community structure, nor for mild taphonomic conditions or low environmental variability in the study area. Study areas vary greatly in character, from rather stereotypic temperate siliciclastic shelves and bights (Corpus Christi, Mannin Bay) to high-energy straits and shorefaces (San Juan Channel, Chihama shelf), shelves affected by strong seasonal upwelling and decadal climate oscillations (wide Patagonia shelf, narrow southern California Bight), and tropical and temperate lagoons (Smugglers Bay, Mugu Lagoon).

Time-averaged death assemblages do differ significantly in composition from snapshot pictures of living assemblages at fine spatial, station-level scale—as expected if species differ in life span (rates of mortality) and durability of skeletal remains. However, in spite of this live-dead disagreement in community composition within stations, death assemblages partly preserve the *compositional ordination* that characterizes living assemblages (as revealed by positive rank correlations of the first PCO axis between living and death assemblages) and capture *environmental and spatial gradients* (as revealed by distance-based RDA of principal coordinates and other tests). Although the equal community responses of living and death assemblages to gradients do not need to be based on the same species associations, the good agreement in individual species responses indicates that the same species underlie the community response of living and death assemblages to environmental and spatial gradients.

Nine data sets of course represent a limited basis for uncovering the mechanisms that permit death assemblages to capture gradients. The finding that, for example, only ~50% of death assemblages return a correct compositional ordination can be discouraging but can

be affected by the use of one ordination axis only—when we explore pairwise compositional dissimilarities (which underlie ordinations and preserve the complete information about community structure), we find that ~70% of death assemblages show a significant rank correlation in dissimilarities between living and death assemblages (Tomašových and Kidwell 2009). Inspection suggests that the preservation of gradients is not favored by any particular methodology (e.g., mesh size, sample size, number of stations) or environmental circumstances (number of facies, shelf versus estuary, protection versus exposure to water energy). The causes of failure—and thus protocols for identifying the most reliable death assemblages—will be resolved only by acquiring station-level taphofacies data (e.g., are those data sets with poor fidelity affected by higher or more differential destruction, or are their constituent species characterized by especially heterogeneous durability?).

We suggest that the preservation of compositional ordinations and environment gradients can be partly related to structural redundancy in community structure that is inherently associated with multispecies assemblages (e.g., owing to multiple overlapping species distributions in species-rich communities, and/or owing to partly nested species responses to environmental gradients). This redundancy is revealed by the presence of more than one mutually exclusive subset of species that significantly capture compositional dissimilarities based on the full set of species; between-sample relationships can be preserved and remain significant even when a large proportion of species is randomly removed from the molluscan data sets (Fig. 8). Therefore, preservation of all species is not required to capture an environmental gradient.

### Conclusions

This analysis of nine molluscan data sets from modern coastal regions reaches positive outcomes for two key working assumptions of paleoecology:

1. The presence of niche differences among molluscan species in living communities. Species abundances do vary significantly along environmental gradients, with living com-

munities generally behaving according to the species-sorting and mass-effect metacommunity models, rather than being dominated by dispersal limitation and demographic and environmental stochasticity. This is the first study to partition environmental and spatial components and to evaluate metacommunity structure in subtidal benthic communities.

2. A lack of substantial loss or degradation of these patterns by postmortem processes. Death assemblages identify the dominance of non-neutral models in mollusk communities, as do living assemblages. Species niche positions along bathymetric and facies gradients in death assemblages are mostly significantly positively rank-correlated to species positions in living assemblages. Community responses to depth and facies gradients are similarly captured by living and death assemblages. Finally, death assemblages have a preservation potential of spatial gradients that is equal to that of living assemblages, or they show higher spatial structure. Although it is possible that some environment-specific taphonomic processes accentuate the community response of death assemblages to environmental gradients, the relatively high fidelity of individual species responses to depth and facies gradients suggests that primarily ecological signals are preserved by molluscan death assemblages.

This analysis of the environmental resolution of death assemblages thus provides a first-order approximation of the reliability of niche analyses in paleoecological analyses, and justifies fine-scale niche and paleoenvironmental analyses of the marine molluscan fossil record. Taxonomic dissimilarity tests reveal that death assemblages do differ significantly in composition from living assemblages, as expected from taphonomic processes and the inherent limits of comparing time-averaged death assemblages with non-averaged data for living assemblages. However, we suggest that the preservation potential of environmental and spatial structure by these death assemblages, despite these compositional differences, can be partly enhanced by some structural redundancy in composition of multispecies assemblages. Models simulating random species loss in nine molluscan data

sets show that between-sample relationships can be preserved and remain significant even when a large proportion of species is randomly removed from data sets.

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