

ADDITIVE DIVERSITY PARTITIONING IN PALAEOBIOLOGY: REVISITING SEPKOSKI'S QUESTION

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Abstract: Using Whittaker's concepts of alpha, beta, and gamma diversity, Sepkoski asked how global diversity was assembled at scales ranging from the community to the province. In the years since, ecologists have recast diversity in terms of additive partitions where total diversity can be decomposed into sample-level alpha diversity plus the sum of a series of beta diversity terms that reflect progressively larger spatial scales. Given that marine alpha diversity represents a tiny fraction of global diversity, Phanerozoic global diversity patterns must be dominated by changes in beta diversity at one or more scales. A ballooning ecological literature demonstrates wide variation in beta diversity among

ecosystems, regions, and taxa, suggesting that large changes in beta diversity on evolutionary timescales are likely. But the question is which scales are the most important. Several recent palaeontological studies help to constrain beta diversity within sedimentary basins, and the emergence of sample-based databases puts an answer to Sepkoski's question within reach. A new method for calculating diversity partitions for richness is introduced, which allows the calculation of each species' contribution to alpha and beta diversity, as well as the contribution of each sampling unit to beta diversity.

Key words: diversity, palaeoecology, marine.

In two formative studies of vegetational changes along environmental gradients in the United States, Whittaker (1956, 1960) distinguished three types of diversity. Alpha diversity, so named because it was measured with Fisher's alpha (Fisher 1943), was the diversity in an individual stand (sampling area) or community. Beta diversity was proposed as a measure of the variation in taxonomic composition along an environmental gradient. Gamma diversity was the combined diversity for a range of environments present in a region. Since then, the concepts of all three have changed. Alpha is now regarded as the species richness at the finest scale of observation, but is generally not measured with Fisher's alpha. Gamma is generally the richness at the largest scale of observation. Beta diversity is commonly expressed as the ratio (Whittaker 1960, 1972) or the difference (Lande 1996) between gamma and alpha diversity. Regardless of how it is measured, beta diversity reflects the increase in diversity at larger spatial or temporal scales.

The Phanerozoic record of alpha diversity has been used to evaluate the biological significance of global diversity trends in the marine fossil record (Bambach 1977). For example, the similar trajectories of genus-level diversity within collections and global family-level diversity were taken as evidence that global-scale patterns were not an artefact of available rock volume as had

been suggested (Raup 1972, 1976) and that they were biologically meaningful (Sepkoski *et al.* 1981). As global-scale diversity patterns continue to be re-evaluated (Alroy *et al.* 2001, 2008; Peters and Foote 2001; Smith 2001, 2007; Jablonski *et al.* 2003; Wagner *et al.* 2007; McGowan and Smith 2008; Miller and Foote 2009; Kiessling *et al.* 2010), patterns in alpha diversity are likewise being re-examined, particularly with regard to the role of taphonomy and lithification in perceptions of diversity (Powell and Kowalewski 2002; Bush and Bambach 2004; Kowalewski *et al.* 2006; Wagner *et al.* 2006; Hendy 2009).

Ecological studies of the present consistently show that beta is a significant, if not the most significant, contributor to gamma diversity (e.g. Summerville and Crist 2005; Benedick *et al.* 2006; Gabriel *et al.* 2006; Kattan *et al.* 2006; Veech and Crist 2007; Navarrete and Halffter 2008; Rodriguez-Zaragoza and Arias-Gonzalez 2008). Likewise, a simple comparison of global marine diversity (1000–2500 genera during most of the post-Cambrian; Sepkoski 1997) and average diversity within habitats (20–60 species for the richest habitat; Bambach 1977) demonstrates the enormous discrepancy between the two. Assuming a conservative average of three species per genus (Krug *et al.* 2008), beta diversity must represent over 99 per cent of the global diversity signal. Understanding the Phanerozoic

history of alpha diversity is important in its own right because it sheds light on the changing structure of ecological communities (Kowalewski *et al.* 2006; Wagner *et al.* 2006), but the contribution of alpha diversity is far too small to play a central role in the interpretation or evaluation of global diversity. Even if these studies underestimate alpha diversity (for example, many Neogene samples in the Paleobiology Database exceed 100 species), the gulf between gamma and alpha is still gigantic. If we want to understand global diversity, we must understand the sources and magnitudes of beta diversity.

Valentine (1970, 1971; Valentine *et al.* 1978) proposed that provinciality exerts the dominant control on global marine diversity and argued that the observed increase in Phanerozoic diversity reflected an increased number of provinces through geological time. Sepkoski (1988) followed with a challenging question about what drives global diversity patterns, namely to what extent do global changes in diversity reflect community-level changes (alpha diversity) or some aspect of beta diversity, such as onshore-offshore differentiation, the waxing and waning of specialised habitats like reefs and hardgrounds, or provinciality? What makes Sepkoski's question particularly interesting is how he framed it, in particular, the idea that diversity might be decomposed into a series of partitions and that some partitions might be substantially larger than others.

MEASURING BETA DIVERSITY

In his original conception of beta diversity, Whittaker (1956) proposed measuring the ecological similarity of samples with the Jaccard Coefficient (also called the coefficient of community), that is, the ratio of the number of shared taxa to the total number of taxa in a pair of samples. To measure the beta diversity along a gradient, the ecological similarity of an endpoint along the gradient could be measured relative to successively more distant samples along the gradient. At some gradient position, the similarity with the endpoint would be 50 per cent, marking a half-change in composition. Using this new point as the starting point, the locations of successive half-changes could be found farther along the gradient, until the total length of the gradient could be measured in terms of the number of half-changes. Although Whittaker's original formulation of beta was explicitly cast in terms of position along an environmental gradient, numerous beta measures have since been proposed, many of which measure the overlap in taxon composition between samples or sets of samples, without regard to position along a gradient (see Koleff *et al.* 2003 for a thorough review of beta measures).

Whittaker (1977) later recognised the multiple scales of taxonomic variation among sampling units. In doing so, he redefined gamma diversity as diversity at the landscape scale and added provincial-scale differentiation (delta diversity) and global-scale diversity (epsilon). Although the terms delta and epsilon never became widely accepted, ecologists held onto the concept that diversity could be measured at multiple scales and that diversity should increase with the scale of a study. The diversity at any particular scale is an inventory (α) diversity, and the change in diversity between scales is known as turnover (β) diversity.

Alpha, beta, and gamma diversity also have a strong relationship to the shape of individual-based rarefaction curves and sample-based rarefaction curves (also called collectors curves; Gotelli and Colwell 2001; Olszewski 2004). Individual-based rarefaction curves describe taxon richness as the number of individuals censused increases (Hurlbert 1971; Raup 1975). When all individuals from a study area are pooled, their individual-based rarefaction curve provides an estimate of gamma, or total, diversity over a spectrum of sampling intensity. If individuals are randomly distributed among samples, a sample-based rarefaction curve will be identical to an individual-based rarefaction curve, indicating a lack of beta diversity. However, as individuals of taxa become increasingly aggregated within samples, the two curves will diverge as beta diversity increases.

TWO APPROACHES TO DIVERSITY PARTITIONING

Whittaker (1960, 1972) related mean inventory diversity at a local scale (α) to the inventory diversity at a larger spatial scale (γ) through a multiplicative factor, β :

$$\gamma = \bar{\alpha}\beta.$$

Similarly, diversity at an even larger scale (ε) would be equal to mean gamma diversity multiplied by a factor, δ :

$$\varepsilon = \bar{\gamma}\delta.$$

In this way, diversity could be examined at a series of progressively larger spatial scales, although raising the question of whether codifying each scale of diversity with a Greek letter really adds to an understanding of diversity (cf. Rosenzweig 1995; Kowalewski *et al.* 2006).

Although Sepkoski (1988) framed his paper in Whittaker's terms, he measured beta diversity with the Jaccard coefficient to avoid the distorting effects of variable numbers of samples. Even so, the point remains that diversity can be considered at a variety of spatial scales, with beta diversity reflecting the importance of variation at each scale in contributing to the total diversity of a system.

MacArthur *et al.* (1966), Levins (1968), Lewontin (1972) and Allan (1975) showed that diversity could also be partitioned additively rather than multiplicatively, with Lande (1996) later making the explicit connection to the alpha, beta, and gamma diversities of Whittaker. In additive diversity partitioning, beta is redefined as the diversity that is added by examining a larger spatial scale, that is, the difference between gamma and mean alpha diversity.

$$\gamma = \bar{\alpha} + \beta$$

In this formulation, beta diversity can be thought of as the diversity among a set of samples that is missing from an average sample (Veech *et al.* 2002). Progressively larger spatial scales are easily incorporated. For a study considering local diversity and three successively larger spatial scales, global diversity (γ) is

$$\gamma = \bar{\alpha} + \bar{\beta}_1 + \bar{\beta}_2 + \bar{\beta}_3$$

where mean α , mean β_1 , and mean β_2 are the means over the entire region (e.g. Okuda *et al.* 2004; Text-fig. 1).

Additive diversity partitioning has several advantages over multiplicative diversity partitioning (Veech *et al.* 2002; Heim 2009). Foremost, alpha, beta and gamma diversity share the same units in additive diversity partitioning and can be compared directly, whereas beta and delta are dimensionless ratios in the multiplicative approach (Lande 1996). Additive diversity partitioning is also ideally suited for multiple hierarchical levels of sampling because the beta diversity at each level is measured on the same scale (e.g. Wagner *et al.* 2000; Crist *et al.* 2003; Okuda *et al.* 2004), whereas the beta and delta of the multiplicative approach cannot be compared directly. Additive diversity partitioning can be applied not only to

richness, but also to Shannon's H and Simpson's D , which can provide a more informative picture of diversity changes (Lande 1996). Finally, additive diversity partitions can be recast as percentages of gamma diversity, allowing one to see not only the absolute changes in the size of a partition but also their relative (i.e. multiplicative) changes.

An alternative approach to measuring additive partitions

Additive partitions are typically calculated by first measuring gamma diversity, then finding mean alpha diversity and finally calculating their difference to give beta diversity. Alternatively, additive partitions may be calculated by measuring the contribution of each taxon to alpha and beta diversity. The contribution of the j th taxon to alpha diversity is

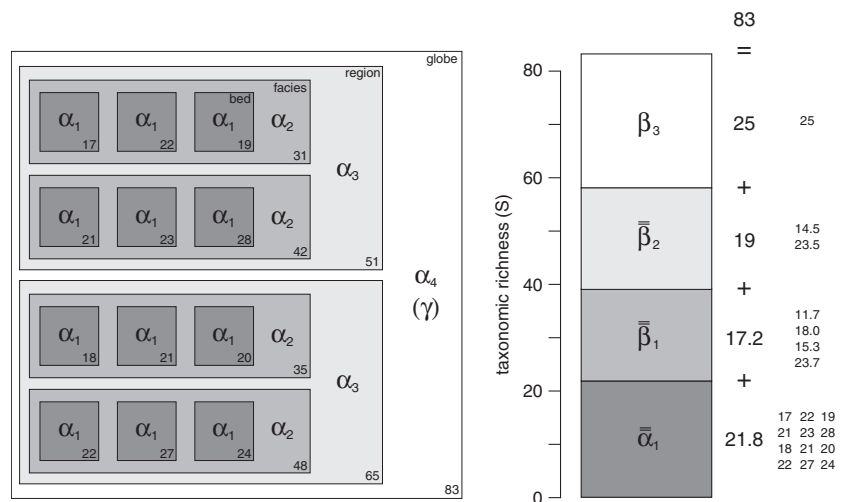
$$\alpha_j = \frac{n_j}{N}$$

where n_j is the number of sampling units that contain the j th taxon and N is the total number of sampling units. Similarly, the contribution of the j th taxon to beta diversity is

$$\beta_j = \frac{n_{-j}}{N}$$

where n_{-j} is the number of sampling units that do not contain the j th taxon. Mean alpha diversity of a group of sampling units is given by the sum of the alpha contributions from all taxa, with beta diversity among those sampling units being the sum of all beta contributions of the taxa. The advantage of this approach is that it allows the computation of the contribution of each sampling unit to beta diversity:

TEXT-FIG. 1. Schematic of sampling design of additive diversity partitioning, with four levels of inventory diversity (α_1 through α_3 , and γ) and three levels of turnover diversity (β_1 through β_3). Values of diversity are shown as a worked example of the calculation of diversity partitions.



$$\beta_i = \sum_{j=1}^p \frac{\beta_j}{n_j} x_{ij}$$

where i is the sampling unit, p is the total number of taxa (that is, gamma diversity), and x_{ij} is the presence (one) or absence (zero) of taxon i in sampling unit j . This approach could be used, for example, to determine which habitats contribute most to landscape-scale beta or which provinces contribute most to global-scale beta. R code for implementing these calculations is included in Appendix S1.

Using this formulation, a simple example illustrates how increased diversity is accommodated. Suppose there are ten sites, each with ten taxa unique to that site. Each site has an alpha diversity of 10, leading to a mean alpha diversity of 10. As the total (γ) diversity is 100, the beta diversity is the difference, or 90. If one endemic taxon is added to a single site, the alpha diversity of that site is now 11, but the mean alpha diversity is 10.1. The total (γ) is now 101, so beta diversity is 90.9 taxa. When that single taxon was added, it contributed 0.1 taxa to the alpha diversity and 0.9 taxa to the beta diversity. If, instead, a single cosmopolitan taxon had been added, the alpha of all collections would be raised by one, increasing mean alpha diversity by one. Gamma diversity would likewise be raised by one, and as the difference of gamma and mean alpha, beta would show no change. In short, as taxa are added, they may contribute partly to alpha and partly to beta, depending on how they are distributed among the sites. Sampling units with a large number of endemic or restricted taxa contribute more to beta diversity than sampling units dominated by widespread or cosmopolitan taxa.

DIVERSITY MEASURES FOR ADDITIVE PARTITIONING

Additive diversity can be applied to any measure measured that exhibits strict concavity (Lewontin 1972; Lande 1996). A diversity metric is strictly concave if the metric in a pooled set of samples is always greater than or equal to the average value of the metric among the samples; equality occurs when the samples are identical. Three diversity metrics exhibit strict concavity: richness, Shannon's H , and Simpson's D (Lande 1996). The term 'diversity' has a wide range of meanings among ecologists with little consensus. Some allow it to be used for any measure that describes the number and abundance of taxa, but others restrict it to simply a count of taxa. I use the term in the broader sense, as is typical of the additive diversity partitioning literature, but I try to be specific about how diversity is measured in any given study (cf. Spellerberg and Fedor, 2003).

Richness

Richness (S), the number of taxa within a sample, is the most intuitive and widely used metric for additive partitioning. Richness weights rare taxa equally with abundant taxa and is therefore highly sensitive to sampling effort (Lande 1996). Even when sampling effort is held constant, richness is generally dominated by rare taxa.

Shannon's H

Shannon's H (also called Shannon information and Shannon entropy; Box 1) is defined as

$$H = - \sum_{i=1}^n p_i * \log(p_i)$$

BOX 1

Shannon's H was developed originally for a mathematical theory of communication and shared the form of Gibbs' thermodynamic entropy (Gibbs 1902; equation 450, p. 137), which has roots going back to Boltzmann (1866). Although Claude Shannon (1948) was the first to present the metric in its familiar form, it is frequently also called the Shannon–Weaver index, the Shannon–Wiener index, and the Shannon–Weiner index (Spellerberg and Fedor 2003). Margalef (1957, translated from Spanish in Margalef 1958) introduced Shannon's metric to ecologists and attributed it to Shannon alone. Warren Weaver's name became associated with the metric because he edited the volume in which Shannon's original paper appeared, and because he and Shannon subsequently co-authored a frequently reprinted book (Shannon and Weaver 1949) that discusses the metric. At least as early as 1964 (Lloyd and Ghelardi 1964), Norbert Wiener's name was linked to the metric presumably because he authored an influential book on cybernetics (Wiener 1948), which included an integral formulation of entropy (p. 76) in the form of Gibbs' (1902) and because Shannon acknowledges the influence of Wiener (Spellerberg and Fedor 2003). Complicating matters, Norbert Wiener's name is frequently misspelled as Weiner. In short, although many authors have published on entropy, Shannon (1948) was the first to present it in the form commonly used by ecologists today. For this reason, the metric should be called Shannon's H or Shannon Entropy, but not Shannon–Weaver, Shannon–Wiener or Shannon–Weiner.

where p_i is the proportion of a sample represented by taxon i . The minimum value for Shannon's H occurs when all taxa but one have an abundance of one, and Shannon's H increases with richness and the total number of individuals. Shannon's H reaches a maximum at $\ln S$, when all taxa are equally abundant. Because Shannon's H is based on proportions rather than a simple count of taxa, it is less dominated by the effects of rare taxa than is richness. Shannon's H is an entropy measure, but can be converted to a diversity measure by the transformation, Shannon diversity = $\exp(H)$ (Jost 2006).

Simpson's D

Simpson's concentration (λ) is related to the probability that any two randomly selected individuals from a population belong to the same taxon (Simpson 1949):

$$\lambda = \sum_{i=1}^n p_i^2.$$

The minimum value of lambda is $1/S$, and it occurs when all taxa are equally abundant. Lambda reaches a maximum approaching one when most individuals belong to a single taxon. As a result, the inverse of Simpson's concentration is often used as a measure of diversity (Jost 2006). Because common taxa contribute much more to lambda than do rare taxa, Simpson's lambda is a measure of dominance.

$$D = 1 - \lambda$$

Simpson's D is a measure of evenness equal to and is also known as the Gini Coefficient (Lande 1996). Hurlbert's PIE is an unbiased estimator of the probability of inter-specific encounter and is equal to Simpson's D multiplied by $N/N - 1$, where N is the number of individuals (Hurlbert 1971; Olszewski 2004). Of the three measures suitable for additive diversity partitioning, Simpson's D is the least sensitive to rare taxa. Simpson's D is also the least biased at small sample sizes and has the smallest standard error (Lande 1996).

Richness, Shannon's H , and Simpson's D can be used in concert to understand how all parts of an abundance distribution contribute to diversity in the broad sense. Richness provides information on the rare tail of the taxon abundance distribution, whereas Simpson's D reflects the abundant end of the distribution and Shannon's H is an intermediate measure.

These and other diversity measures can be performed with the vegan package for R (Oksanen *et al.* 2009) and

with the software package PAST (Hammer and Harper 2005).

THREE ECOLOGICAL QUESTIONS

Among ecologists, additive diversity partitioning has raised three classes of questions. At the most basic level is a discussion about pattern: how is landscape-scale diversity assembled, that is, does it primarily reflect high community-level diversity or strong differentiation? Second, do the observed relative sizes of partitions reflect anything more than random sampling? Finally, and most importantly, what ecological processes control the sizes of diversity partitions?

What are the important sources of diversity?

A survey of modern landscape-scale studies of additive diversity partitioning demonstrates consistently high values of beta in trees, herbs, insects, aquatic invertebrates, fishes, and birds (Table 1). Although in some cases, beta may be as low as 25 per cent, total beta is commonly >70 per cent. Time and resources prevent comprehensive sampling at the largest spatial scale in these studies, and as a result, gamma (total) diversity is almost certainly underestimated. Increased numbers of sample localities would not likely increase mean alpha diversity, but they would increase beta, making it likely that all of these betas are minimum estimates.

Many of these studies sampled at four spatial scales, corresponding approximately to a site (quadrat, for example), a habitat, a location composed of several habitats and a region or landscape containing multiple locations. Patterns in beta diversity across these scales are inconsistent. For example, beta diversity among sites is larger than beta diversity among habitats in only about half of the studies. The same is true when comparing beta among habitats to beta among locations. This heterogeneity is an important feature, and it may reflect differences in the precise scaling of measurements in the study areas, differences in the type of ecosystem studied or organismal differences. Regardless of its origin, there appears to be no simple rules to the size of beta at progressively larger scales.

Many studies have also compared spatial turnover with temporal turnover (usually seasonal, but sometimes annual) to estimate the magnitude of temporal change and to scale it against a spatial factor. Again, results are mixed. In some cases, increased spatial coverage yields more diversity than longer temporal coverage (e.g. Tylianakis *et al.* 2005; Boonzaaijer *et al.* 2007; Sobek *et al.* 2009). Others find that temporal turnover is an important

TABLE 1. Percentage contribution of diversity partitions to total (γ) diversity for a range of modern-day organisms and habitats.

Study	alpha	beta micro-scale	beta meso-scale	beta macro-scale
Forest plants, Italy Chiarucci <i>et al.</i> 2008	3 subplot	4 among subplots	31 among plots	62 among regions
Forest plants, United States Chandy <i>et al.</i> 2006	44 plot	24 among plots	20 among research area	12 among subregions
Agricultural weeds, Germany Gabriel <i>et al.</i> 2006	3–16 plot	5–16 among plots	17–37 among fields	14–25 among region
Prairie plants, United States Wilsey <i>et al.</i> 2005	25 site	75 among sites		
Butterflies on farms, Sweden Rundlof <i>et al.</i> 2008	67–73 field	27–33 among field		
Butterflies, Great Basin, United States Fleishman <i>et al.</i> 2003	40 site	21 among canyon segments	25 among canyons	14 among mountain ranges
Agricultural arthropods, Europe Hendrickx <i>et al.</i> 2007	40–51 local	49–60 within landscape		
Insects, midwestern United States Gering <i>et al.</i> 2003	9 tree	11/21 among trees/ among stands	29 among sites	29 among ecoregions
Aquatic invertebrates, Sweden Stendera and Johnson 2005	5–7 site	44–46 among sites	16 among ecoregions	32–33 among bioregions
Reef fish, Caribbean Rodriguez-Zaragoza and Arias-Gonzalez 2008	10 site	20 among sites	20 among habitats	50 among reefs
Riverine fish, Hungary Eros 2007	21 site	37 among sites	41 between habitat	
Riverine fish, United States Pegg and Taylor 2007	17–36 site	16–23 among sites	17–29 among reaches	
Birds, United States Veech and Crist 2007	13 point	31 among points	56 within landscape	
Birds, Great Basin, United States Fleishman <i>et al.</i> 2003	13 site	18 among canyon segments	36 among canyons	33 among mountain ranges
Coastal wetland birds, Brazil Guadagnin <i>et al.</i> 2005	6/62 site (fragments only/lagoons included)	94/38 among site (fragments only/ lagoons included)		

component of beta diversity (Devries *et al.* 1999; Summerville and Crist 2005; Hirao *et al.* 2007). The amount of beta diversity varies seasonally in some cases (Murakami *et al.* 2008), but doesn't in others (Walla *et al.* 2004). Such heterogeneity is important because it suggests that beta diversity at various scales may change over geologic time as taxonomic composition and ecological structure change within communities, landscapes and provinces.

Several studies have contrasted the role of beta diversity in terms of taxonomic diversity and functional diversity. Two important recent studies reach the same conclusion that beta diversity may be high in taxonomic terms, but may be much lower in terms of functional diversity, suggesting a high degree of functional redundancy among taxa (Ricotta and Burrascano 2008; de Bello *et al.* 2009). From an evolutionary viewpoint, this contrast between taxonomic and functional diversity raises the questions of how and why functional redundancy within ecosystems has varied over geologic timescales.

Is the signal statistically different from random?

Because sampling at any level within a hierarchy will never completely capture all of the diversity at that level, it is possible that observed values of beta diversity merely reflect the chance effects of sampling rather than true ecological structure. Several approaches to this problem have been developed, including ANOVA-like analyses (Couteron and Pelissier 2004) and analytical formulas for confidence intervals (Kiflawi and Spencer 2004). By far the most common approach is randomisation (e.g. Crist *et al.* 2003, Veech 2005; Freestone and Inouye 2006; Cornell *et al.* 2007; Deblauwe *et al.* 2008; Ribeiro *et al.* 2008). Randomisation tests can be either individual-based or sample-based and can be performed with the PARTITION software (Crist *et al.* 2003).

Individual-based randomisation tests whether the observed diversity partitions could have been generated by a random distribution of individuals at the lowest level

of the sampling hierarchy. To accomplish this, individuals at the lowest level are randomly shuffled among all of the samples. This shuffling is done while preserving the total number of individuals in each taxon and the total number of individuals in each sample, that is, randomising without replacement. The number of sampling units at each level of the hierarchy is maintained as in the original sampling scheme. After randomisation, the sizes of all diversity partitions are calculated. This process is repeated 1000–10 000 times to generate mean values and confidence limits for the size of each diversity partition. The observed partitions are compared to the randomised partitions to identify partitions that contain either more or less diversity than would be predicted by a random distribution of individuals among samples. Because this approach involves one randomisation for the entire sampling hierarchy, the partitions in any one randomisation are additive, just as they are in the original sampling.

Sample-based randomisation tests whether the observed partitions reflect sampling design. In it, samples at the $i-1$ level are randomised relative among samples at the i level for all that comprise the same sample at the $i-1$ level. For example, suppose insects were sampled at the levels of a single tree, a stand of trees, a forest, a region and a continent. To assess beta diversity at the level of a stand of trees, trees would be randomly shuffled among stands found within a single forest. This randomisation and calculation of beta at this level would be repeated 1000–10 000 times to provide null estimates of beta and its confidence interval, which would be compared to the observed estimate of beta. This process would be repeated separately for each level in the hierarchy. Because the randomisation at each level is performed separately, the diversity partitions among all of the levels are not additive as they are in the original data or in an individual-based randomisation.

Although richness is strongly controlled by sample size (Hurlbert 1971; Raup 1975), rarefaction is not required in these randomisation tests or in the original calculation of the diversity partitions because alpha diversity is weighted by sample size, such that larger samples contribute more strongly to the estimate of diversity than do smaller samples (Crist *et al.* 2003).

What are the underlying controls on beta diversity?

Beta diversity reflects the differences in taxonomic composition among sampling areas. Identifying the processes responsible for beta diversity requires comparison to some external data, such as the environmental characteristics of sites or geographical distances among them. Comparison with ordinations (e.g. Eros 2007) and regression against external variables (e.g. Hofer *et al.* 2008) are

useful techniques for establishing the controls on beta diversity. Although chance has an effect on beta diversity, niche differences and environmental heterogeneity, as well as geographical distance and dispersal limitation, play dominant roles.

Most modern ecological studies of additive diversity partitioning have focussed on habitat patches within landscapes, and they have most commonly attributed beta diversity to niche differences and environmental heterogeneity (e.g. Stendera and Johnson 2005; Gabriel *et al.* 2006; Eros 2007; Buckley and Jetz 2008). Because habitat patches are heterogeneous and because taxa differ in all aspects of their niches (optimum, breadth and maxima), patches differ in their taxonomic composition and in the rank abundances of taxa (Kattan *et al.* 2006). In terrestrial studies, which dominate research into diversity partitioning, physical factors are often implicated and include such factors as canopy coverage and soil temperature (Navarrete and Halffter 2008), moisture (Lindo and Winchester 2008), solar and topographical variability (Hofer *et al.* 2008), climate heterogeneity (Veech and Crist 2007) and elevation (Pineda and Halffter 2004). Many studies document the importance of physical complexity of a habitat in increasing beta diversity (e.g. Benedick *et al.* 2006; Deblauwe *et al.* 2008; Economo and Keitt 2008). Chemical factors are also important for beta diversity, such as the use of fertilisers (Chalcraft *et al.* 2008; Klimek *et al.* 2008) or organic farming methods (Rundlof *et al.* 2008). Biotic factors also affect diversity partitioning, such as invasive taxa (Hulme and Bremner 2006), the presence of predators and parasites (Brockhurst *et al.* 2004), the diversity of prey taxa (Tylianakis *et al.* 2006), the existence of biotic gradients (Belmaker *et al.* 2008), and body size and diet breadth (Summerville *et al.* 2006).

Environmental heterogeneity is commonly thought of in spatial terms, but temporal heterogeneity can be equally important. For example, seasonality exerts a strong control in leaf quality and the abundance of predators, and as a result, their patterns of alpha and beta diversity have a strong seasonal component (Devries and Walla 2001; Murakami *et al.* 2008). Disturbance, which has both spatial and temporal components, also raises heterogeneity and beta diversity (Polley *et al.* 2005; Verdu *et al.* 2007; Klimek *et al.* 2008).

Although diversity is generated by heterogeneity at a wide range of spatial scales, dispersal limitation and geographical distance play an increasing role at the largest scales (Freestone and Inouye 2006; Veech and Crist 2007). Dispersal tends to increase diversity at the alpha level, but has a homogenising effect at larger scales, reducing both gamma and beta diversity (Mouquet and Loreau 2003; Cadotte and Fukami 2005). The degree to which dispersal limitation matters depends greatly on the organism and setting; for example, insects display

dispersal limitation (Tylianakis *et al.* 2006; Navarrete and Halffter 2008), but corals do not (Cornell *et al.* 2007). Distance itself is not the only consideration, and habitat isolation and fragment size can significantly impact diversity (MacArthur and Wilson 1967; Hubbell 2001; Pineda and Halffter 2004). For example, beta diversity of epiphytes is lower in isolated trees than in forests (Flores-Palacios and Garcia-Franco 2008).

Controls on diversity partitioning commonly show complicated variations, across space, through time, and among taxa, and a few examples illustrate this complexity. In one study, beta diversity in butterflies was affected by vertical zonation within forests and by regional differences, but varied little through time (Walla *et al.* 2004). In other studies of forest butterflies, seasonality contributed to beta, but differentially among the canopy and understory (Devries and Walla 2001). In a study of rocky intertidal sessile invertebrates, a latitudinal gradient elevated beta diversity in lower latitudes relative to high latitudes, but the effect was primarily felt at larger spatial scales (Okuda *et al.* 2009). Furthermore, the latitudinal gradient was expressed primarily in richness, a reflection of rare taxa, but not in Simpson's *D*, an indicator of common taxa (Okuda *et al.* 2004). Similarly, ecoregional differences controlled richness in another study, but Simpson's *D* and Shannon's *H* were governed by local factors (Summerville *et al.* 2003). Even within single areas, taxa differ in what controls their diversity patterns: butterfly diversity was dominated by alpha, but not for birds, and the importance of beta increases at progressively larger spatial scales for birds, but not for butterflies (Fleishman *et al.* 2003).

The complexity of these patterns in modern-day settings has an important implication for palaeontology: the great range of patterns and controls on diversity partitioning seen today among taxa and at different spatial scales suggests it is likely that beta diversity may change markedly over geological time. The question raised by the complexity of these patterns is whether 'the explanation of these facts [will] degenerate into a tedious set of case histories, or is there some common pattern running through them all' (MacArthur 1972, p. 169).

PALAEOLOGICAL APPLICATIONS, SO FAR

The majority of modern ecological studies of additive diversity partitioning have been conducted in terrestrial and aquatic settings (but see Price 2002; Okuda *et al.* 2004, 2009; Cornell *et al.* 2007; Belmaker *et al.* 2008; Rodriguez-Zaragoza and Arias-Gonzalez 2008). Although the patterns and principles from terrestrial and aquatic settings might inform what could be expected in marine

settings, direct understanding of diversity partitioning of subtidal marine invertebrates is known from relatively few studies, both modern and ancient.

Before diversity partitioning can be applied in the ancient past, the critical question is whether the marine fossil record has sufficient fidelity for observed diversity partitions to be meaningful. Initial results suggest it does (Tomasovych and Kidwell 2009). Using eleven regional data sets from siliciclastic soft-bottom settings, Tomasovych and Kidwell (2009) compared diversity partitioning at the alpha (sample) level and beta (among-samples within a region) level. Beta diversity is consistently lower among death assemblages than in living assemblages by approximately 25 per cent. Alpha diversity is correspondingly greater in death assemblages than living assemblages. Gamma (within region) diversity is only slightly greater in death assemblages. These patterns are attributed to time-averaging, which allows for the mixing of assemblages through time over relatively small spatial scales. As a result, the diversity of death assemblages is somewhat greater than living assemblages, and fewer distinct community types are recognised within death assemblages. Similar effects were noted in several modern studies, where rapidly conducted or spatially limited sampling depressed alpha diversity and raised among-sample beta diversity (e.g. Devries and Walla 2001; Kattan *et al.* 2006; Greenstreet and Piet 2008). This is encouraging news, because it suggests that alpha level diversity of readily preserved taxa may be captured more reliably in the fossil record than by sampling techniques in modern environments (cf. Kidwell 2008).

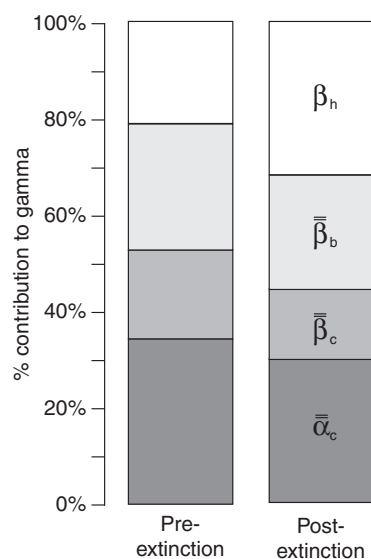
That the fossil record is a source of reliable data for diversity partitioning is important, because studies of the fossil record add exciting new dimensions to diversity partitioning studies: how diversity partitions change in response to long-term biotic events and whether these changes are consistent or idiosyncratic. Three studies have so far explored the response of marine invertebrate diversity partitioning to regional changes, with one focusing on the restructuring following a regional extinction event, and two examining the responses to biotic invasions.

The effects of regional extinction

Layou (2007) developed a general null model to predict how a pulse of extinction should affect the sizes of diversity partitions within collections, beds, habitats and regionally. In her model, total regional (γ) diversity is the sum of mean collection diversity, among-collections (within a bed) diversity, among-beds (within a habitat) diversity and among-habitats (within the region) diversity. In her model, the relative per cent contribution of alpha diversity and of beta diversity at all levels are relatively constant at

moderate and nonselective extinction intensities (<75–80 per cent extinction). At higher levels of extinction, alpha diversity increases at the expense of all beta diversities as the per cent of extinction increases, and beds, collections and habitats become more similar to one another. When extinction is selective for rare taxa, alpha diversity steadily increases across all values of per cent extinction, primarily at the expense of among-habitat beta diversity, suggesting that the loss of rare taxa primarily has the effect of making habitats more similar to one another in taxonomic composition. For extinction selective for abundant taxa, beta diversity at the highest level increases at the expense of all other diversity partitions, up to exceptionally intense extinctions (>60 per cent extinction).

Applying her model to a Late Ordovician regional extinction of benthic invertebrates in the eastern United States (Patzkowsky and Holland 1993), Layou (2007) found decreases in alpha and the two smallest scales of beta diversity, but an increase in among-habitat beta diversity (Text-fig. 2). These results are consistent with the abundant-selective extinction model for moderate extinction intensities, consistent with the observed 40 per cent extinction for this event (Patzkowsky and Holland 1997). The change in relative sizes of partitions is driven here mostly by a 17 per cent drop in alpha diversity, with total beta diversity showing <1 per cent increase. Layou's (2007) approach is particularly valuable because her null model makes predictions about changes in diversity partitions and elevates the study beyond the purely descriptive.



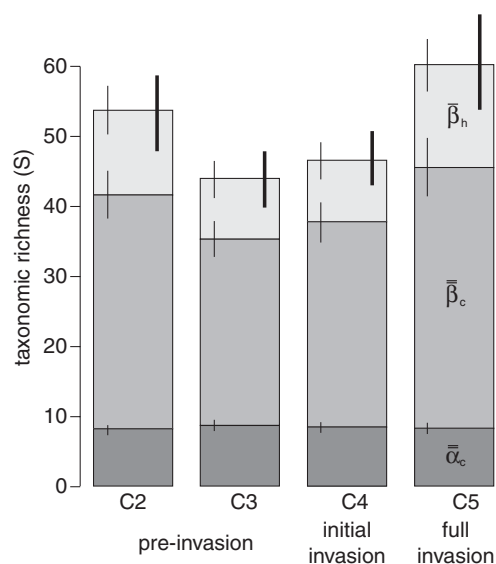
TEXT-FIG. 2. Additive diversity partitions as a percentage of gamma diversity, before and after a regional extinction in the Late Ordovician of the eastern United States. Beta diversities correspond to among-collections (c; within-bed), among-beds (b; within-habitat), and among-habitat (h; within-landscape). Figure modified from Layou (2007).

The effects of biotic invasions

To understand the effects of migration on diversity partitioning, Heim (2008) developed a random branching model of evolution that incorporated migration among three continents. His results show that decreased migration rates foster differentiation among continents, mirroring the results of ecological investigations into the role of dispersal at smaller scales (e.g. Mouquet and Loreau 2003; Cadotte and Fukami 2005). Increased migration can increase global diversity by lowering the probability that a taxon will go extinct, because global extinction of a taxon requires its separate extinction on each of the continents. This effect of migration stands in contrast to ecological studies at smaller scales where increased dispersal lowers gamma diversity (e.g. Mouquet and Loreau 2003; Cadotte and Fukami 2005). Heim (2009) also reported that all models proceeded to an equilibrium diversity determined by the relative rates of origination, extinction and migration and that the time to equilibrium is generally equal to or longer than the average Phanerozoic stage.

Patzkowsky and Holland (2007) studied changes in diversity partitioning among benthic invertebrates during a Late Ordovician biotic invasion on the Cincinnati Arch in the eastern United States. Their sampling consisted of collections within two habitats, and through four depositional sequences, giving partitions for alpha diversity, among-collection beta diversity, and between-habitat beta diversity. Through four depositional sequences collectively spanning 5 myr, alpha diversity remained nearly unchanged, compared to marked increases in among-collection beta diversity (41 per cent) and among-habitat beta diversity (68 per cent) as a result of the invasion, producing a net 37 per cent increase in diversity across the region (Text-fig. 3). In contrast, partitions based on Simpson's *D* showed virtually no change and were dominated by the alpha level, suggesting that diversity changes during the biotic invasion were dominated by less abundant to rare taxa. This is supported by the presence of several dozen genera known from museum collections to be invaders but that were never encountered in the study. This pattern of higher partitions being dominated by rare taxa is common in modern ecological studies.

Patterns of partitioning varied within habitats during this invasion. For example, richness in the shallow subtidal showed a modest but statistically insignificant decline, whereas deep subtidal richness was constant. Among-collection beta diversity in richness showed a much greater increase in the deep subtidal (55 per cent) than in the shallow subtidal (27 per cent). Likewise, alpha diversity as Simpson's *D* showed a slight but statistically insignificant rise in the deep subtidal, but fell in the shallow subtidal. Within-habitat beta diversity for Simpson



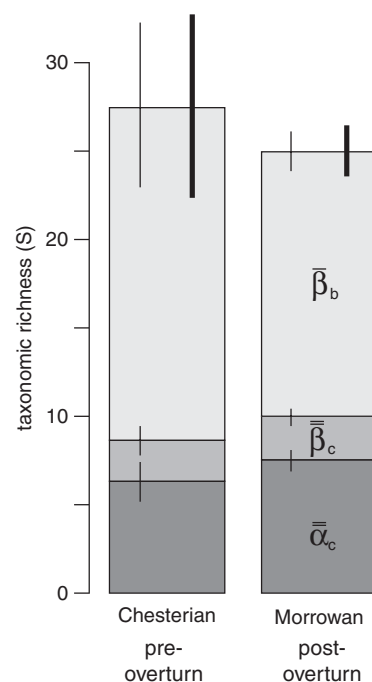
TEXT-FIG. 3. Additive diversity partitions during a Late Ordovician biotic invasion in the eastern United States. Beta diversities correspond to among-collections (c; within-habitat) and among-habitat (h; within-landscape). Thin vertical bars indicate 95 per cent confidence interval on individual diversity partitions; thick vertical bar at top indicates 95 per cent confidence interval on total (γ) diversity. Figure modified from Patzkowsky and Holland (2007).

rose by 21 per cent in the shallow subtidal, but by 33 per cent in the deep subtidal. These suggest that the diversity of common taxa fell within collections in the shallow subtidal and that the differentiation among samples within a habitat rose more for abundant taxa in the deep subtidal than the shallow subtidal.

An ordination analysis of these data (Holland and Patzkowsky 2007) sheds light on these partitions. Ordination indicated that the primary control on the taxonomic composition and abundance structure of collections is related to water depth, with substrate consistency as a secondary control. Furthermore, because a depositional sequence reflects 1–2 myr of geological time, faunal turnover within a sequence adds to differences among collections. Although segregation of samples into shallow subtidal and deep subtidal habitats helps isolate that aspect of faunal variation in the diversity partitions, some amount of faunal turnover still occurs with depth within a habitat, as well as faunal variation related to substrate consistency, patchiness and temporal turnover.

Faunal turnover events

Heim (2009) examined changes in brachiopod diversity partitioning across the mid-Carboniferous (Mississippian/Pennsylvanian) boundary, a time of both immigra-



TEXT-FIG. 4. Additive diversity partitions during a regional biotic overturn, with both extinction and migration, in the Carboniferous of the south-central United States. Beta diversities correspond to among-collections (c; within-beds) and among-beds (b; within-habitat). Confidence limits are shown as in Text-fig. 3. Figure modified from Heim (2009).

tion and regional extinction in the mid-continent of the United States. In terms of richness, brachiopods show a slight increase in alpha diversity and within-bed diversity, and a slight decrease in among-bed diversity, but none of the changes were statistically significant (Text-fig. 4). Heim measured evenness with E_{ss} , a metric that asymptotically approaches Simpson's D as the number of taxa goes to infinity (Peters 2004). Evenness increased within collections, but decreased for both within-bed and among-bed beta diversity, but none of these changes were statistically significant. If the patterns are real, but statistically insignificant owing to low sample sizes, they would suggest that communities became richer, with increased patchiness on beds, but decreased differentiation within the region, and that these changes are driven primarily by changes in the most abundant taxa. On the whole, however, changes in the sizes of the diversity partitions were modest (maximum of 24 per cent change) during this time of faunal turnover.

PROMISING DIRECTIONS

Even as interest renews in characterising Phanerozoic marine global diversity patterns, there is a growing

realisation that interesting insights also lie at smaller scales, particularly in spatial patterns of diversity (e.g. Miller 1997; Vermeij and Leighton 2003; Jablonski 2009). Additive diversity partitioning offers palaeobiology a way to dissect global diversity, to rank the relative contributions of diversity at all scales from the patch to the province, and to understand the causes of diversity changes at those scales.

Sampling issues

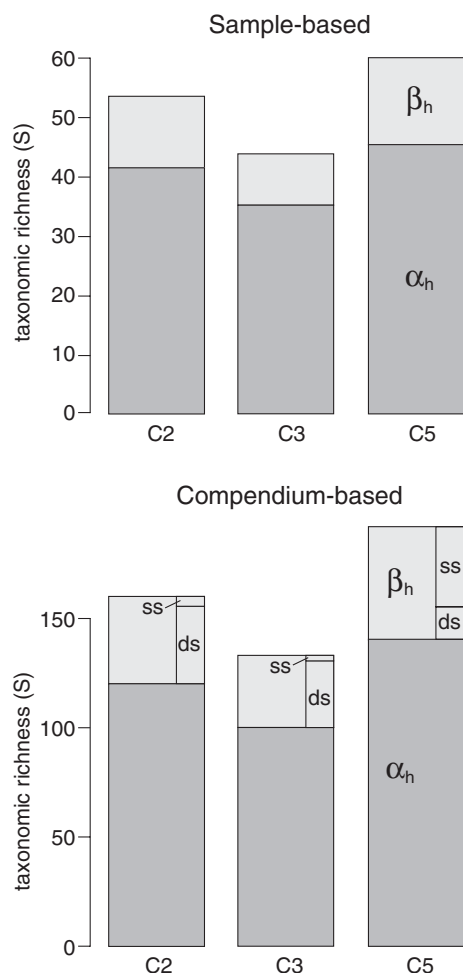
Sampling is the principal hurdle for applying additive diversity partitioning to the fossil record, and the issue presents itself in at least three ways. First, there is the question of sampling within geological units (i.e. beds, depositional facies and sedimentary basins) and how this corresponds to relevant ecological units (Kowalewski *et al.*, 2006; Scarponi and Kowalewski, 2007). In part, geologically defined sampling units are required partly out of necessity; they are what palaeontologists have to work with. There is also a broad correspondence of these geological sampling units with ecologically meaningful units. The scale of a sampled bed is approximately equivalent to the scale of a box core containing time-averaged dead fauna, for example. At least in marine environments, depositional facies are defined by grain size, bedding and sedimentary structures, many of which reflect features that are important to benthic invertebrates, such as shear stress, substrate consistency and oxygen availability. Depositional basins are large-scale sampling units of approximately the same scale as ecological landscapes. Other sampling units may be possible in the fossil record, and it will be critical to evaluate the differences in scale among studies when comparing their results, particularly when dealing with organisms of varying dispersal capabilities (cf. Gaston and Blackburn, 2000).

Second, additive partitioning requires that sampling intensity be equal across all elements at a given scale, in other words, the sampling design should be balanced. For example, in a sampling design consisting of depositional sequences, depositional facies and beds, the size of each sampled bed should be comparable, each facies should have the same number of beds, and each sequence should have the same sampled facies. If sampling is incomplete at one level, such as too few samples within a particular facies, the diversity in that facies will be depressed relative to other facies. This will lower the mean alpha diversity at that level, lowering the beta diversity for the level below and raising the beta diversity at the level above. Conversely, overly intense sampling at one level will raise the mean alpha diversity at that level, elevating beta diversity for the level below and depressing the beta diversity of the level above.

Layout (2007) and Heim (2009) were aware of additive diversity partitioning at the onset of their study and developed balanced sampling designs. The sampling in Patzkowsky and Holland (2007) was conducted prior to learning of additive partitioning and was therefore not balanced. To achieve a balanced design, Patzkowsky and Holland (2007) removed those habitats that could not be sampled consistently through time, removed depositional sequences that lacked a core set of shared habitats and subsampled to equalise the sampling intensity within habitats. A similar strategy could be used in other studies designed without additive diversity partitioning in mind.

Finally, sampling poses a challenge in bridging from regional-scale studies to the global scale. The iconic pattern of global diversity (e.g. Sepkoski 1997) was estimated from tabulations of first and last occurrences of taxa. Such compendia include many taxa so rare that they are known from only a few specimens and are unlikely to be encountered in any bed-scale sampling. For example, an intensive study in the Ordovician of the Cincinnati Arch encountered 57 genera within 1900+ samples (Holland *et al.* 2001), yet 185 genera have been reported historically from these strata. Although some of these genera may have been encountered in the field yet not recognised as a distinct genus (e.g. some ramose trepostomes), the majority were too rare to be found. These rare taxa dominate genus-level diversity within a compendium-based analysis, but would be absent in a collection-based study. The extent to which rare taxa alter temporal diversity patterns depends on the variation in taxon abundance distributions through time (Kosnik and Wagner 2006; Wagner *et al.* 2006). Promising approaches to capturing this rare tail have recently been developed (Harnik, 2009).

This compendium effect of rare taxa can be compared to the diversity partitions of Patzkowsky and Holland (2007) using a compilation of all reported taxa from the type Cincinnati (http://www.uga.edu/strata/cincy/fauna; Text-fig. 5). Among-habitat beta diversity is 16–24 per cent of the within-habitat mean alpha diversity in the sample-based data, but is 33–37 per cent in the compendium-based data. In short, the compendium contains almost double the number of rare taxa limited to a single habitat than a sample-based study indicates. Whether the compendium pattern is a better reflection of reality is difficult to know, as patterns of sampling intensity in that compendium cannot be determined. The more important issue is that compendium-derived diversity estimates cannot be reconciled with sample-based diversity estimates, particularly when they are compiled at greatly different scales (e.g. Sepkoski's (2002) compendium vs. local collections). For example, the compendium-scale diversity is nearly triple the sample-based diversity in the example above (Text-fig. 5).



TEXT-FIG. 5. Additive diversity partitions during a Late Ordovician biotic invasion in the eastern United States, illustrating the differences between diversity partitions calculated from field censuses (upper figure, modified from Patzkowsky and Holland 2007) and from a compendium of reported genera (lower figure). Diversity partitions reflect alpha diversity within a habitat (equal to sum of collection-level alpha diversity and among-collections beta diversity of Text-fig. 3) and among-habitat beta diversity. Note that the relative contributions of the shallow subtidal (ss) and deep subtidal (ds) to among-habitat beta diversity are shown for the compendium-based analysis, based on the new approach to calculating diversity partitions presented in this paper. The faunal invasion prior to and during the C5 sequence marks a substantial reversal in the relative contributions to beta diversity of these two habitats.

More recently, global diversity has been estimated through sample standardisation techniques applied to compilations of local occurrences (e.g. Alroy *et al.* 2008). Such approaches ease the problem of comparing diversity at greatly different scales by maintaining a constant sampling effort through time, but so far have not been balanced with respect to provinces or sedimentary

environments. The structure of the Paleobiology Database makes balanced subsampling feasible, and conducting it will require targeted addition of new data from specific sedimentary environments. A promising development is the shareholder quorum subsampling method (Alroy, 2010), which provides an objective and consistent way to define sampling quality, makes sampling intensity equivalent at different scales and corrects for unbalanced sampling.

Changes that could be investigated

Modern ecologists are increasingly interested in the question of diversity partitioning, both from the aspect of documenting the spatial scaling of diversity to guide conservation policy and from the perspective of understanding how ecological processes shape diversity at a range of scales. Additive diversity partitioning is an exciting and timely opportunity for palaeobiologists because palaeobiological data are uniquely suited for understanding the evolution of diversity partitioning. Many aspects at the regional scale are easily within reach, such as changes in onshore–offshore partitioning and changes in partitioning within habitats. In particular, it is relatively easy to address how these change in response to external factors such as migration and extinction (e.g. Layou 2007; Patzkowsky and Holland 2007; Heim 2009), or relative to global-scale phenomena such as Ordovician radiation, the Palaeozoic plateau in diversity, or the Mesozoic–Cenozoic rise in diversity. Larger-scale issues such as provinciality (e.g. Valentine 1971; Valentine *et al.* 1978; Miller *et al.* 2009) or latitudinal gradients (Roy *et al.* 2000; Valentine *et al.* 2008) could also be addressed through additive diversity partitioning, although the larger spatial scale will make balanced sampling more difficult.

Not only can taxonomic diversity be addressed through additive partitioning, but other forms of diversity can as well. Ecologists have noted how differing patterns of functional and taxonomic diversity indicate substantial functional redundancy among taxa. Existing methods of describing marine functional diversity are well developed (e.g. Bambach *et al.* 2007; Novack-Gottshall 2007) and lend themselves to additive partitioning. Such approaches could address how functional redundancy is affected, for example, by immigration events and regional extinctions.

Several modern ecologists have asked questions about the relative importance of seasonal variations versus spatial variations in diversity, particularly of insects. These studies pose interesting palaeobiological counterparts, such as how much was a particular extinction or migration event worth compared to the increase in diversity achieved by sampling another habitat. These questions have particular relevance for the interpretation of

diversity patterns in single sections or small regions, where facies changes at a boundary can overwhelm the true patterns of origination or extinction (e.g. Holland 2000; Smith *et al.* 2001).

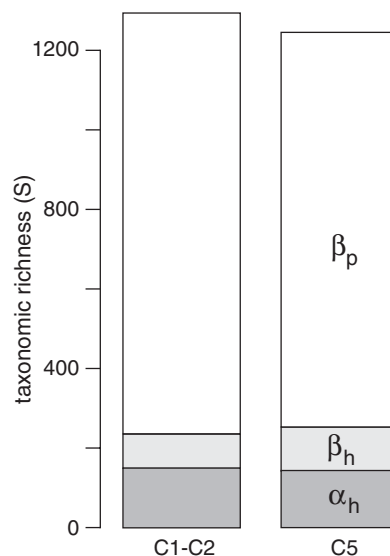
Revisiting Sepkoski's question

Sepkoski (1988, p. 221) famously asked 'Alpha, beta, or gamma – where does all the diversity go?' The ultimate goal of additive diversity partitioning in the marine fossil record is the complete partitioning of Phanerozoic diversity into all of its components. Such a partitioning would greatly facilitate the interpretation of Phanerozoic diversity by reducing the question to scales at which diversity may be more interpretable, such as the number of provinces, the latitudinal configuration of habitable space, the intensity of onshore–offshore gradients and the complexity of local habitats.

Although the complete partitioning of Phanerozoic diversity is not at hand (but may soon be), preliminary data suggest that provinciality may be by far the most dominant single source of global diversity. Using two intervals of the Late Ordovician from the compendium of genera from the type Cincinnati and comparing these to global genus diversity from Sepkoski (1997) suggest that mean within-habitat alpha diversity and among-habitat beta diversity comprise <20 per cent of global diversity, with the remaining 80 per cent reflecting provinciality (Text-fig. 6). In this analysis, the mean habitat diversity is based on shallow subtidal, deep subtidal and offshore habitats and therefore spans much of the fossiliferous habitat for this time. The analysis assumes that the type Cincinnati is a reasonable proxy for global within-habitat and among-habitat diversity. Given the exceptional preservation, abundance and diversity of fossils from this region, it is likely that the size of these two partitions is overestimated relative to most regions and that the estimate of beta diversity because of provinciality is a minimum estimate.

This estimated 20 per cent contribution of the onshore–offshore gradient to global diversity is far less than Sepkoski's (1988) 50 per cent estimate. Part of this discrepancy may reflect differences between collection-based approaches like Sepkoski (1988) and compendium-based approaches, such as presented here.

In terms of additive diversity partitioning, global diversity could change in two ways. First, one or more of the diversity partitions could change in absolute size, while also changing its proportional size relative to the other partitions. Such a change would indicate a basic restructuring of how global diversity is assembled. Alternatively, the absolute size of all of the diversity partitions could change by the same proportional amount, such that their



TEXT-FIG. 6. Global diversity partitioning during the Late Ordovician. Global genus diversity is based on Sepkoski (1997). Regional mean within-habitat diversity (alpha h) and among-habitat diversity (beta h) are based on an unpublished compendium of genus occurrences from the Late Ordovician of the Cincinnati Arch, USA. Provincial-scale beta diversity (beta p) dominates global diversity during the Late Ordovician.

relative proportions remained constant. This type of change would imply that there is a relatively fixed structure to global diversity. Observed modern variation in partitions among taxa, habitats and geographical regions, coupled with observed ancient changes in the sizes of diversity partitions, favours the first scenario, whereas parallel changes in mean within-collection (α) and global diversity (e.g. Sepkoski *et al.* 1981; Alroy *et al.* 2008) argue for the latter scenario.

The relative sizes of these diversity partitions imply their relative contributions to changes in global diversity. Large changes in diversity would require a large change in partition size and larger partitions are more likely to show large variance in their size through time. For example, even if global (γ) diversity and local (alpha-collection) diversity show similar trajectories (e.g. Sepkoski *et al.* 1981) or show similar per cent changes through time (e.g. Alroy *et al.* 2008), local diversity per se cannot be driving the global diversity pattern because the changes in mean alpha diversity are so much smaller than global diversity. For example, if mean alpha diversity increased by ten genera, with no accompanying change in any beta diversity, that is, by adding ten cosmopolitan genera, then global diversity would increase by only ten genera. If, however, the ten genera added to each local collection were endemic in some way, either by environmental restriction or provinciality, then the beta diversity terms will increase, leading to a much greater rise in global diversity.

Thus, the relative sizes of the diversity partitions suggest that large Phanerozoic changes in diversity are driven primarily by changes in the degree of provinciality (cf. Valentine 1970, 1971; Valentine *et al.* 1978; Heim 2008), to lesser degree by onshore–offshore variation, and to a still lesser degree by changes in local alpha diversity (cf. Kowalewski *et al.* 2002; Crampton *et al.* 2006). None of the among-habitat or smaller-scale partitions in Layou (2007), Patzkowsky and Holland (2007), or Heim (2009) are substantial at the scale of global diversity, even though all of these studies were conducted over intervals of substantial ecological change. Counting the number of provinces has been notoriously difficult, and a recent approach has sought to measure directly the degree of geographical differentiation, called geodispersity (Miller *et al.* 2009). Their analysis indicates that the amount of geodispersity has not changed substantially over the scale of the Phanerozoic, but holds out the possibility that geodispersity may have changed substantially over shorter timescales. Identifying the dominant sources of Phanerozoic diversity and their changes remain open questions, and additive diversity partitioning is a promising avenue for answering them.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. R code to calculate partition contributions

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

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