

Paleobiology

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Abstract.—Paleoecological analyses that test for spatial or temporal variation in diversity must consider not only sampling and preservation bias, but also the effects of temporal scale (i.e., time-averaging). The species-time relationship (STR) describes how species diversity increases with the elapsed time of observation, but its consequences for assessing the effects of time-averaging on diversity of fossil assemblages remain poorly explored. Here, we use a neutral, dispersal-limited model of metacommunity dynamics, with parameters estimated from living assemblages of 31 molluscan data sets, to model the effects of within-habitat time-averaging on the mean composition and multivariate dispersion of assemblages, on diversity at point (single station) and habitat scales (pooled multiple stations), and on beta diversity. We hold sample size constant in STRs to isolate the effects of time-averaging from sampling effects. With increasing within-habitat time-averaging, stochastic switching in the identity of species in living (dispersal-limited) assemblages (1) decreases the proportional abundance of abundant species, reducing the steepness of the rank-abundance distribution, and (2) increases the proportional richness of rare, temporally short-lived species that immigrate from the neutral metacommunity with many rare species. These two effects together (1) can shift the mean composition away from the non-averaged (dispersal-limited) assemblages toward averaged assemblages that are less limited by dispersal, resembling that of the metacommunity; (2) allow the point and habitat diversity to increase toward metacommunity diversity under a given sample size (i.e., the diversity in averaged assemblages is inflated relative to non-averaged assemblages); and (3) reduce beta diversity because species unique to individual stations become shared by other stations when limited by a larger but static species pool. Surprisingly, these scale-dependent changes occur at fixed sample sizes and can become significant after only a few decades or centuries of time-averaging, and are accomplished *without* invoking ecological succession, environmental changes, or selective postmortem preservation. Time-averaging results in less inflation of diversity at habitat than at point scales; paleoecological studies should thus analyze data at multiple spatial scales, including that of the habitat where multiple bulk samples have been pooled in order to minimize time-averaging effects. The diversity of assemblages that have accumulated over 1000 years at point and habitat scales is expected to be inflated by an average of 2.1 and 1.6, respectively. This degree of inflation is slightly higher than that *observed* in molluscan death assemblages at these same spatial scales (1.8 and 1.3). Thus, neutral metacommunity models provide useful quantitative constraints on directional but predictable effects of time-averaging. They provide minimal estimates for the rate of increase in diversity with time-averaging because they assume no change in environmental conditions and in the composition of the metacommunity within the window of averaging.

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Accepted: 27 January 2010

Introduction

To what extent can compositional or diversity differences among communities arise from differences in time-averaging alone? Time-averaging, i.e., the accumulation of skeletal remains from multiple non-contemporaneous generations into a single assemblage, is a general scaling phenomenon affecting fossil assemblages because burial rates are mostly slower than the turnover

rates of producers (Johnson 1960; Fürsich 1978; Behrensmeyer 1982; Fürsich and Aberhan 1990; Behrensmeyer and Hook 1992; Bennington and Bambach 1996; Kowalewski et al. 1998). The decrease in temporal resolution imposed by time-averaging means that the assemblage encompasses both (1) fluctuations in the abundances of species that died over the duration of time-averaging, pooling them into one sampling unit, and (2) a longer

history that can include change in environmental conditions and in the composition of the regional species pool, mixing species that did not co-occur alive (e.g., Fürsich and Kaufmann 1984). Time-averaging also affects two other components of temporal scale in that it increases the total temporal extent and decreases the temporal separation among assemblages (e.g., discussions of scale in Allen and Star 1982; Allen and Hoekstra 1992; Palmer and White 1994; Bengtsson et al. 2002). Time-averaging almost certainly varies among fossil assemblages in different settings owing to systematic differences in net sedimentation rates, bioturbation rates, and skeletal destruction rates (Thayer 1983; Sepkoski et al. 1991; Kidwell and Bosence 1991; Kidwell and Brenchley 1994; Holland and Patzkowsky 1999; Hendy and Kamp 2004; Tomašových 2006; Finnegan and Droser 2008; see Kidwell 1997 for review). Consequently, the effects of time-averaging on diversity need to be distinguished from diversity differences that arise from spatial or temporal variation in ecological mechanisms (for studies attempting to discriminate these effects, see Staff et al. 1986; Bush and Bambach 2004; Scarponi and Kowalewski 2007).

Mechanisms that affect species diversity are known to change with increasing temporal as well as spatial scale in present-day communities (Sale 1998; Storch and Gaston 2004; Gray et al. 2005; Harte et al. 2005; Pech et al. 2007; Dornelas and Connolly 2008; Zillio and He 2010), and so the increase in temporal scale that occurs with time-averaging has potential to modify the composition and diversity of *fossil* assemblages. For example, Miller and Cummins (1993) found that time-averaging increases diversity at a higher rate in communities with clumped individuals than in communities with randomly distributed individuals. The species-time relationship (STR) observed in modern systems describes how richness increases with the time span over which the assemblage is sampled: just as sampled diversity increases as the area sampled increases, so does diversity increase with the elapsed time of observation (Preston 1960). The effects of time-averaging on fossil diversity are thus

analogous to moving up and down along the slope of an STR (Staff and Powell 1988; Rosenzweig 1998).

Here, we explore the consequences of time-averaging on diversity and other community attributes by using STRs while holding sample size constant, in contrast to standard STRs where the effects of growing assemblage size are coupled with the effects arising from ecological mechanisms (Preston 1960). To simulate the effects of time, we adopt individual-based neutral but spatially implicit community models that incorporate sampling and natural stochastic variation in birth, death, migration, and sampling rates (Durrett and Levin 1996; Bell 2000; Hubbell 2001; Borda-de-Água et al. 2002), allowing these to play out over intervals up to 1000 years. We focus on modeling the community dynamics within single habitats, and thus adopt the neutral assumption that species are equal in their per capita response to environment. First, we use the neutral model to estimate the effects of increasing time-averaging on the mean composition of assemblages and their dispersion in multivariate space, using a database of modern benthic marine samples of living communities to estimate parameters. Second, we model the change in sampled diversity at point (single station in a modern environment, or single bulk sample in a paleoecological analysis) and habitat scales (data pooled from multiple stations within a single habitat) as well as the change in beta diversity (among-station differences) and the change in rank-abundance distributions (RADs). In a companion study, we use a similar approach to test for the effects of time-averaging on *temporal* variation in species composition (Tomašových and Kidwell 2010). Although postmortem destruction and transportation rates can be incorporated into models of fossil preservation (e.g., Miller and Cummins 1990; Cutler 1993; Olszewski 2004), we think that within-habitat time-averaging constitutes the first-order mechanism determining the nature of death assemblages in most environments, and can be generalized across community types and environments (Behrensmeyer and Chapman 1993; Miller and Cummins 1993).

Quantitative models that predict the change in diversity with increasing temporal scale are needed to (1) determine whether differences in diversity patterns can be produced by time-averaging alone or whether they remain scale-invariant (Harte and Kinzig 1997; Sizling et al. 2009), (2) evaluate whether the effects of temporal scaling are directional or simply add noise to the outcomes of paleoecological analyses (e.g., Miller and Cummins 1993; McGill 2003; McGill et al. 2005), and (3) rescale composition and diversity between averaged and non-averaged assemblages. Peterson (1976, 1977) anticipated the effect of time on diversity of time-averaged assemblages by comparing single averaged (death) assemblages to the accumulation of multiple consecutive non-averaged (living) assemblages. A *directional* effect of temporal scale on the composition and diversity of fossil assemblages is implied by systematic differences observed between molluscan time-averaged death assemblages and non-averaged snapshot samples of living assemblages. First, alpha diversity of time-averaged death assemblages at habitat scales commonly exceeds that of counterpart living assemblages (Kidwell 2001, 2002; Lockwood and Chastant 2006; Olszewski and Kidwell 2007; for foraminiferal examples, see Murray 2003; Horton and Murray 2006). Second, time-averaged death assemblages do have lower beta diversity; i.e., they show less habitat-to-habitat differences in composition within a region than do living assemblages (Tomašových and Kidwell 2009). Such differences can be expected to occur when death assemblages are characterized by higher sample sizes, but theory-driven explanations for such differences at *fixed* sample sizes are lacking.

Methods and Analyses

Approach to Scaling.—From the accumulation of individuals that died over an increasing time span and their subsequent sampling, modeling studies can predict the change in diversity with increasing time-averaging—that is, how diversity scales with time. Such accumulation is equivalent to STRs that describe community changes with increasing time span of sampling *and* with increasing

numbers of sampled individuals (Preston 1960; Rosenzweig 1998; McKinney and Frederick 1999; Adler and Lauenroth 2003; Adler et al. 2005; White et al. 2006). Although it is also possible that sample sizes are equal even when time-averaging differs (e.g., Olszewski 2004), a first-order assumption is that the raw numbers of dead individuals tend to increase with the degree of time-averaging.

To determine if elapsed time has any effect on diversity other than those arising from increasing sample size in standard STRs, Coleman curves have been used to predict diversity for increasingly larger durations of elapsed time under random sampling of a static species pool (Coleman 1981; Coleman et al. 1982; White 2004). Diversity increases because, in the *absence* of dispersal limitation, the probability of sampling individuals of rare species from the regional metacommunity increases (White 2004, 2007; McGlenn and Palmer 2009). This procedure yields diversities equivalent to those predicted by rarefaction (Brewer and Williamson 1994). Therefore, rarefaction can be adequate for rescaling assemblages that differ in the degree of time-averaging.

However, such random sampling models rarely fully explain STRs in ecological time series (White 2004; White et al. 2006). Second-order approximations that account for the effects of ecological mechanisms are thus needed to describe changes in diversity with increasing time-averaging. Two-phase STR models and other approaches can separate sampling (statistical) effects from ecological mechanisms (White 2004; Fridley et al. 2006; McGlenn and Palmer 2009). Here, however, we evaluate the effects of time-averaging on diversity at a fixed sample size in terms of numbers of individuals because (1) marine fossil assemblages can rarely be standardized to an equal original seafloor surface area owing to the net effect of population turnover rates, sedimentation rates, mixing rates, and rates of preservation; (2) sample size differences among fossil assemblages can arise from sampling procedures that are unrelated to time-averaging; and (3) the increase in diversity produced by time-averaging under a fixed sample size ultimately corresponds to

effects *unrelated* to sampling. This last point allows us to identify the ecological component of temporal species turnover.

Several species-area, species-time, and occupancy-area models have been proposed (Williamson et al. 2001; He et al. 2002; Tjørve 2005; He and Condit 2007; Dengler 2009), but their parameters depend on sampling design, spatial resolution, intersample distance, and survey extents, as well as on the species pool structure and several other assumptions (Carey et al. 2007). Here, we use exponential and power models that fit STRs well (White et al. 2006). The ability of exponential models to capture this change in diversity is evaluated with linear regression on log-transformed time-span data ($S = b + a \log T$) and for power models with nonlinear regression on untransformed data ($S = bT^a$) (Loehle 1990; Dengler 2009), where S is species diversity (or other community attribute), T is duration of time-averaging, and b and a are fitted parameters. In the exponential model, a is a fitted linear slope. In the power model, a is a fitted exponent so that slope increases as time-averaging increases. The goodness-of-fit is assessed with R^2 adjusted by the number of degrees of freedom.

Assemblage Composition and Diversity.—The taxonomic composition of a set of local assemblages can be summarized by two components: centroid location (mean composition of multiple local assemblages) and dispersion of assemblages (dissimilarity among local assemblages and their centroid) in multivariate space defined by species abundances in local assemblages, i.e., in Euclidean space represented by principal coordinates (Anderson et al. 2006). Dispersion among assemblages is a dissimilarity-based measure of beta diversity that is monotonically related to beta diversity based on partitioning of regional diversity (Jost 2007; Gaston et al. 2007). Rate of change in mean assemblage composition is measured as the change in the dissimilarity between centroids of non-averaged (i.e., species composition represented by the smallest (1-year) time span) and averaged assemblages. Rate of change in dispersion is measured by change in dispersion among increasingly averaged

assemblages. In other words, this is one way of measuring how beta diversity among a set of local assemblages changes as time-averaging increases. The significance of the change in dispersion is assessed with a test for homogeneity of multivariate dispersions (Anderson 2006; Anderson et al. 2006).

Between-centroid dissimilarity and dispersion among assemblages are evaluated with two metrics. The Jaccard dissimilarity, based on presence-absence data, is related to the probability that two randomly chosen species from two assemblages do not belong to any of the species shared by the two assemblages (Koleff et al. 2003). The Horn-Morisita dissimilarity, based on proportional abundance data, is related to the probability that two randomly drawn *individuals* from two assemblages do not belong to the same species, relative to the probability of randomly drawing two individuals of the same species from one or another assemblage alone (Horn 1966). Comparisons of non-averaged with averaged assemblages are size-standardized here because differences in species richness arising from differences in numbers of individuals can magnify differences in composition among assemblages (Lande 1996; Chao et al. 2005).

We use three orders of diversity measures that differ in their sensitivity to abundant and rare species (Hill 1973; Jost 2006). *Species richness* (diversity of order zero; i.e., only species' presence is used) is disproportionately sensitive to rare species in characterizing diversity; the *Shannon entropy* (diversity index of order one) is equally sensitive to abundant and rare species because species are weighted by their proportional abundance; and the *Gini-Simpson index* (diversity index of order two) is disproportionately sensitive to the most abundant species. To express the diversity values generated by the Shannon entropy and the Gini-Simpson index in terms comparable to species richness (their effective number of species), these diversity indices are transformed into *numbers equivalents* defined as the exponential of Shannon entropy and as $1/(1-\text{Gini-Simpson index})$ (Jost 2007). In contrast to untransformed diversity indices, (1) numbers equivalents put diversity of differ-

ent orders to the same measurement scale; (2) numbers equivalents are characterized by the doubling property, i.e., combining two equally large communities that do not share any species doubles the diversity (Hill 1973); and (3) ratios of the numbers equivalents have reasonable mathematical behavior that does not suffer from the false inflation characterizing raw indices (Jost 2006). We also partition the *habitat* diversity of each data set (multiple stations pooled) into independent *point* alpha (within sampling stations) and beta components (among stations), again using numbers equivalents.

Here, the ratio in the effective species richness (i.e., the ratio in the numbers equivalents) between averaged and non-averaged assemblages defines the inflation factor by which the *sampled* diversity is increased (or diminished) by time-averaging. We explore changes in the dominance structure at point and habitat scales using the Gini-Simpson index and changes in the proportion of rare species using the number of species represented by singletons and doubletons, both under a fixed sample size. To compare changes in shapes of RADs between non-averaged and averaged assemblages, we evaluate 12 data sets where the mean size of the living assemblages exceeds 75 individuals (see Supplement Table 1 in the online supplementary information at <http://dx.doi.org/10.1666/08092.s1>).

Simulations of Within-Habitat Time-Averaging

We model dispersal-limited metacommunity dynamics using an island-mainland structure, where several semi-isolated local assemblages are surrounded by a very large and static panmictic species pool (metacommunity) that acts as a source of immigrants and its abundance structure is at speciation-extinction equilibrium (Hubbell 2001; Volkov et al. 2003; Holyoak et al. 2005). Semi-isolated local assemblages that receive immigrants from other local assemblages rather than from a large and common species pool represent an alternative model of metacommunity that can characterize systems with strong dispersal limitation (Volkov et al. 2007). Here, meta-

community dynamics refers to species immigration rates from the panmictic species pool (metacommunity) to multiple sites, the multispecies interactions that govern recruitment and extinction rates at local scales, and the properties of the neutral (logseries-like) metacommunity determined by speciation-extinction at large spatial scales (Hubbell 2001). We use neutral individual-based simulations that model changes in the abundance of species that are characterized by equal per capita birth, death, and immigration rates and lead to a steady-state rank-abundance distribution (RAD) in non-averaged (living) assemblages. The size of local living assemblages remains in steady state in time (i.e., zero-sum dynamics). The immigration rates of species that are abundant in the metacommunity exceed the immigration rates of rare species. The difference between local non-averaged assemblages and the metacommunity tends to increase as dispersal limitation increases (Lande 1993; Hubbell 2001): a stochastic random walk in assemblage composition is less constrained by immigration from the metacommunity, and is instead more affected by demographic stochasticity in local birth and death rates. Neutral models have already been used to predict how diversity scales with increasing spatial scale (Borda-de-Água et al. 2002, 2007).

Neutral metacommunity dynamics predict sampling and natural variability in species composition on the basis of: (1) local assemblage (sample) size (J), here represented by the average density of individuals in the living assemblage collected at the roughly meter-scale spatial resolution of one station; (2) the biodiversity number (θ); and (3) the dispersal number (I) (Hubbell 2001; Etienne and Olff 2004a; He and Hu 2005). Both the biodiversity number (a dimensionless measure of metacommunity abundance structure and metacommunity diversity) and the dispersal number (a measure of dispersal limitation defined as the effective number of immigrants that compete with the $J - 1$ individuals when one spot in the local assemblages becomes free [Etienne and Olff 2004a,b]) are estimated by maximum-likelihood methods from the species-abundance

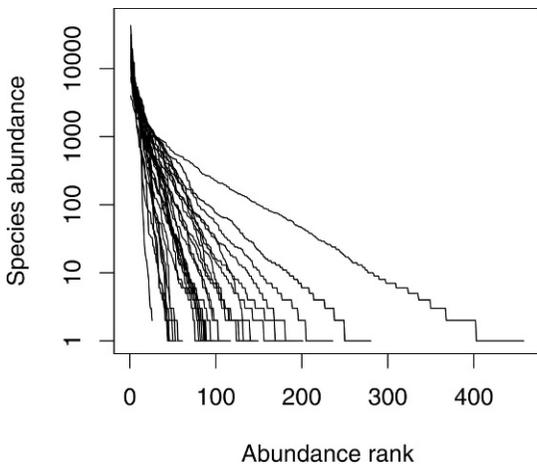


FIGURE 1. Rank-abundance distributions (RADs) of 31 molluscan metacommunities, modeled using Etienne's (2005) species generator algorithm that simulates metacommunity structures for a given fundamental biodiversity number θ estimated from species-abundance distributions of multiple living assemblages, and metacommunity size = 100,000 individuals. The raw abundance of a species (log scale) is displayed against its ranked abundance. These RADs vary from steep and straight lines (low θ) to J-shaped curves (high θ) where many rare species are encountered.

distributions of multiple living assemblages based on the genealogical approach that traces immigrating ancestors to all individuals in local assemblages (Etienne and Olff 2004a). The per capita immigration rate m is related to the dispersal number I as $m = I/(I + J - 1)$. These assemblages occupy the same habitat and are linked to the metacommunity with the same dispersal (Etienne 2007; see Etienne 2009 for another sampling formula for multiple samples that relaxes the condition of equal dispersal limitation). To find the expected *metacommunity* RADs for 31 data sets, we adopt Etienne's (2005) species-generator algorithm that simulates metacommunity structures for a given Jm and θ . We arbitrarily use 100,000 individuals for Jm , which is otherwise unknown. Modeled metacommunities have logseries-like species-abundance distributions (i.e., the abundance classes with rare species have the most species). They range from steep and straight geometric-like RADs (data sets with low θ) to less steep J-shaped RADs with an excess of rare species (data sets with larger θ) (Fig. 1). For calculating population turnover rates, we assume a life span of three years, which is the mode of

marine molluscan life spans as compiled by Powell and Cummins (1985).

The number of stations simulated per habitat corresponds to the number of stations in each data set. Depending on the probability of immigration, random mortality events are followed either by self-recruitment from the local assemblage or by immigration from the metacommunity (Hubbell 2001; Chave et al. 2002; Etienne and Alonso 2006). The probability of immigration m is $I/I + J$, and the probability of self-recruitment b is $1 - m$. This approach is comparable to simulation of time-averaging by McGill (2003). However, after living assemblages attain steady-state local diversity, *individuals* are uniformly sampled from the pool of individuals that died over the period of time-averaging, until the count equals the mean sample size of non-averaged assemblages. Numbers of individuals per species are calculated for seven intervals of time-averaging (5, 25, 50, 100, 200, 500, and 1000 years). This range of averaging corresponds to the durations documented in molluscan death assemblages from in marine environments (Flessa et al. 1993; Flessa and Kowalewski 1994; Meldahl et al. 1997; Kidwell et al. 2005; Kosnik et al. 2007). The change in dissimilarity between the centroid locations of consecutive groups of living assemblages as a function of elapsed time (here, over 1000 years) is used to measure the rate of temporal change in the composition of living assemblages (e.g., Collins et al. 2000; Collins 2000). Changes in centroid location, dispersion, and sampled diversity are averaged over 1000 simulations. All analyses were performed using the R language (R Development Core Team 2009). The source code for the simulations is available in Supplement 2 online at <http://dx.doi.org/10.1666/08092.s2>.

Parameters and Data Sets

The parameter space for modeling is large: it is defined by the RAD and the size of the metacommunity, by dispersal limitation between the metacommunity and the local assemblage, by the number of individuals in local assemblages, by the number of local assemblages, and by population turnover rates (e.g., McGlenn and Palmer 2009). Rather

than exploring all possible combinations, we model the effects of time-averaging using the *living* assemblages of 31 empirical marine molluscan data sets as a source of parameter values (Supplement Table 1). Each data set reflects sampling at a single moment of time at more than four different places (spatially replicate stations) within a single habitat characterized by constant sediment type and water depth (the sources of 27 data sets are available in supplementary information at <http://dx.doi.org/10.1666/08092.s1>; four data sets from the Southern California Bight are available in Data Dryad, <hdl.handle.net/10255/dryad.1225>). The spatial resolution of individual stations in our data sets is mostly between 0.1 and 1 m², with a mean $J = 91$ living individuals per station). The mean number of sampled assemblages per habitat is eight (min = 4 stations; mean $J = 664$ living individuals per habitat), which generally corresponds to an order-of magnitude decrease in spatial resolution, and to a several-fold increase in spatial extent because distances between stations range from 10 m to several kilometers. Neutral models do not possess stabilizing mechanisms that would ensure temporal constancy in assemblage composition and thus change at a higher rate than is predicted in models with intraspecific density dependence or life-history trade-offs (Chave et al. 2002; Tilman 2004; Volkov et al. 2007). A high proportion of molluscan data sets sampled in relatively homogeneous environments show spatial variation in composition that is comparable to or only slightly different from that predicted by neutral models (Supplement Fig. 1, <http://dx.doi.org/10.1666/08092.s1>).

All 31 data sets are from subtidal soft-sediment habitats that were relatively undisturbed by human activities at the time of sampling, but that reflect a range of grain sizes (muds to gravels and sea grass), climates (tropical to cool temperate), and settings (tidal lagoons, well-mixed estuaries, protected coastal bights, back-reef shelves, high-energy straits, and open continental shelves [see Supplement 1]). For comparison with modeled results from *living* assemblages, we note

that these data sets show systematic differences in diversity between living (non-averaged) and death (time-averaged) assemblages (Fig. 2). First, living (non-averaged) assemblages are characterized by significantly higher dispersion in species composition (Fig. 2A) and higher beta diversity within habitats (Fig. 2B) than are death assemblages. A decrease in dispersion and beta diversity from living assemblages to death assemblages is also evident among multiple habitats within a region (Tomašových and Kidwell 2009). Second, species diversity is consistently higher in death (time-averaged) assemblages at both point and habitat scales (Fig. 2B), and the inflation in diversity at local scales in death assemblages is larger than the inflation in diversity at habitat scales (Fig. 2B).

Results

Change in Mean Assemblage Composition.—The change in dissimilarity between centroids of non-averaged and increasingly averaged assemblages is expected to be zero in the absence of directional changes in mean assemblage composition. Between-centroid Jaccard dissimilarity in fact increases (mean slope = 0.015 in exponential model), and changes by ~25% under time-averaging of 1000 years (Fig. 3A). Between-centroid Horn-Morisita dissimilarity remains more or less constant (Fig. 3B). However, the centroid location of the averaged assemblages remains within the multivariate space defined by non-averaged assemblages because between-centroid dissimilarity does not exceed the dissimilarity among non-averaged assemblages (Fig. 3C,D). The change in centroid location is equally approximated by the exponential model and the power model (Table 1).

Change in Dispersion.—The average dissimilarity between assemblages and their centroid (i.e., dispersion or spatial variation in species composition) is consistently reduced with increasing time-averaging, and this reduction can become significant after several decades or centuries (Fig. 4). After 1000 years, dispersion among averaged assemblages is reduced by 20% using Jaccard dissimilarity and by 45% using Horn-Morisita dissimilarity: dispersion based on abundance indices is

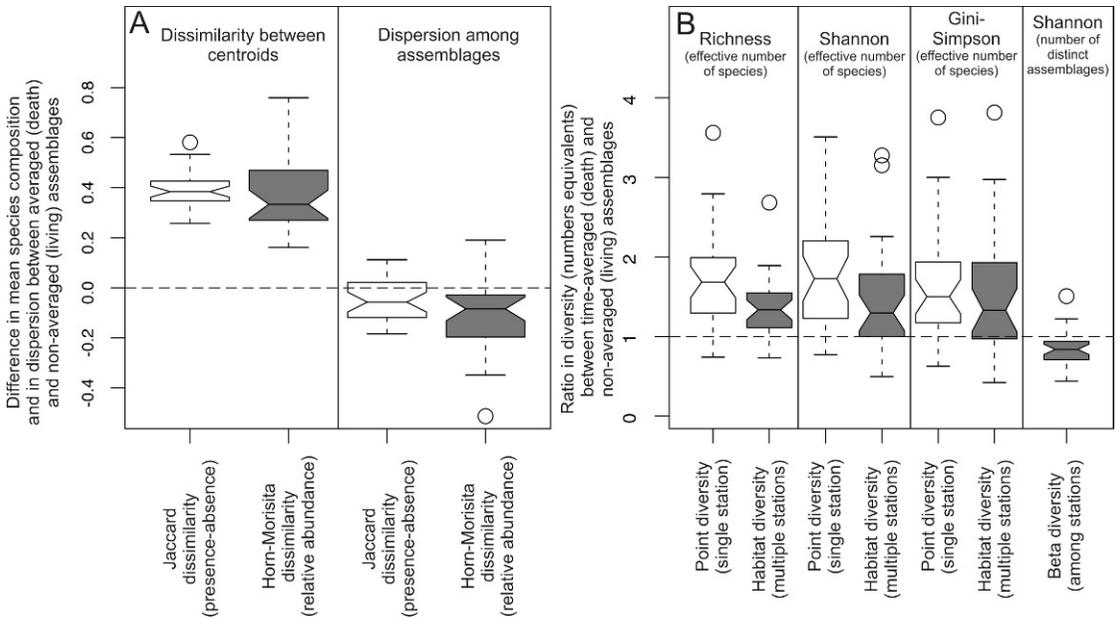


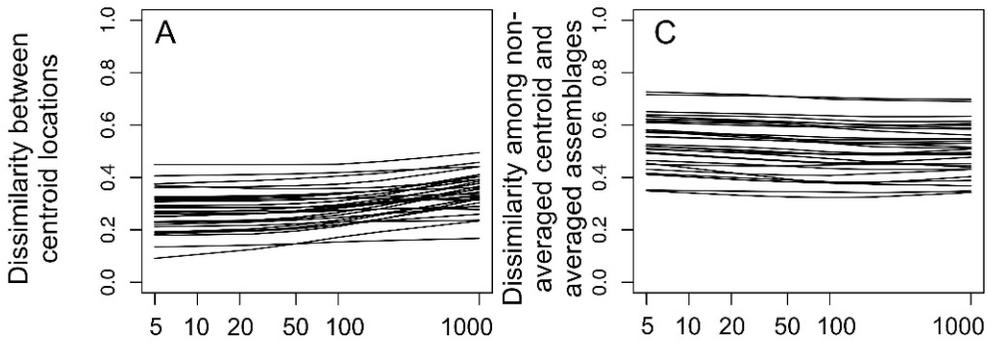
FIGURE 2. Observed differences between non-averaged (living) and averaged (death) assemblages for 31 molluscan data sets. A, The mean composition of death assemblages differs significantly from that of counterpart living assemblages, and dispersion among death assemblages is smaller than among living assemblages, using both presence-absence (Jaccard) and relative abundance (Horn-Morisita) measures of dissimilarity. B, Death assemblages are more diverse than living assemblages at both local and habitat spatial scales, and are more similar in composition within a habitat (beta diversity). Point and habitat diversities are expressed in terms of the effective number of species and beta diversity in terms of the number of distinct communities (Hill 1973). Sample sizes between individual pairs of living and death assemblages were equalized by resampling without replacement before comparing their diversities. Beta diversity is estimated with Shannon entropy because this index can be partitioned into independent alpha and beta components when the sizes of assemblages are unequal (Jost 2007). Boxplots denote medians and the 25 and 75 quartiles, notches mark the approximate 95% confidence intervals on the median (on the basis of the function `boxplot.stats()` in `grDevices` package, R Development Core Team 2007), whiskers denote values that are 1.5 times the interquartile range, and white circles mark extreme values.

reduced at a higher rate than is dispersion based on presence-absence indices (Table 1, Fig. 4). Coefficients of determination in the exponential model (mean $R^2 = 0.88$ using Jaccard dissimilarity and $R^2 = 0.84$ using Horn-Morisita dissimilarity) are slightly larger than in the power model (mean $R^2 = 0.84$ and 0.78). The change in assemblage dispersion with time-averaging can thus be approximated by the exponential model ($D = b + a \log T$), where D is the average dissimilarity between assemblages and their centroid, T is the duration of time-averaging, b is the dispersion among non-averaged assemblages, and a is the fitted scaling slope.

Change in Diversity.—Even with a fixed sample size, diversity increases with time-averaging for all measures (columns in Fig. 5). The change in sampled diversity is better approximated by power models at

point scales but the support for power and exponential models becomes similar at habitat scales, and the change in beta diversity is better explained by exponential models (Table 1). The slopes remain curvilinear in semi-log and log-log plots (Fig. 5). Point and habitat diversity expressed in terms of effective number of species increases more rapidly using species richness than using Gini-Simpson index (Table 1). The mean power-function exponent of sampled richness for diversities of three orders at *point* sampling scales is 0.14–0.17 (Table 1, Fig. 6A), but variation among exponents is relatively high. Sampled *habitat* diversity increases more slowly than point diversity (mean exponent = 0.05–0.08; Table 1, Fig. 6B). Sampled beta diversity expressed in terms of number of distinct assemblages decreases consistently with increasing time-averaging, matching the expect-

Jaccard dissimilarity (presence-absence)



Horn-Morisita dissimilarity (relative abundances)

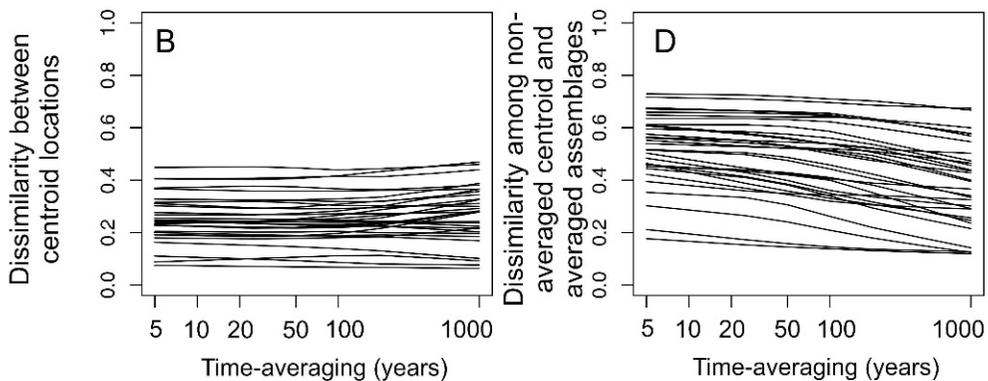


FIGURE 3. Effects of time-averaging on mean assemblage composition (expressed by dissimilarity between the centroids of non-averaged and averaged assemblages) defined by presence-absence data (Jaccard) and proportional abundances (Horn-Morisita). The centroid location drifts away from the initial (non-averaged) location when using presence-absence data because of their sensitivity to the accumulation of new (rare) species (A). In contrast, the location of the centroid is relatively unaffected using proportional abundances (B). However, the locations of individual averaged assemblages remain within the multivariate cloud defined by non-averaged assemblages: the average distance between the centroid of non-averaged assemblages and the individual locations of averaged assemblages remains static or is reduced (C, D).

ed reduction in dispersion among assemblages (average exponent = 0.05–0.08, average reduction after 1000 years = 0.62–0.76; Fig. 6C). After 1000 years of time-averaging, the average inflation factor is 2.1 (SD = 0.55) for sampled point richness and 1.6 (SD = 0.29) for sampled habitat richness, with a wide spread from 1 to ~3, and similar inflation factors characterize Shannon entropy and Gini-Simpson index (Fig. 7). The power function exponents for diversity changes are thus variable but their range can still provide potential boundary conditions for data sets with unknown degrees of time-averaging.

The rates of increase in sampled richness at point and habitat scales and the rate of decrease in sampled beta richness correlate

positively with the rate of change in mean composition of non-averaged (living) assemblages on the basis of both Jaccard dissimilarity (Spearman r [point] = 0.95, $p < 0.0001$; Spearman r [habitat] = 0.86, $p < 0.0001$; Spearman r [beta] = 0.81, $p < 0.0001$) and Horn-Morisita dissimilarity (Spearman r [point] = 0.93, $p < 0.0001$; Spearman r [habitat] = 0.89, $p < 0.0001$; Spearman r [beta] = 0.73, $p < 0.0001$). However, all of these rates of diversity change also correlate positively with metacommunity structure as described by the Gini-Simpson index (Spearman r [point] = 0.59, $p = 0.0005$; Spearman r [habitat] = 0.6, $p = 0.0004$, Spearman r [beta] = 0.39, $p = 0.03$). To conclude, the change in diversity with time-averaging is steeper when

TABLE 1. Average coefficients of determination and average slopes and exponents of exponential and power functions for between-centroid dissimilarity, dispersion among assemblages, and three levels of diversity for the exponential and power models.

	Power function (R^2)	Power function - mean exponent	Power function - standard deviation of exponent	Exponential function (R^2)	Exponential function - mean slope	Exponential function - standard deviation of slope
Between-centroid distance - Jaccard index	0.77	0.059	0.042	0.78	0.015	0.0081
Between-centroid distance - HM index	0.38	0.01	0.04	0.45	0.003	0.0084
Dispersion - Jaccard index	0.84	-0.044	0.021	0.88	-0.018	0.007
Dispersion - Horn-Morisita index	0.78	-0.1	0.051	0.84	-0.036	0.014
Point diversity - species richness	0.95	0.139	0.064	0.92	1.66	1.2
Point diversity - exp(Shannon entropy)	0.91	0.168	0.079	0.87	1.15	0.8
Point diversity - 1/(1-Gini-Simpson)	0.88	0.168	0.081	0.84	0.84	0.62
Habitat diversity - species richness	0.93	0.082	0.038	0.92	2.72	2.06
Habitat diversity - exp(Shannon entropy)	0.83	0.067	0.047	0.84	1.2	1.4
Habitat diversity - 1/(1-Gini-Simpson)	0.71	0.054	0.048	0.74	0.71	1.07
Beta diversity - species richness	0.84	-0.049	0.024	0.87	-0.15	0.12
Beta diversity - exp(Shannon entropy)	0.87	-0.077	0.027	0.91	-0.2	0.13
Beta diversity - 1/(1-Gini-Simpson)	0.83	-0.084	0.031	0.89	-0.21	0.12

(1) the temporal change in species composition among living assemblages is stronger, and (2) the metacommunity has high species evenness.

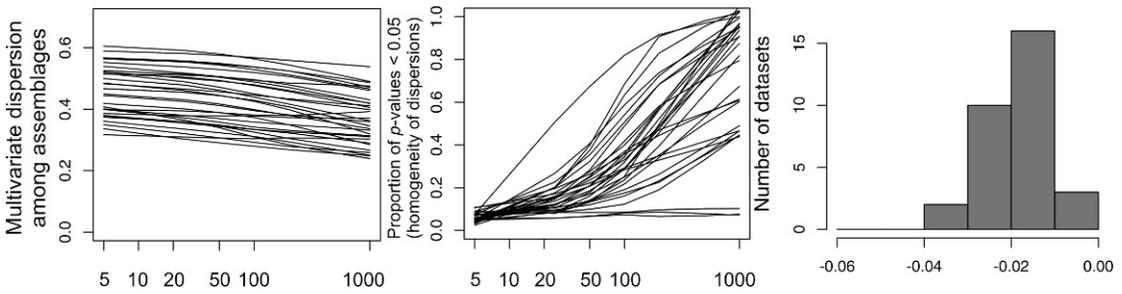
Change in Rank-Abundance Distributions.—With time-averaging, the Gini-Simpson index increases, indicating that the dominance of the most abundant species decreases, creating a flatter abundance structure at point scales (Fig. 8). Concurrently, the proportion of singleton and doubleton species increases; that is, the assemblage becomes enriched in rare species (Fig. 8C,D). In the 12 data sets where the mean size of living assemblages is >75 individuals, modeled RADs change with time-averaging from straight geometric-like curves to more J-shaped logseries-like curves (Fig. 9). First, these changes involve the *most abundant* species in the non-averaged assemblage becoming less abundant and species with intermediate abundance ranks becoming more abundant. Second, the proportion of rare species (relative to the total number of

species) increases, and the RADs of local assemblages thus begin to resemble the RADs of the modeled metacommunities. RADs observed in death assemblages are also on average less steep and more J-shaped than those observed in living assemblages (Fig. 9).

Discussion

Within-Habitat Time-Averaging Can Shift Mean Assemblage Composition.—With increasing time-averaging, local (non-averaged) assemblages become less dispersal-limited, their species dominance is reduced, and new rare species are added. The mean assemblage composition of dispersal-limited assemblages thus shifts toward the mean composition of averaged assemblages (less limited by dispersal), resembling the static panmictic metacommunity for a given sample size. The mean composition of non-averaged assemblages is expected to be the same as that of averaged assemblages only when local non-averaged assemblages are random samples from the

A. Jaccard dissimilarity (presence-absence)



B. Horn-Morisita dissimilarity (relative abundances)

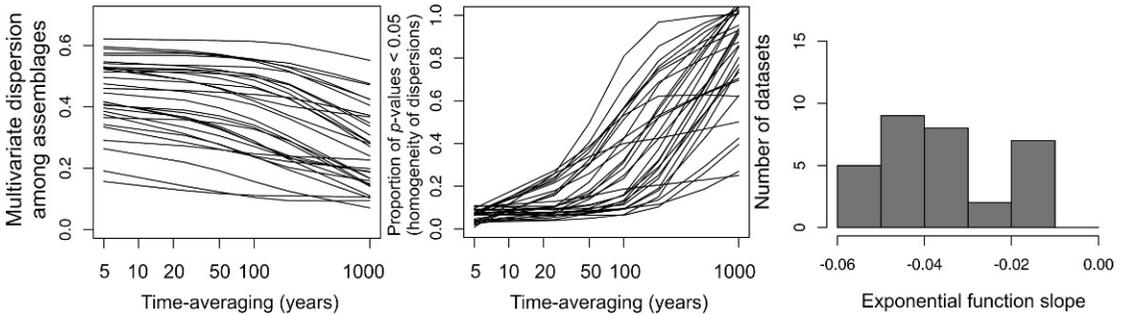


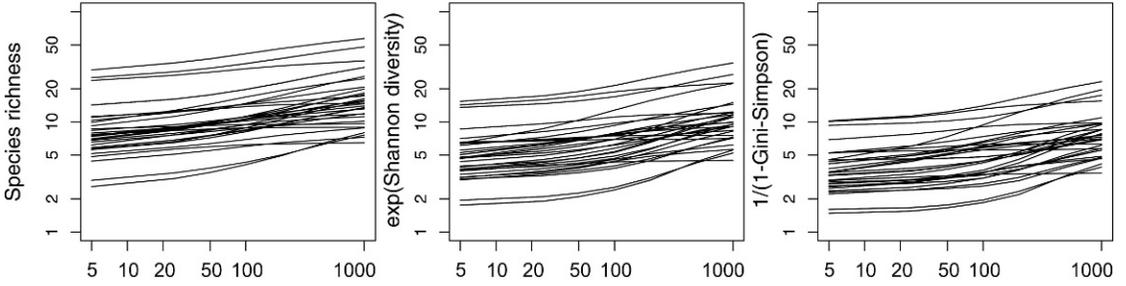
FIGURE 4. Time-averaging significantly reduces dispersion among assemblages (average dissimilarity among assemblages and centroid in multivariate space) regardless of the dissimilarity measure used, but at a lower rate using Jaccard dissimilarity (A) than using Horn-Morisita dissimilarity (B) (left column). Based on 100 simulations, the proportion of tests finding a significant reduction in dispersion increases and, with some exceptions, most data sets show a significant decrease in dispersion after only several decades to centuries (middle column). The slopes of the exponential functions describing the reduction in dispersion are restricted to a relatively narrow range of values between 0 and -0.06 (right column).

metacommunity. We note that an increase in spatial scale would similarly decrease dispersal limitation and would change RADs toward flatter curves (Hubbell 2001; Chisholm and Lichstein 2009). Shifts in mean species composition can thus be accomplished by time-averaging *without* invoking ecological succession or environmental change, assuming dispersal-limited metacommunity dynamics, in contrast to the constant composition expected in local assemblages without dispersal limitation. However, the shift in mean assemblage composition with time-averaging is small, in that it remains within multivariate space encompassed by non-averaged assemblages. The shift would be stronger if we relaxed the assumption of a static metacommunity composition over the duration of time-averaging.

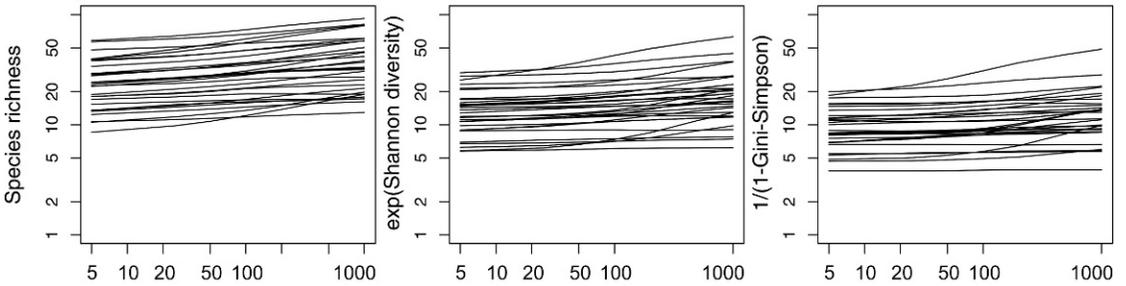
Within-habitat Time-Averaging Decreases Among-Site Variation in Composition and Beta Diversity.—Our simulations find that

averaged assemblages are characterized by significantly lower dispersion among assemblages in multivariate space and by lower beta diversity than non-averaged assemblages (Figs. 4, 5). These changes concur with qualitative expectations of time-averaging; i.e., local assemblages shift toward their mean assemblage composition. On one hand, the reduced variation in composition of time-averaged assemblages is related to pooling: temporal fluctuations in species abundances are averaged out owing to homogenization of dead individuals of species from non-contemporaneous generations (e.g., Peterson 1977; Martin et al. 2002; Terry 2008; Tomašových and Kidwell 2010). This positive relationship between variance and the resolution of analysis is a general scaling rule (Wiens 1989; Levin 1992; Lande 1996). Individual non-averaged assemblages temporally drift within a multivariate space that is shared with other non-averaged assemblages and is

A. Point diversity (single station)



B. Habitat diversity (multiple stations)



C. Beta diversity (among stations)

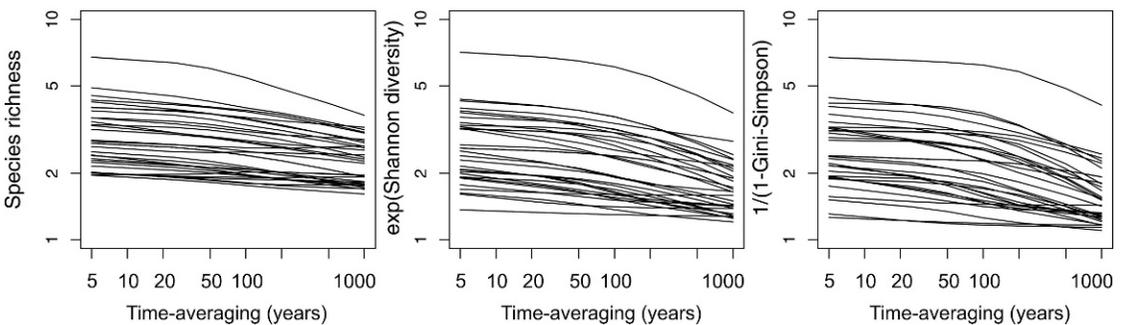


FIGURE 5. Expected accumulation of species in averaged assemblages with increasing time-averaging (log-log plots), showing a relatively rapid increase in sampled diversity at point scales (single stations) (A), a slower increase in sampled diversity at habitat scales (B), and a decrease in sampled beta diversity (C). The slopes of these functions remain curvilinear in log-log plots (used here), and are robust to the diversity measures of three orders (columns). Sampled diversity is expressed in terms of species richness (diversity of order zero; left column) and the effective number of species and communities based on Shannon entropy (diversity of order one; middle column) and the Gini-Simpson index (diversity of order two; right column).

constrained by the static metacommunity species pool. Temporal changes within individual *stations* thus translate into spatial changes among stations. Each station becomes less limited by dispersal with increasing time-averaging, thus becoming more similar to other stations. Spatial variation in species composition among stations is therefore also reduced with increasing time-averaging, even in the absence of postmortem transportation (McKinney and Allmon 1995; Russell 1998). On the other hand, time-

averaging leads to the accumulation of new species and thus *adds* new variation to the spatial variation in species composition. This phenomenon slows the decrease in dispersion when presence-absence measures are used because they are sensitive to species richness, but even there it does not obliterate the homogenizing effect of pooling consecutive assemblages (Figs. 4, 5C).

Within-Habitat Time-Averaging Increases Diversity at Point and Habitat Scales.—In the absence of dispersal limitation, the increase in

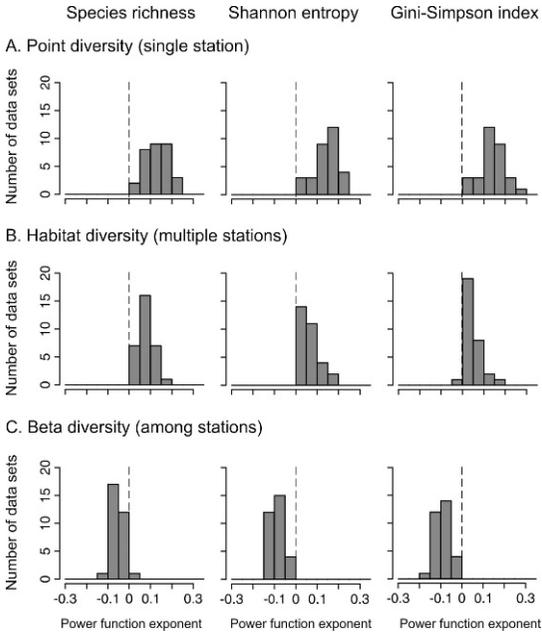


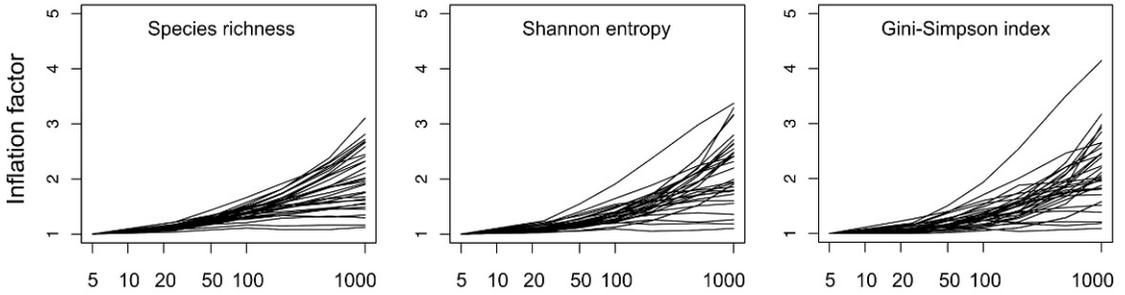
FIGURE 6. Frequency distributions of scaling exponents for change in sampled diversity of three orders (species richness, Shannon entropy, and Gini-Simpson index) expected with increasing within-habitat time-averaging. Scaling exponents, which indicate the rate of change in diversity, decrease from point (A) to habitat (B) scales, and the range of exponents is restricted to a relatively narrow range of values between 0 and 0.3. Sampled diversity thus increases at a slower rate with increasing time-averaging at the habitat scale than at the point scale. In contrast, beta (among-station) diversity decreases with increasing time-averaging and lies within a very narrow range (between 0 and -0.2) (C). This decrease matches the expected reduction in dispersion among assemblages (see Fig. 2). Sampled diversity expressed as in Figure 4.

diversity with increasing sample size in standard STRs arises from the increased probability of sampling individuals of rare species from the regional metacommunity (White 2004, 2007; McGlenn and Palmer 2009). The predictions for STR when a neutral metacommunity model is used are comparable to those for a pure sampling model only when immigration to local assemblages is not limited, because non-averaged assemblages represent random samples from the metacommunity (Green and Plotkin 2007; McGlenn and Palmer 2009). In that case, the sampled diversity of the averaged assemblages should not exceed that of the non-averaged assemblages (i.e., “ergodic within-habitat mixing” [Olszewski and Kidwell 2007]).

In contrast, under *dispersal-limited* metacommunity dynamics, time-averaged habitat diversity can be larger than the habitat-scale diversity of non-averaged assemblages without invoking environmental change or post-mortem transportation from other habitats. Averaged assemblages can contain species that are present in the species pool and have a potential to immigrate into the habitat over the duration of time-averaging, but that are not recorded by non-averaged (dispersal-limited) assemblages distributed in space at any single moment. Most standard STRs of present-day communities in stable environments also do not conform to a pure sampling model (White 2004, 2007; Adler et al. 2005; White et al. 2006), and time-averaging is thus probably always coupled with an increase in diversity that is larger than expected under a random sampling of the static habitat species pool. We note that changes in composition related to ecological succession or temporal environmental changes are increasingly likely as time-averaging exceeds a few years or decades. Time-averaging will obviously have stronger effects on diversity in communities characterized by a high rate of change in composition (e.g., Peterson 1977; Fürsich and Aberhan 1990), owing to high dispersal limitation or high temporal variation in environmental conditions. However, local assemblages drawn from relatively even and diverse metacommunities can also show stronger effects of time-averaging: with each consecutive pooling, more species can be added into local assemblages and more species can co-occur within local assemblages, further reducing beta diversity and inflating alpha diversity. The magnitude of time-averaging effects is thus driven both by rates of change in the composition of assemblages at local spatial scales and by the metacommunity structure governed by speciation-extinction dynamics at larger spatial scales (He and Legendre 2002; McGlenn and Palmer 2009).

Time-Averaging Flattens Rank-Abundance Distributions.—Under a fixed sample size, the change in diversity is forced through a flattening of the RAD in time-averaged assemblages (e.g., Kosnik and Wagner 2006),

A. Point diversity (single station)



B. Habitat diversity (multiple stations pooled)

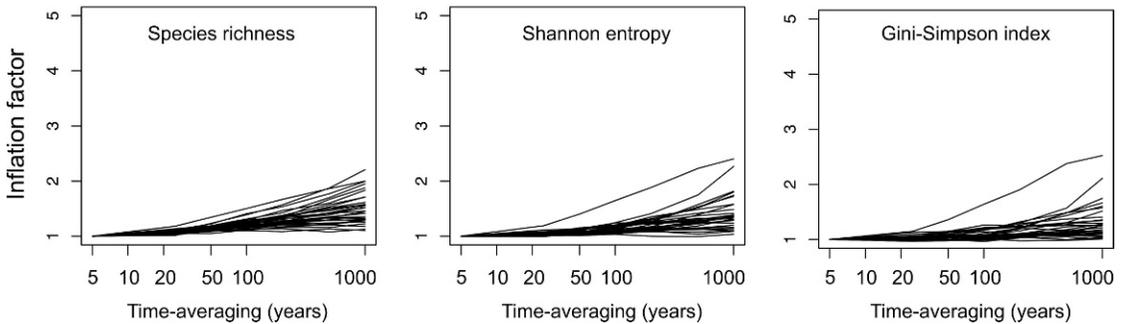


FIGURE 7. Expected change in inflation factors for sampled diversity at point (A) and habitat (B) scales with increasing within-habitat time-averaging. Inflation factors are the ratio of sampled diversity in averaged assemblages relative to that in non-averaged assemblages. Sampled diversity expressed as in Figure 4.

and this shift is possible when species' proportional abundances in local assemblages change over the course of time-averaging owing to dispersal-limited metacommunity dynamics (or owing to non-neutral dynamics in temporally variable environments). Rank-abundance structure does in fact change with increasing time-averaging at a fixed sample size, owing to compensatory mechanisms that reduce species dominance. The sensitivity of RADs to an increase in temporal scale is comparable to an increase in spatial scale (e.g., Wilson et al. 1998). We find two primary effects.

First, with an increase in time duration, the identity of the *dominant* species in non-averaged (living) assemblages switches temporally among several different species, which reduces the proportional abundance of all of them in the averaged assemblage (Fig. 8A). The decrease in resolution thus flattens the dominance structure of averaged assemblages (Fig. 9) because any temporal increase in the abundance of one species is compensated by a temporal decrease in the

abundance of one or more other species under a steady state of abundance structure of living assemblages (Hubbell 2001). This reduction in averaged abundance mainly affects relatively common species, which change rank but mostly remain present in successive generations. Compensatory effects are not restricted to neutral zero-sum models—they also characterize competition-driven communities composed of species that exhibit density dependence and unequal niche responses to environmental variation (Vasseur and Fox 2007; Loreau and de Mazancourt 2008; Ranta et al. 2008).

Some studies in natural systems have found that, when absolute population densities are used, positive covariation in species abundances is more common than negative covariation (Houlahan et al. 2007). The neutral model can also lead to positive covariation among *absolute* species abundances when the zero-sum constraint is relaxed (Loreau and de Mazancourt 2008), but an overall negative covariation is still expected when *proportional* abundances are used because

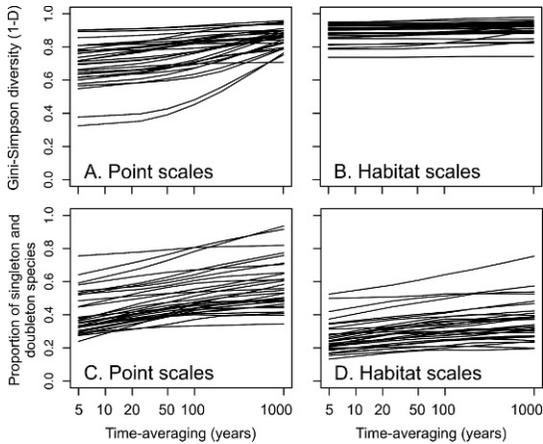


FIGURE 8. With time-averaging, the dominance of abundant species substantially decreases at point scales whereas the reduction in species dominance is minor at habitat scales (Gini-Simpson index) (A, B). The proportional richness of rare species (species represented by singletons and doubletons) increases at both point and habitat spatial scales (C, D).

they effectively obey the zero-sum rule (Loreau and de Mazancourt 2008). In addition, positive covariance is not expected to *increase* species dominance with increasing time-averaging because species do not switch ranks: all species increase (or decrease) in absolute abundance, maintaining their original proportional abundances.

Second, with an increase in time duration, the proportion of rare species represented by only one or two individuals increases (Fig. 8), so that the averaged assemblage acquires a tail of rare species approaching that expected in the metacommunity under a given sample size. The high richness of rare species that characterizes neutral (logseries-like) metacommunities (Fig. 1) is related to the way new species are introduced into the neutral metacommunity, namely as singletons (“point-mutation” speciation [Hubbell 2001; Zillio and Condit 2007]). Therefore, to keep the excess of rare species in the metacommunity at speciation-extinction equilibrium, species must preferentially originate at small population sizes (Hubbell 2001). At local scales, species that are abundant in the metacommunity have higher immigration and lower local extinction rates than rare species owing to mass effects (they are replenished by new immigrant individuals)

and a lower susceptibility to extinction (Hanski 1982; Brown 1984; Nee et al. 1991; Gaston et al. 1997, 2000). However, at any time step there is a high probability that some rare species can immigrate because the metacommunity has disproportionately more rare species than do dispersal-limited (non-averaged) assemblages. The proportion of rare species found locally can thus be expected to increase with time-averaging because, at each time step, different rare species but roughly the same abundant species are present in the local non-averaged assemblage (Magurran and Henderson 2003; Magurran 2007). The effect of time averaging on the proportion of rare species can, however, differ when other speciation modes dominate the metacommunity dynamics (e.g., when species, rather than individuals, have the same probabilities to speciate; Haegeman and Etienne 2009).

McGill (2003) observed that time-averaging coupled with temporal autocorrelation (e.g., dispersal limitation) can lead to a negative (left) log-skew of initially lognormal species-abundance distributions under *increasing* sample size, also demonstrating that time-averaged species-abundance distributions can be skewed toward rare species relative to the lognormal metacommunity (see also Green and Plotkin 2007; Šizling et al. 2009) (Fig. 10A). However, with the exception of extreme dispersal limitation (when abundant species become highly dominant and most other species become rare), we find that at fixed sample sizes, increasingly averaged assemblages drawn from the same lognormal distribution do not change in their skew on a log scale (Fig. 10A). Increasingly averaged assemblages drawn from a logseries distribution change toward a positive (right) log-skew, i.e., toward the metacommunity where most species are represented by singletons (Fig. 10B). To conclude, the log-skew of the averaged assemblages at fixed sample sizes can reveal information about the attributes of the metacommunity distribution.

Implications

Using Time-Averaged Data to Infer Metacommunity Models.—A neutral model serves as a

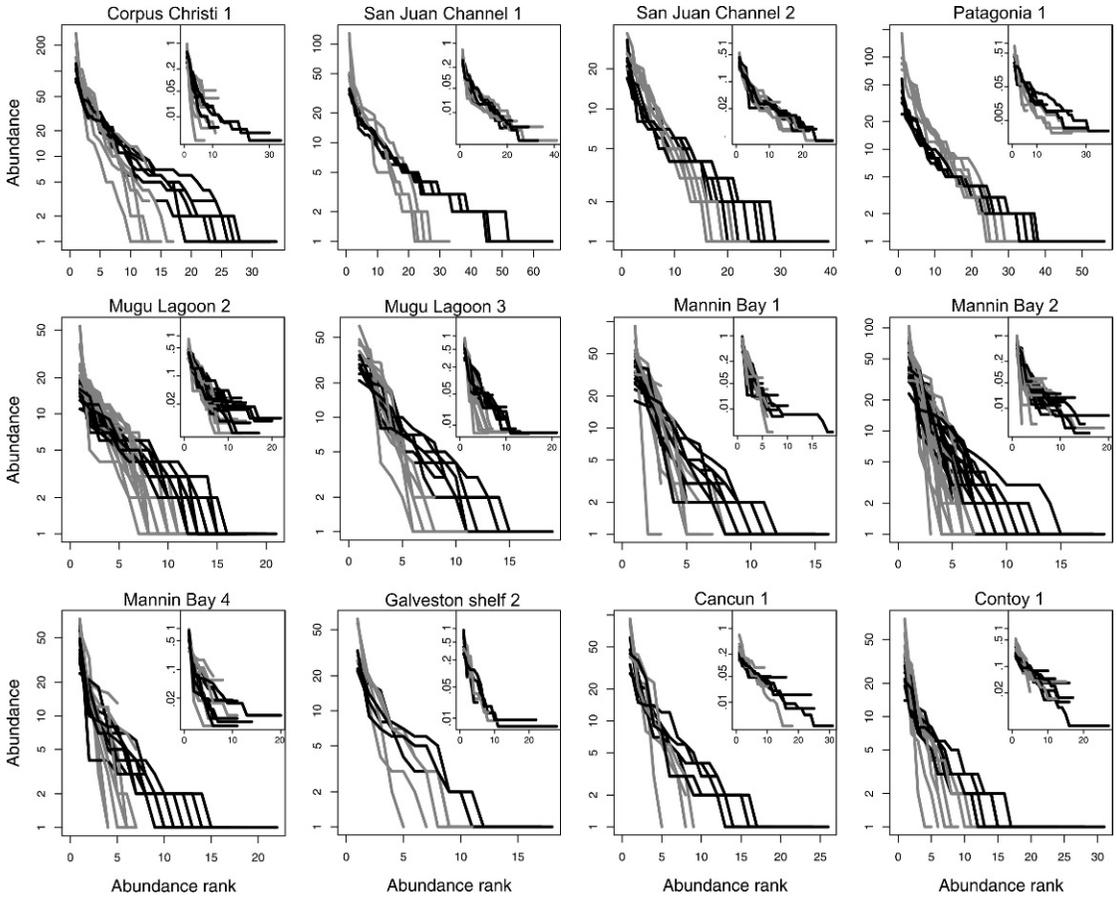


FIGURE 9. *Modeled* decrease in species dominance and increase in the proportion of rare species between non-averaged assemblages (gray) and assemblages averaged for 1000 years (black) in 12 habitat-level data sets where the mean size of living assemblages exceeds 75 individuals. Rank-abundance distributions *observed* in averaged (death) assemblages (small insets) are also on average less steep and more J-shaped than those observed in non-averaged (living) assemblages. In simulations, sample sizes of non-averaged and averaged assemblages are equal (standardized to mean sample size observed in each data set). Each curve in a plot corresponds to the rank-abundance distribution produced by simulation of one individual station in the designated habitat. In analyses of observed data, living and death assemblages sampled at the same station were size-standardized, but sample sizes remain different among stations owing to large variation in the number of individuals.

null model for recognizing the operation of species-sorting and other non-neutral meta-community models, where intraspecific density-dependence and trade-offs in growth rates can lead to highly stable compositions (Pandolfi 1996; Clark and McLachlan 2003; Leibold et al. 2004; Gotelli and McGill 2005; McGill et al. 2005). Spatial variation in composition among non-averaged assemblages is thus expected to be higher in neutral than in non-neutral models where such mechanisms operate (e.g., Chave and Leigh 2002; Munoz et al. 2008). On one hand, our finding that time-averaged assemblages tend to be *more* constant in species composition

than non-averaged assemblages means that assemblages from neutral systems that have been averaged over larger temporal scales can mimic *non*-neutral assemblages that have been averaged over smaller temporal scales. On the other hand, pooling of communities that are non-neutral at small *spatial* scales can lead to an averaged assemblages whose parameters conform to the neutral model at larger spatial scales, because averaging over multiple habitats equalizes the distribution of species that differ in per capita growth rates or in habitat requirements (Purves and Pacala 2005; Ricklefs 2007; Allouche and Kadmon 2009). Standard predictions of the neutral

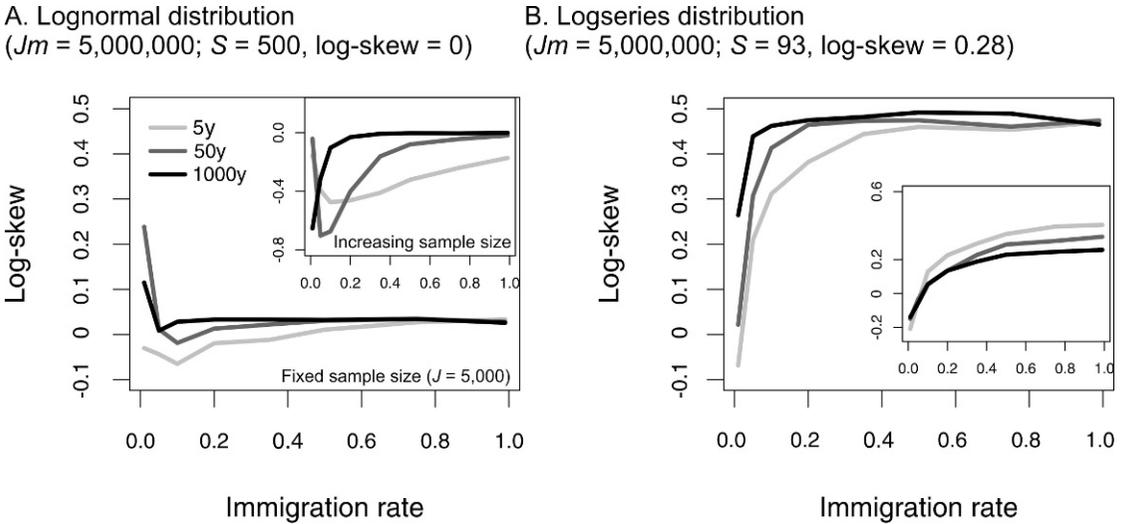


FIGURE 10. The change in log-skew of the assemblages averaged over 5 (light gray), 50 (dark gray), and 1000 (black) years (and the proportional richness of rare species) depends on whether sample size increases or remains fixed. A, At fixed sample sizes ($J = 5000$), increasingly averaged assemblages drawn from the same lognormal distribution either remain lognormal or change toward a *right* skew on a log scale under extreme dispersal limitation. In contrast, under increasing sample size (inset), averaged assemblages change toward a *left* skew on a log scale under dispersal limitation, in accord with McGill (2003). B, At fixed sample sizes, increasingly averaged assemblages drawn from a logseries distribution change toward a *right* log-skew, i.e., toward the metacommunity where most species are represented by singletons. Under increasing sample size (inset), averaged assemblages change toward a *left* skew, similarly as lognormal distributions. In these figures, the effects of time-averaging are assessed with the simulation approach used by McGill (2003). We assume that generations are discrete and one year corresponds to one time step. Distribution parameters are: lognormal $\mu = 0$, $\sigma = 1$; logseries $\alpha = 6.88$.

model for small temporal scales (Hubbell 2001; Etienne and Olff 2004a; Etienne 2005, 2007; McGill et al. 2005) thus must be scaled up when they are to be applied to time-averaged assemblages because the predictions of different metacommunity models converge at larger temporal scales (Tomašových and Kidwell 2010).

Evaluating Variations in Alpha and Beta Diversity.—Understanding the effects of time-averaging on diversity allows us to evaluate temporal variations in alpha and beta diversity (e.g., Sepkoski 1988; Staff and Powell 1988; Adrain et al. 2000; Powell and Kowalewski 2002; Peters 2004; Kowalewski et al. 2006; Wagner et al. 2006; Alroy et al. 2008) because inflation factors can be used to evaluate whether a given diversity increase might be explained by differences in time-averaging alone. Several findings here are relevant to this issue.

First, both the exponents of power functions and the inflation factors (ratios of averaged to non-averaged diversity) become smaller as the spatial resolution of sampling is

coarsened—diversity is less sensitive to variation in time-averaging at the habitat scale than at the point, single-station scale because temporal turnover is expected to decrease at larger spatial scales (Figs. 6, 7) (Adler et al. 2005). This effect is expected when temporal and spatial turnover in species composition is limited by a static species pool or by a species pool where temporal turnover is slower than spatial turnover (McGlinn and Palmer 2009). Similarly, spatial diversity patterns become less scale-dependent at large spatial scales as spatial species turnover slows down and species-abundance distributions can converge toward a particular limiting shape (Harte et al. 2009; Kurka et al. 2010). Although Phanerozoic trends in sampled alpha diversity have been refined by using individual bulk samples that correspond to the spatial resolution of point diversity (i.e., assemblages collected at roughly meter-scale spatial resolution) (Powell and Kowalewski 2002; Bush and Bambach 2004; Kowalewski et al. 2006), the inflationary effects of time-averaging on diversity are likely to be high at such small

spatial scales. Sampling designs that evaluate diversity patterns with replicates at *multiple* spatial scales (e.g., Hayek and Buzas 1997; Bennington 2003; Buzas and Hayek 2005; Webber 2005; Zuschin et al. 2006; Johnson et al. 2007) can thus minimize the effects of differential time-averaging by evaluating diversity at larger than local spatial scales.

Second, the inflation factors for sampled diversity predicted here from neutral modeling of non-averaged (living) assemblages are remarkably similar to empirical estimates of diversity inflation in time-averaged death assemblages based on live-dead studies, especially given that naturally time-averaged death assemblages are additionally subject to postmortem bias and that our models provide rather conservative estimates of the effects of time-averaging because they assume no environmental change. For example, at the *habitat* scale, we found a mean inflation of 1.25 for molluscan death assemblages on continental shelves that are relatively unaffected by human activities (Kidwell 2008). In our present study of 31 data sets from unmodified habitats, the mean *observed* inflation of diversity at habitat scales is 1.3 (Fig. 2) and the *modeled* inflation using the living assemblages is 1.6 under time-averaging of 1000 years (Fig. 7). At *point* scales, which we have not previously calculated, the mean *observed* inflation in our 31 data sets is 1.8 (Fig. 2) and the *modeled* inflation is 2.1 (Fig. 7). The discrepancy between the observed and modeled inflation factors is difficult to assess because absolute estimates of time-averaging for the 31 data sets are not available and individual data sets may well differ in their degree of time-averaging by an order of magnitude or more. We nonetheless think that our modeled inflation factors provide useful minimum and maximum estimates of the magnitude of time-averaging effects under the durations explored by our model (from 1 to 1000 years).

As an example, Bush and Bambach (2004) observed that raw bulk-sample (point) richness, uncorrected for taphonomic, latitudinal, and environmental effects, increased in fossil macrobenthic assemblages between the Paleozoic and Late Cenozoic by a factor of 1.84

(sample size of 100 individuals). They modeled the inflation of point (bulk-sample) diversity caused by a hypothesized increase in time-averaging (Kidwell and Brenchley 1994) by applying inflation factors of 1.2–1.6 to their Paleozoic assemblages (they evaluated changes in genus rather than species diversity, but most genera in our molluscan data sets are monospecific). The 1.2 inflation estimate was taken from Kidwell's (2002) *habitat*-scale empirical estimate for modern molluscan death assemblages. If we used instead the higher inflation factors for diversity at *point* scales found by us here (observed at 1.8, modeled at 2.1; Figs. 2 and 7), the adjusted alpha diversity of Paleozoic assemblages would approach the mean *raw* (1.84) values observed in Late Cenozoic assemblages, at least for Paleozoic assemblages that originally contained a large proportion of aragonitic species (Bush and Bambach 2004: Fig. 4). Similarly, Kowalewski et al. (2006) observed that point (bulk-sample) species richness increased between the Jurassic and Miocene–Pleistocene by a factor of at least 1.6 (at a sample size of 30 individuals) and 1.9 (at a sample size of 90 individuals). The outcomes of both studies thus come close to or partially overlap the range of values that can arise from variation in time-averaging. That said, secular trends in scales of time-averaging as related to long-term changes in population turnover rates, bioturbation rates, and preservation rates remain poorly explored (e.g., modern brachiopods can sustain scales of time-averaging similar to those of mollusks in carbonate environments [e.g., Carroll et al. 2003; Krause et al. 2010]), and adjustments for latitudinal bias may in fact exceed and oppose those of time-averaging (so that the biologically driven secular increase in diversity would be stronger than the raw trend [Bush and Bambach 2004: Fig. 7]). Moreover, an increase in time-averaging might lead to greater postmortem damage, i.e., that the expected inflation in species diversity is counteracted to some extent by a higher loss of species having fragile shells. Such an effect might explain, for example, why observed inflation factors in molluscan death assemblages are lower than modeled

estimates. On the other hand, increasing time-averaging by a single order of magnitude—from decadal to centennial scale—might still boost inflation factors because of the potential to capture more natural environmental variability per site, thus promoting averaging across multiple habitats (environmental condensation), which falls outside of our model of strictly within-habitat time-averaging. To get a sense of the magnitude of effect of such condensation, we note that habitat-scale inflation values are significantly higher in time-averaged death assemblages from shelves that have been subject to human modification (eutrophication, bottom-trawling) than on pristine shelves (2.16 ± 0.52 versus 1.25 ± 0.48 [Kidwell 2008]), indicating that environmental condensation does increase inflation factors significantly. Clearly, more work is needed before time-averaging correction factors can be applied rigorously.

Finally, this study makes a testable prediction about the inverse relationship between alpha and beta diversity that should exist if trends in diversity arise from an increase in time-averaging. Thus, an increase in alpha diversity that is *not* accompanied by a reduction in beta diversity implies that the trend is biological in origin rather than the product of a change in time-averaging. We note, however, that an increase in alpha and decrease in beta diversity (the prediction of time-averaging) is also predicted by some models of metacommunity dynamics under conditions of decreasing dispersal ability (Loreau and Mouquet 1999; Mouquet and Loreau 2002, 2003), which might arise from a temporal shift to gentler paleogeographic and environmental gradients or from a shift from non-planktonic to planktonic modes of larval dispersal. Thus, although our modeling puts the predictions of time-averaging on a firm theoretical basis, care is still required to discriminate among possible drivers of spatial and temporal variation in diversity.

Conclusions

This modeling study provides the first theory-derived estimates for the impact of time-averaging on assemblage composition and diversity under *fixed* sample sizes and

over temporal scales (up to 1000 years) that are relevant to fossil assemblages. Systematic effects on diversity were expected to occur when time-averaged assemblages have higher sample sizes than non-averaged assemblages, but we show that within-habitat time-averaging also affects diversity at fixed sample sizes. Our estimates of the effects of time-averaging on species composition, diversity, dispersion, and rank-abundance distributions (RADs) are independent of empirical estimates based on *observed* differences between non-averaged (living) and time-averaged (death) assemblages (e.g., Kidwell 2002, 2007; 2008): information about death assemblages does not enter into the parameters of our modeling process, which is based on the attributes of living assemblages only.

The rate of change in diversity with increasing time-averaging under a fixed sample size provides a measure of the temporal species accumulation rate that is partly comparable to the slope of a standard species-time relationship (STR), but factors out the effects of increasing sample size from the effects of other ecological processes. With the exception of dispersal-*unlimited* metacommunity models, diversity increases because immigration probability increases in time and local RADs become flatter and change toward the metacommunity RAD. We show that within-habitat time-averaging alone systematically modifies the composition and diversity of time-averaged away from that of non-averaged (living) assemblages: it leads to higher diversity at both point and habitat scales, and to lower beta diversity and higher species co-occurrence. Most of these effects are linked to a flattening in the shape of the RAD—that is, species abundances become equalized as a consequence of temporal switching among multiple abundant species. In addition, rare species increase to constitute a larger proportion of all species present if new species in the metacommunity originate at small population sizes. These changes arise within the first few decades to centuries of pooling dead individuals, even when the model is restricted to within-habitat time-averaging and the metacommunity structure is constant.

Neutral models thus provide conservative predictions of the effects of increasing temporal scale on species composition, diversity, and RADs. Importantly, we find that the effects of time-averaging are directional and predictable: time-averaging does not simply introduce noise nor, on the other hand, simply collapse variation observed among spatially replicate samples of the living assemblage in any given increment of time. The rates at which diversity increases with increasing time-averaging at point scales are driven by the rate of temporal change in composition of living assemblages (controlled by the degree of dispersal limitation and environmental variability acting at local scales) but also by metacommunity structure (controlled by speciation-extinction dynamics at larger spatial scales). Finally, the effects of time-averaging on diversity can be minimized by evaluating trends at the larger habitat spatial scales rather than at point (bulk-sample) scales because time-averaging inflates diversity at a slower rate as the spatial resolution of sampling decreases.

Acknowledgments

We thank A. Bush and S. Peters for critical reviews. We are grateful to authors for making unpublished data available and providing additional insights into their study areas and methods (W. A. White, K. Linse, M. A. Kowalewski, T. A. Rothfus, D. W. J. Bosence, J. E. Warne, A. I. Miller, G. M. Staff, E. N. Powell) and for the generous cooperation of scientists across southern California who have made it possible for us to build the California shelf data sets (D. B. Cadien, Los Angeles County Sanitation District; R. G. Velarde and K. Barwick, San Diego Metropolitan Water Department; S. C. Johnson, Aquatic Bioassay and Consulting Laboratories, Ventura; S. Holt, MEC-Weston Solutions, Inc.; S. B. Weisberg and A. Ranasinghe, Southern California Coastal Water Research Project; L. T. Groves and J. H. McLean, Los Angeles County Natural History Museum). We are also grateful to D. S. Gorsline, R. G. Douglas, B. Thompson, and W. Etter for their help in locating and preserving unpublished "live" data from southern California. This

research was supported by the National Science Foundation (EAR-0345897) and the University of Southern California Sea Grant Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce (NA07OAR4170008). We thank the University of Chicago "Death at Noon" group for useful discussions. A. Tomašových also thanks the Slovak Research and Development Agency (APVV-0248-07) and Slovakian Scientific Grant Agency (VEGA 2/0068/08) for their support.

Literature Cited

- Adler, P. B., and W. K. Lauenroth. 2003. The power of time: spatiotemporal scaling of species diversity. *Ecology Letters* 6:749–756.
- Adler, P. B., P. E. White, W. K. Lauenroth, D. M. Kaufman, A. Rassweiler, and J. A. Rusak. 2005. Evidence for a general species-time-area relationship. *Ecology* 86:2032–2039.
- Adrain, J. M., S. R. Westrop, B. D. E. Chatterton, and L. Ramsköld. 2000. Silurian trilobite alpha diversity and the end-Ordovician mass extinction. *Paleobiology* 26:625–646.
- Allen, T. F. H., and T. W. Hoekstra. 1992. *Toward a unified ecology*. Columbia University Press, New York.
- Allen, T. F. H., and T. B. Star. 1982. *Hierarchy: perspectives for ecological complexity*. University of Chicago Press, Chicago.
- Allouche, O., and R. Kadmon. 2009. A general framework for neutral models of community dynamics. *Ecology Letters* 12:1287–1297.
- Alroy, J., M. Aberhan, D. J. Bottjer, M. Foote, F. T. Fürsich, P. J. Harries, A. J. W. Hendy, S. M. Holland, L. C. Ivany, W. Kiessling, M. A. Kosnik, C. R. Marshall, A. J. McGowan, A. I. Miller, T. D. Olszewski, M. E. Patzkowsky, S. E. Peters, L. Villier, P. J. Wagner, N. Bonuso, P. S. Borkow, B. Brenneis, M. E. Clapham, L. M. Fall, C. A. Ferguson, V. L. Hanson, A. Z. Krug, K. M. Layou, E. H. Leckey, S. Nuernberg, C. M. Powers, J. A. Sessa, C. Simpson, A. Tomašových, and C. C. Visaggi. 2008. Phanerozoic trends in the global diversity of marine invertebrates. *Science* 321:97–100.
- Anderson, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245–253.
- Anderson, M. J., K. E. Ellingsen, and B. H. McCordle. 2006. Multivariate dispersion as a measure of beta diversity. *Ecology Letters* 9:683–693.
- Behrensmeyer, A. K. 1982. Time resolution in fluvial vertebrate assemblages. *Paleobiology* 8:211–227.
- Behrensmeyer, A. K., and R. E. Chapman. 1993. Models and simulations of taphonomic time-averaging in terrestrial vertebrate assemblages. In S. M. Kidwell and A. K. Behrensmeyer, eds. *Taphonomic approaches to time resolution in fossil assemblages*. *Short Courses in Paleontology* 6:125–149. Paleontological Society, Knoxville, Tenn.
- Behrensmeyer, A. K., and R. W. Hook. 1992. Paleoenvironmental contexts and taphonomic modes. Pp. 15–136 in A. K. Behrensmeyer et al. eds. *Terrestrial ecosystems through time*. University of Chicago Press, Chicago.
- Bell, G. 2000. The distribution of abundance in neutral communities. *American Naturalist* 155:606–617.
- Bengtsson, J., K. Engelhardt, P. Giller, S. Hobbie, D. Lawrence, J. Levine, M. Vila, and V. Wolters. 2002. Slippin' and slidin' between the scales: the scaling components of biodiversity-ecosystem functioning relations. Pp. 209–220 in M. Loreau, S.

- Naem, and P. Inchausti, eds. Biodiversity and ecosystem functioning. Oxford University Press, Oxford.
- Bennington, J. B. 2003. Transcending patchiness in the comparative analysis of paleocommunities: a test case from the Upper Cretaceous of New Jersey. *Palaios* 18:22–33.
- Bennington, J. B., and R. K. Bambach. 1996. Statistical testing for paleoecology recurrence: Are similar fossil assemblages ever the same? *Palaeogeography, Palaeoclimatology, Palaeoecology* 127:107–133.
- Borda-de-Água, L., S. P. Hubbell, and M. McAllister. 2002. Species-area curves, diversity indices, and species abundance distributions: a multifractal analysis. *American Naturalist* 159:138–155.
- Borda-de-Água, L., S. P. Hubbell, and F. He. 2007. Scaling biodiversity under neutrality. Pp. 347–375 in Storch et al. 2007.
- Brewer, A., and M. Williamson. 1994. A new relationship for rarefaction. *Biodiversity and Conservation* 3:373–379.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. *American Naturalist* 124:255–279.
- Bush, A. M., and R. K. Bambach. 2004. Did alpha diversity increase during the Phanerozoic? Lifting the veils of taphonomic, latitudinal, and environmental biases. *Journal of Geology* 112:625–642.
- Buzas, M., and L. A. C. Hayek. 2005. On richness and evenness within and between communities. *Paleobiology* 31:199–220.
- Carey, S., A. Ostling, J. Harte, and R. del Moral. 2007. Impact of curve construction and community dynamics on the species-time relationship. *Ecology* 88:2145–2153.
- Carroll, M., M. Kowalewski, M. G. Simões, and G. A. Goodfriend. 2003. Quantitative estimates of time-averaging in terebratulid shell accumulations from a modern tropical shelf. *Paleobiology* 29:381–402.
- Chao, A., R. L. Chazdon, R. K. Colwell, and T.-J. Shen. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters* 8:148–159.
- Chave, J., and E. G. Leigh Jr. 2002. A spatially explicit neutral model of β -diversity in tropical forests. *Journal of Theoretical Biology* 62:153–168.
- Chave, J., H. C. Muller-Landau, and S. A. Levin. 2002. Comparing classic community models: theoretical consequences for patterns of diversity. *American Naturalist* 159:1–23.
- Chisholm, R. A., and J. W. Lichstein. 2009. Linking dispersal, immigration and scale in the neutral theory of biodiversity. *Ecology Letters* 12:1385–1393.
- Clark, J. S., and J. S. McLachlan. 2003. Stability of forest biodiversity. *Nature* 423:635–638.
- Coleman, B. D. 1981. On random placement and species-area relations. *Mathematical Biosciences* 54:191–215.
- Coleman, B. D., M. A. Mares, M. R. Willig, and Y.-H. Hsieh. 1982. Randomness, area, and species richness. *Ecology* 63:1121–1133.
- Collins, S. L. 2000. Disturbance frequency and community stability in native tallgrass prairie. *American Naturalist* 155:311–325.
- Collins, S. L., F. Micheli, and L. Hartt. 2000. A method to determine rates and patterns of variability in ecological communities. *Oikos* 91:285–293.
- Cutler, A. H. 1993. Mathematical models of temporal mixing in the fossil record. In S. M. Kidwell and A. K. Behrensmeier, eds. *Taphonomic approaches to time resolution in fossil assemblages*. Short Courses in Paleontology 6:169–187. Paleontological Society, Knoxville, Tenn.
- Dengler, J. 2009. Which function describes the species-area relationship best? A review and empirical evaluation. *Journal of Biogeography* 36:728–744.
- Dornelas, M., and S. R. Connolly. 2008. Multiple modes in a coral species abundance distribution. *Ecology Letters* 11:1008–1016.
- Durrett, R., and S. Levin. 1996. Spatial models for species-area curves. *Journal of Theoretical Biology* 179:119–127.
- Etienne, R. S. 2005. A new sampling formula for neutral biodiversity. *Ecology Letters* 8:253–260.
- . 2007. A neutral sampling formula for multiple samples and an “exact” test of neutrality. *Ecology Letters* 10:608–618.
- . 2009. Maximum likelihood estimation of neutral model parameters for multiple samples with different degrees of dispersal limitation. *Journal of Theoretical Biology* 257:510–514.
- Etienne, R. S., and D. Alonso. 2006. Neutral community theory: how stochasticity and dispersal limitation can explain species coexistence. *Journal of Statistical Physics* 128:485–510.
- Etienne R. S., and H. Olff. 2004a. A novel genealogical approach to neutral biodiversity theory. *Ecology Letters* 7:170–175.
- . 2004b. How dispersal limitation shapes species-body size distributions in local communities. *American Naturalist* 163:69–83.
- Finnegan, S., and M. L. Droser. 2008. Reworking diversity: effects of storm deposition on evenness and sampled richness, Ordovician of the Basin and Range, Utah and Nevada, USA. *Palaios* 23:87–96.
- Flessa, K. W., and M. Kowalewski. 1994. Shell survival and time-averaging in nearshore and shelf environments: estimates from the radiocarbon literature. *Lethaia* 27:153–165.
- Flessa, K. W., A. H. Cutler, and K. H. Meldahl. 1993. Time and taphonomy: quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat. *Paleobiology* 19:266–286.
- Fridley, J. D., R. K. Peet, E. van der Maarel, and J. H. Willems. 2006. Integration of local and regional species-area relationships from space-time species accumulation. *American Naturalist* 168:133–143.
- Fürsich, F. T. 1978. Influence of faunal condensation and mixing on preservation of fossil benthic communities. *Lethaia* 11:243–250.
- Fürsich, F. T., and M. Aberhan. 1990. Significance of time-averaging for paleocommunity analysis. *Lethaia* 23:143–152.
- Fürsich, F. T., and E. G. Kaufmann. 1984. Palaeoecology of marginal marine sedimentary cycles in the Albian Bear River Formation of south-western Wyoming. *Palaeontology* 27:501–536.
- Gaston, K. J., T. M. Blackburn, and J. H. Lawton. 1997. Interspecific abundance-range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology* 66:579–601.
- Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. Abundance-occupancy relationship. *Journal of Applied Ecology* 37(Suppl. 1):39–59.
- Gaston, K. J., K. L. Evans, and J. J. Lennon. 2007. The scaling of spatial turnover: pruning the thicket. Pp. 181–222 in Storch et al. 2007.
- Gotelli, N. J., and B. J. McGill. 2005. Null versus neutral models: what’s the difference? *Ecography* 29:793–800.
- Gray, J. S., A. Bjørgaerter, and K. I. Ugland. 2005. The impact of rare species on natural assemblages. *Journal of Animal Ecology* 74:1131–1139.
- Green, J. L., and J. B. Plotkin. 2007. A statistical theory for sampling species abundances. *Ecology Letters* 10:1037–1045.
- Haegeman, B., and R. S. Etienne. 2009. Neutral models with generalized speciation. *Bulletin of Mathematical Biology* 71:1507–1519.
- Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38:210–221.
- Harte, J., and A. P. Kinzig. 1997. On the implications of species-area relationships for endemism, spatial turnover, and food web patterns. *Oikos* 80:417–427.
- Harte, J., E. Conlisk, A. Ostling, J. L. Green, and A. B. Smith. 2005. A theory of spatial structure in ecological communities at multiple spatial scales. *Ecological Monographs* 75:179–197.

- Harte, J., A. B. Smith, and D. Storch. 2009. Biodiversity scales from plots to biomes with a universal species-area curve. *Ecology Letters* 12:789–797.
- Hayek, L. C., and M. A. Buzas. 1997. Surveying natural populations. Columbia University Press, New York.
- He, F., and R. Condit. 2007. The distribution of species: occupancy, scale, and rarity. Pp. 32–50 in Storch et al. 2007.
- He, F., and X.-S. Hu. 2005. Hubbell's fundamental biodiversity parameter and the Simpson diversity index. *Ecology Letters* 8:386–390.
- He, F., and P. Legendre. 2002. Species diversity patterns derived from species-area models. *Ecology* 83:1185–1198.
- He, F., K. W. Gaston, and J. Wu. 2002. On species occupancy-abundance models. *Écoscience* 9:119–126.
- Hendy, A. J. W., and P. J. J. Kamp. 2004. Late Miocene to early Pliocene biofacies of Wanganui and Taranaki Basins, New Zealand: Applications to paleoenvironmental and sequence stratigraphic analysis. *New Zealand Journal of Geology and Geophysics* 47: 769–785.
- Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54:427–432.
- Holland, S. M., and M. E. Patzkowsky. 1999. Models for simulating the fossil record. *Geology* 27:491–494.
- Holyoak, M., M. A. Leibold, N. Mouquet, R. D. Holt, and M. F. Hoopes. 2005. Metacommunities: a framework for large-scale community ecology. Pp. 1–31 in M. Holyoak, M. A. Leibold, and R. D. Holt, eds. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago.
- Holyoak, M., M. A. Leibold, and R. D. Holt, eds. 2005. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago.
- Horn H. S. 1966. Measurement of "overlap" in comparative ecological studies. *American Naturalist* 100:419–424.
- Horton, B. P., and J. W. Murray. 2006. Patterns in cumulative increase in live and dead species from foraminiferal time series of Cowpen Marsh, Tees Estuary, UK: implications for sea-level studies. *Marine Micropaleontology* 58:287–315.
- Houlahan, J. E., D. J. Currie, K. Cottenie, G. S. Cumming, S. K. M. Ernest, C. S. Findlay, S. D. Fuhlendorf, U. Gaedke, P. Legendre, J. J. Magnuson, B. H. McArdle, E. H. Muldavin, D. Noble, R. Russell, R. D. Stevens, T. J. Willis, I. P. Woiwod, and S. M. Wozell. 2007. Compensatory dynamics are rare in natural ecological communities. *Proceedings of the National Academy of Sciences USA* 104:3273–3277.
- Hubbell, S. P., 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, N.J.
- Johnson, R. G. 1960. Models and methods for the analysis of the mode of formation of fossil assemblages. *Geological Society of America Bulletin* 71:1075–1086.
- Johnson, K. G., J. A. Todd, and J. B. C. Jackson. 2007. Coral reef development drives molluscan diversity increase at local and regional scales in the late Neogene and Quaternary of the southwestern Caribbean. *Paleobiology* 33:24–52.
- Jost, L. 2006. Entropy and diversity. *Oikos* 113:363–375.
- . 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427–2439.
- Kidwell, S. M. 1997. Time-averaging in the marine fossil record: overview of strategies and uncertainties. *Geobios* 30:977–995.
- . 2001. Preservation of species abundance in marine death assemblages. *Science* 294:1091–1094.
- . 2002. Time-averaged molluscan death assemblages: palimpsests of richness, snapshots of abundances. *Geology* 30:803–806.
- . 2007. Discordance between living and death assemblages as evidence for anthropogenic ecological change. *Proceedings of the National Academy of Sciences USA* 104:17701–17706.
- . 2008. Ecological fidelity of open marine molluscan death assemblages: effects of post-mortem transportation, shelf health, and taphonomic inertia. *Lethaia* 41:199–217.
- Kidwell, S. M., and D. W. J. Bosence. 1991. Taphonomy and time-averaging of marine shelly faunas. In P. A. Allison and D. E. G. Briggs, eds. *Taphonomy: releasing the data locked in the fossil record*. Topics in Geobiology 9:115–209. Plenum, New York.
- Kidwell, S. M., and P. J. Brenchley. 1994. Patterns in bioclastic accumulation through the Phanerozoic: changes in input or destruction? *Geology* 22:1139–1143.
- Kidwell, S. M., M. M. R. Best, and D. S. Kaufmann. 2005. Taphonomic trade-offs in tropical marine death assemblages: Differential time-averaging, shell loss, and probable bias in siliciclastic vs. carbonate facies. *Geology* 33:729–732.
- Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* 72:367–382.
- Kosnik, M. A., and P. J. Wagner. 2006. Effect of taxon abundance distributions on expected numbers of sampled taxa. *Evolutionary Ecology Research* 8:195–211.
- Kosnik, M. A., Q. Hua, G. E. Jacobsen, D. S. Kaufman, and R. A. Wüst. 2007. Sediment mixing and stratigraphic disorder revealed by the age-structure of *Tellina* shells in Great Barrier Reef sediment. *Geology* 35:811–814.
- Kowalewski, M., G. A. Goodfriend, and K. W. Flessa. 1998. High-resolution estimates of temporal mixing within shell beds: the evils and virtues of time-averaging. *Paleobiology* 24:287–304.
- Kowalewski, M., W. Kiessling, M. Aberhan, F. T. Fürsich, D. Scarponi, S. L. Barbour Wood, and A. P. Hoffmeister. 2006. Ecological, taxonomic, and taphonomic components of the post-Paleozoic increase in sample-level species diversity of marine benthos. *Paleobiology* 32:533–561.
- Krause, R. A. Jr., S. L. Barbour, M. Kowalewski, D. S. Kaufman, C. S. Romanek, M. G. Simões, and J. F. Wehmiller. 2010. Quantitative comparisons and models of time-averaging in bivalve and brachiopod shell accumulations. *Paleobiology* 36:428–452.
- Kurka, P., A. L. Šizling, and J. Rosindell. 2010. Analytical evidence for scale-invariance in the shape of species abundance distributions. *Mathematical Biosciences* 223:151–159.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911–927.
- . 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- Lockwood, R., and L. R. Chastant. 2006. Quantifying taphonomic bias of compositional fidelity, species richness, and rank abundance in molluscan death assemblages in from the upper Chesapeake Bay. *Palaio* 21:376–383.
- Loehle, C. 1990. Proper statistical treatment of species-area data. *Oikos* 57:143–145.
- Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *American Naturalist* 172:E48–E66.
- Loreau, M., and N. Mouquet. 1999. Immigration and the maintenance of local species diversity. *American Naturalist* 154:427–440.
- Magurran, A. E. 2007. Species abundance distributions over time. *Ecology Letters* 10:347–354.

- Magurran, A. E., and P. A. Henderson. 2003. Explaining the excess of rare species in natural species abundance distributions. *Nature* 422:714–716.
- Martin, R. E., S. P. Hippensteel, D. Nikitina, and J. E. Pizzuto. 2002. Artificial time-averaging of marsh foraminiferal assemblages: linking the temporal scales of ecology and paleoecology. *Paleobiology* 28:263–277.
- McGill, B. J. 2003. Does Mother Nature really prefer rare species or are log-left-skewed SADs a sampling artefact? *Ecology Letters* 6:766–773.
- McGill, B. J., E.A. Hadly, and B. A. Maurer. 2005. Community inertia of Quaternary small mammal assemblages in North America. *Proceedings of the National Academy of Sciences USA* 102: 16701–16706.
- McGinn, D. J., and M. W. Palmer. 2009. Modeling the sampling effect in the species-time-area relationship. *Ecology* 90:836–846.
- McKinney M. L., and W. D. Allmon. 1995. Metapopulations and disturbance: from patch dynamics to biodiversity dynamics. Pp. 123–183 in D. H. Erwin and R. Anstey, eds. *New approaches to speciation in the fossil record*. Columbia University Press, New York.
- McKinney, M. L., and D. Frederick. 1999. Species-time curves and population extremes: ecological patterns in the fossil record. *Evolutionary Ecology Research* 1:641–650.
- Meldahl, K. H., K. W. Flessa, and A. H. Cutler. 1997. Time-averaging and postmortem skeletal survival in benthic fossil assemblages: quantitative comparisons among Holocene environments. *Paleobiology* 23:207–229.
- Miller, A. L., and H. Cummins. 1990. A numerical model for the formation of fossil assemblages: estimating the amount of post-mortem transport along environmental gradients. *Palaios* 5:303–316.
- . 1993. Using numerical models to evaluate the consequences of time-averaging in marine fossil assemblages. In S. M. Kidwell and A. K. Behrensmeier, eds. *Taphonomic approaches to time resolution in fossil assemblages*. *Short Courses in Paleontology* 6:150–168. Paleontological Society, Knoxville, Tenn.
- Mouquet, N., and M. Loreau. 2002. Coexistence in metacommunities: the regional similarity hypothesis. *American Naturalist* 159:420–426.
- . 2003. Community patterns in source-sink metacommunities. *American Naturalist* 162:544–557.
- Munoz, F. P., Couteron, and B. R. Ramesh. 2008. Beta diversity in spatially implicit neutral models: a new way to assess species migration. *American Naturalist* 172:116–127.
- Murray, J. W. 2003. Patterns in the cumulative increase in species from foraminiferal time-series. *Marine Micropalaeontology* 48:1–21.
- Nee, S., R. D. Gregory, and R. R. May. 1991. Core and satellite species: theory and artefacts. *Oikos* 62:83–87.
- Olszewski, T. D. 2004. Modeling the influence of taphonomic destruction, reworking, and burial on time-averaging in fossil accumulations. *Palaios* 19:39–50.
- Olszewski, T. D., and S. M. Kidwell. 2007. The preservational fidelity of evenness in molluscan death assemblages. *Paleobiology* 33:1–23.
- Palmer, M. W., and P. S. White. 1994. Scale dependence and the species-area relationship. *American Naturalist* 144:717–740.
- Pandolfi, J. M. 1996. Limited membership in Pleistocene coral reef assemblages from the Huon Peninsula, Papua New Guinea: constancy during global change. *Paleobiology* 22:152–176.
- Pech, D., P.-L. Ardisson, E. Bourget, and A. R. Condal. 2007. Abundance variability of benthic intertidal species: effects of changing scale on patterns perception. *Ecography* 30:637–648.
- Peters, S. E. 2004. Evenness of Cambrian-Ordovician benthic marine communities in North America. *Paleobiology* 30:325–346.
- Peterson, C. H. 1976. Relative abundances of living and dead mollusks in two Californian lagoons. *Lethaia* 9:137–148.
- . 1977. The paleoecological significance of undetected short-term temporal variability. *Journal of Paleontology* 51:976–981.
- Powell, E. N., and H. Cummins. 1985. Are molluscan maximum life spans determined by long-term cycles in benthic communities? *Oecologia* 67:177–182.
- Powell, M. G., and M. Kowalewski. 2002. Increase in evenness and sampled alpha diversity through the Phanerozoic: Comparison of early Paleozoic and Cenozoic marine fossil assemblages. *Geology* 30:331–334.
- Preston, F. W. 1960. Time and space and the variation of species. *Ecology* 41:611–627.
- Purves, D. W., and S. W. Pacala. 2005. Ecological drift in niche-structured communities: neutral pattern does not imply neutral process. Pp. 107–138 in D. Burslem, M. Pinard, and S. Hartley, eds. *Biotic interactions in the Tropics*. Cambridge University Press, Cambridge.
- R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org
- Ranta, E., V. Kaitala, M. S. Fowler, J. Laakso, L. Ruokolainen, and R. O'Hara. 2008. Detecting compensatory dynamics in competitive communities under environmental forcing. *Oikos* 117:1907–1911.
- Ricklefs, R. E. 2007. History and diversity: explorations at the intersection of ecology and evolution. *American Naturalist* 170:S56–S70.
- Rosenzweig, M. L. 1998. Preston's ergodic conjecture: the accumulation of species in space and time. Pp. 311–348 in M. L. McKinney and J. A. Drake, eds. *Biodiversity dynamics*. Columbia University Press, New York.
- Russell, G. J. 1998. Turnover dynamics across ecological and geological scales. Pp. 377–404 in M. L. McKinney and J. A. Drake, eds. *Biodiversity dynamics*. Columbia University Press, New York.
- Sale, P. F. 1998. Appropriate spatial scales for studies of reef-fish ecology. *Austral Ecology* 23:202–208.
- Scarponi, D., and M. Kowalewski. 2007. Sequence stratigraphic anatomy of diversity patterns: Late Quaternary benthic mollusks of the Po Plain, Italy. *Palaios* 22:296–305.
- Sepkoski, J. J., Jr. 1988. Alpha, beta, or gamma: where does all the diversity go. *Paleobiology* 14:221–234.
- Sepkoski, J. J., Jr., R. K. Bambach, and M. L. Droser. 1991. Secular changes in Phanerozoic event bedding and the biological overprint. Pp. 298–312 in G. Einsele, W. Ricken and A. Seilacher, eds. *Cycles and events in stratigraphy*. Springer, Berlin.
- Šizling, A.L., D. Storch, J. Reif, and K. J. Gaston. 2009. Invariance in species-abundance distributions. *Theoretical Ecology* 2:89–103.
- Šizling, A.L., D. Storch, E. Šizlingová, J. Reif, and K. J. Gaston. 2009. Species abundance distribution results from a spatial analogy of central limit theorem. *Proceedings of the National Academy of Sciences USA* 106: 6691–6695.
- Staff G. M., and E. N. Powell. 1988. The palaeoecological significance of diversity: the effect of time-averaging and differential preservation on macroinvertebrate species richness in death assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology* 63:73–89.
- Staff, G. M., R. J. Stanton Jr., E. N. Powell, and H. Cummins. 1986. Time-averaging, taphonomy, and their impact on paleocommunity reconstruction: death assemblages in Texas bays. *Geological Society of America Bulletin* 97:428–443.
- Storch, D., and K. J. Gaston. 2004. Untangling ecological complexity on different scales of space and time. *Basic and Applied Ecology* 5:389–400.

- Storch, D., P. A. Marquet and J. H. Brown, eds. 2007. *Scaling biodiversity*. Cambridge University Press, Cambridge.
- Terry, R. C. 2008. Modeling the effects of predation, prey cycling, and time-averaging on relative abundance in raptor-generated small mammal death assemblages. *Palaios* 23:402–410.
- Thayer, C. W. 1983. Sediment-mediated biological disturbance and the evolution of marine benthos. Pp. 479–625 *in* M. J. S. Tevesz and P. L. McCall, eds. *Biotic interactions in Recent and fossil benthic communities*. Plenum, New York.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences USA* 101:10854–10861.
- Tjørve, E. 2005. Shapes and functions of species-area curves: a review of possible models. *Journal of Biogeography* 30:827–835.
- Tomašových A. 2006. Linking taphonomy to community-level abundance: insights into compositional fidelity of the Upper Triassic shell concentrations (Eastern Alps). *Palaeogeography, Palaeoclimatology, Palaeoecology* 235:355–381.
- Tomašových A., and S. M. Kidwell. 2009. Fidelity of variation in species composition and diversity partitioning by death assemblages: time-averaging transfers diversity from beta to alpha levels. *Paleobiology* 35:97–121.
- . 2010. The effects of temporal resolution on species turnover and on testing metacommunity models. *American Naturalist* 175:587–606.
- Vasseur, D. A., and J. W. Fox. 2007. Environmental fluctuations can stabilize food web dynamics by increasing synchrony. *Ecology Letters* 10:1066–1074.
- Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and relative species abundance in ecology. *Nature* 424:1035–1037.
- . 2007. Patterns of relative species abundance in rainforests and coral reefs. *Nature* 450:45–49.
- Wagner, P. J., M. A. Kosnik, and S. Lidgard. 2006. Abundance distributions imply elevated complexity of post-Paleozoic marine ecosystems. *Science* 314:1289–1292.
- Webber, A. J. 2005. The effects of spatial patchiness on the stratigraphic signal of biotic composition (Type Cincinnatian Series; Upper Ordovician). *Palaios* 20:37–50.
- White, E. P. 2004. Two-phase species-time relationships in North American land birds. *Ecology Letters* 7:329–336.
- . 2007. Spatiotemporal scaling of species richness: patterns, processes, and implications. Pp. 325–346 *in* Storch et al. 2007.
- White, E. P., P. B. Adler, W. K. Lauenroth, R. A. Gill, D. Greenberg, D. M. Kaufmann, A. Rassweiler, J. A. Rusak, M. D. Smith, J. R. Steinbeck, R. B. Waide, and J. Yao. 2006. A comparison of the species-time relationship across ecosystems and taxonomic groups. *Oikos* 112:185–195.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- Williamson, M., K. J. Gaston, and W. M. Lonsdale. 2001. The species-area relationship does not have an asymptote! *Journal of Biogeography* 28:827–830.
- Wilson, J. B., H. Gitay, J. B. Steel, and W. M. King. 1998. Relative abundance distributions in plant communities: effects of species richness and of spatial scale. *Journal of Vegetation Science* 9:213–220.
- Zillio, T., and R. Condit. 2007. The impact of neutrality, niche differentiation and species input on diversity and abundance distributions. *Oikos* 116:931–940.
- Zillio, T., and F. He. 2010. Inferring species abundance distribution across spatial scales. *Oikos* 119:71–80.
- Zuschin, M., M. Harzhauser, and K. Sauermoser. 2006. Patchiness of local species richness and its implication for large-scale diversity patterns: an example from the middle Miocene of Paratethys. *Lethaia* 39:65–80.