Stability of regional brachiopod diversity structure across the Mississippian/Pennsylvanian boundary

Noel A. Heim

Abstract.—The middle Carboniferous was an interval of global change when the climate was transitioning from greenhouse to icehouse conditions. Field collections of paleotropical brachiopod assemblages across the Mississippian/Pennsylvanian boundary reveal a taxonomic turnover event in which the overall diversity structure is conserved, despite an apparent regional extinction of 63% of latest Mississippian genera and an apparent regional origination of 50% of earliest Pennsylvanian. An analysis of the global ranges of the brachiopods encountered in the field reveals that turnover was driven primarily by extirpation and immigration rather than true extinctions and originations. Taxonomic richness and evenness are indistinguishable between the latest Mississippian and earliest Pennsylvanian stages. Additive diversity partitioning shows that the within-collection, between-collections (i.e., within-bed), and between-bed diversity components do not change across the Mississippian/Pennsylvanian boundary for richness or evenness. Rank-abundance plots of genera show the same distribution for both stages, but with no correlation between the Mississippian abundances of range-through genera and their abundance in the Pennsylvanian. Detrended correspondence analysis shows a major change in taxonomic composition across that Mississippian/Pennsylvanian boundary and consistency in the general gradient along which genera were distributed. An estimation of spatio-temporal heterogeneity of taxonomic composition within each stage reveals that the earliest Pennsylvanian was significantly more homogeneous. These results suggest that middle Carboniferous brachiopod assemblages from tropical shallow-water carbonate platform settings were organized by some factor that was independent of the specific taxa present. Furthermore, the increased homogeneity in taxonomic composition in the Morrowan did not affect the overall diversity structure. Strong competitive interactions among taxa do not appear to be important in determining the taxonomic compositions and abundances of brachiopod stage-level assemblages.

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Introduction

An important question in ecology and paleoecology is how local and regional communities are assembled from a larger pool of available taxa. Despite the potential shortcomings associated with time-averaging, the fossil record is rich with natural experiments where faunas were decimated and allowed to reform in the aftermath of large environmental perturbations, such as sea-level change. Examining the ecological structure of a fossil assemblage before and after such an event may provide insights into how biological communities are assembled generally. Fossiliferous strata of the Mississippian/Pennsylvanian boundary interval provide one such natural experiment. The Mississippian/Pennsylvanian boundary coincides with a major change in global climate and a global shift in biodiversity dynamics, particularly of

the brachiopods. This boundary is associated with a global extinction event (Raymond et al. 1990; Kelley and Raymond 1991), reduced rates of origination and extinction (Stanley and Powell 2003), a shift from narrowly to widely distributed genera (Powell 2005), and a weakened latitudinal diversity gradient (Powell 2007). The purpose of this research is to test the hypothesis that global climate change associated with the Mississippian/Pennsylvanian boundary induced the reorganization of paleocommunity diversity structure on a regional scale in the paleotropics. The hypothesis is tested with brachiopod assemblages from southern Ozark highlands of Arkansas and Oklahoma, which were situated on a shallow carbonate platform between 8° and 13° south paleolatitude during the middle Carboniferous. Diversity structure is analyzed for richness and even-

ness patterns as well as the processes of migration, all of which have implications for our understanding of interspecific competition over evolutionary time. The results of this study elucidate regional biotic responses to global climate change and regional paleo-community assembly mechanisms. Although the biodiversity of the middle Carboniferous is fairly well understood at the global scale, regional dynamics are not, and regional biodiversity patterns do not always parallel global trends (Miller and Mao 1998; Heim 2008).

The interval from the latest Mississippian through the early Permian (Ziegler et al. 1997; Batt et al. 2007) was characterized by an ice house climate in which much of Gondwana was near the south pole and covered by continental ice sheets (Veevers and Powell 1987), the so-called late Paleozoic ice age. Although the onset of Gondwanan glaciation occurred in the Serpukhovian Stage of the late Mississippian (Mii et al. 1999; Smith and Read 2000; Batt et al. 2007), geological (Frakes 1992) and geochemical (Mii et al. 1999; Batt et al. 2007) paleoclimate proxies indicate that the ice volume during the Bashkirian, the first stage of the Pennsylvanian, was much greater than in the Serpukhovian. Globally, stratigraphic and paleontologic data indicate that the boundary between the Mississippian and Pennsylvanian subsystems was marked by a global fall in sea level (Saunders and Ramsbottom 1986), an increase in glacial deposit frequency (Frakes et al. 1992), and an equatorward shift in the latitudinal extent of coal deposits and carbonate deposition (Frakes et al. 1992). Stable isotope ratios measured from brachiopods collected in the North American mid-continent indicate that the middle to late Serpukhovian was glaciated, but warm relative to the Bashkirian (Mii et al. 1999). A positive shift in $\delta^{18}O$ at the Mississippian/Pennsylvanian boundary suggests a decrease in global temperature, and a positive shift in $\delta^{13}C$ suggests increased organic carbon burial, from which a decrease in atmospheric $p\mathrm{CO}_2$ is inferred.

Field Setting and Methods

A regional field-collected data set is used here to understand the regional impacts of global climate change associated with the Mississippian/Pennsylvanian boundary on brachiopod assemblages from the southern Ozarks. Field data were collected within the regional chronostratigraphic framework for the Carboniferous of North America where the latest Mississippian is the Chesterian Stage and the earliest Pennsylvanian is the Morrowan Stage. Regional stages are used because the base of the global Serpukhovian Stage does not correlate with the base of the North American Chesterian Stage and the regional geology of the southern Ozarks has not been reevaluated in terms of recent global Carboniferous timescales (e.g., Gradstein et al. 2004; Heckel and Clayton 2006). The Mississippian/Pennsylvanian boundary interval is exposed in an east-west trending outcrop belt along the southern flank of the Ozark highlands in northwestern Arkansas and northeastern Oklahoma (Fig. 1). The Mississippian/Pennsylvanian boundary in the southern Ozarks, as in most of North America, is marked by an unconformity. In the Ozarks, the unconformity separates marine strata of Chesterian and Morrowan age and spans nearly two conodont zones (Manger and Sutherland 1992). Keep in mind that because a sizable duration of time is not represented by preserved sediments, nothing can be concluded about the rates of change across the interval. Instead, all that can be observed is whether or not changes occurred. The Chesterian and Morrowan strata of the southern Ozarks were deposited on the passive-margin Arkoma Shelf (Sutherland 1988) between 8° and 13° south of the paleoequator (Scotese 2001). Throughout the middle Carboniferous, a deltaic system to the northeast supplied terrigenous sediments, which produced an east-to-west trend of decreasing sand content within the carbonate rocks and an overall decrease in the proportion of terrigenous rocks (Sutherland 1988; Handford 1995). During the Morrowan, the influence of the deltaic system was so great that separate formation names are applied in Arkansas and Oklahoma (Sutherland and Henry 1977; Sutherland and Manger 1977).

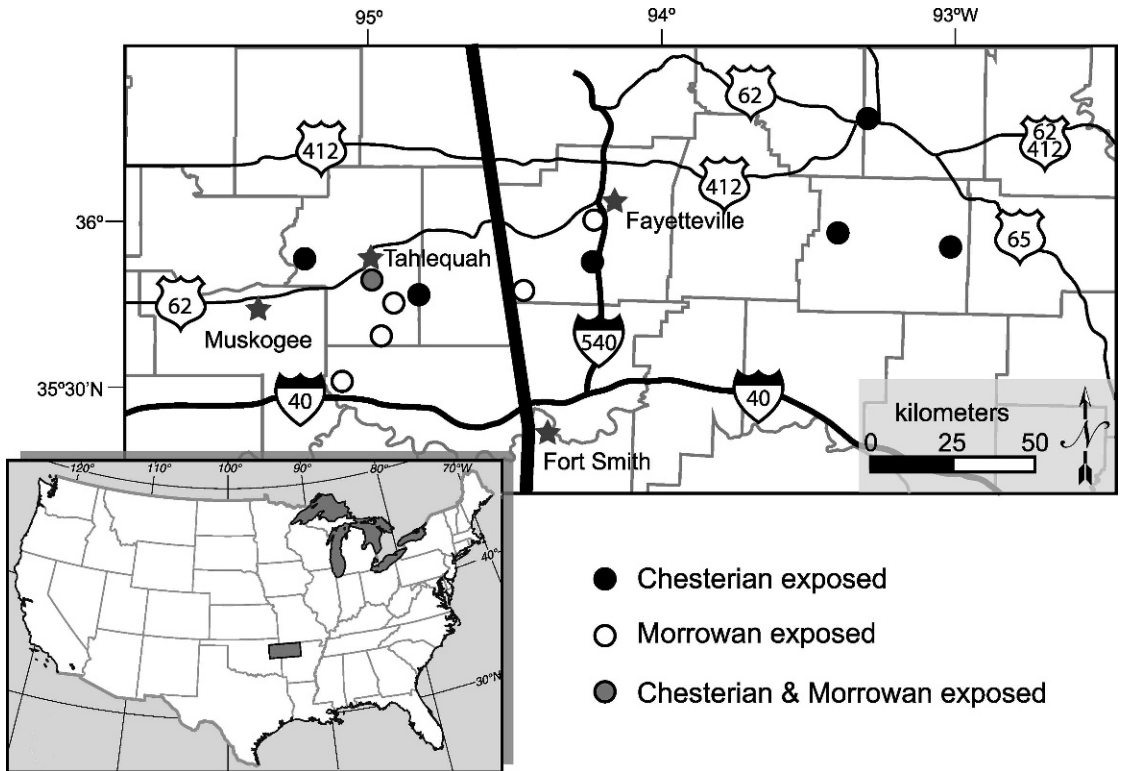Samples were collected within a spatiotemporal hierarchy so that diversity could be

FIGURE 1. Map of collection localities from southwestern Arkansas and northeastern Oklahoma. The solid black circles are Chesterian (Mississippian) localities, the open circles are Morrowan (Pennsylvanian) localities, and the solid gray circles are localities that have both Chesterian and Morrowan rocks exposed. The heavy, nearly vertical line is the border between the states of Arkansas and Oklahoma. The light gray lines outline counties.

analyzed at multiple scales (e.g., Wagner et al. 2000). All collections were taken from shallow subtidal carbonate units. Multiple beds were sampled within the shallow subtidal of the Chesterian and Morrowan Stages, and multiple collections were made from each bed. Each sample was approximately 7.5 liters in volume. A total of 63 collections were made from 22 beds, from the two stages. The collections were made across a 200 km transect trending roughly east-west across northwestern Arkansas and northeastern Oklahoma (Fig. 1). All brachiopods were identified to genus and counted for each collection. Counting was done using the minimum number of individuals method, where the sum of the number of articulated specimens and the greater of the number of brachial or pedicle valves is taken. In total, 48 genera were identified from 2377 individuals. These data are stored in the Paleobiology Database (paleodb.org) and the collections can be

downloaded from reference number 26838 or through a permanent link to the data file listed under Paleobiology Database official publication number 84.

Biodiversity

Extinction and Origination versus Extirpation and Immigration.—Taxonomic turnover between the Chesterian and Morrowan is apparent from simple comparison of the taxonomic lists for the two stages. The Chesterian collections contain a total of 35 brachiopod genera, 22 of which are not found in the Morrowan collections. This corresponds to an apparent regional extinction of 63%. Thirteen genera persist into the Morrowan, which has a total of 26 brachiopod genera. Fifty percent of the Morrowan genera are holdovers from the Chesterian. Global stratigraphic ranges for all of the brachiopod, based on genus occurrences in the Paleobiology Database, genera found in the Ozarks

reveal that the majority of the apparent extinctions and originations were actually extirpations and immigrations, respectively (Fig. 2). Three of the 22 apparent Chesterian extinctions were true global generic extinctions; the rest were extirpations. Similarly, five of the 13 apparent Morrowan originations are true global originations; the rest were immigrants from other regions. From these range data, the Ozark turnover event can be broken down into 9% extinction and 52% extirpation in the Chesterian and 19% origination and 31% immigration in the Morrowan. This, however, does not imply that the Ozarks were the site of origination for the five newly originated genera, simply that those genera had their first global and local occurrences at some time during the Morrowan.

Kelley and Raymond (1991) found that many Southern Hemisphere tropical brachiopod genera shifted their ranges northward toward the equator from the late Mississippian to the early Pennsylvanian coincident with an overall cooling of global climate. That same pattern holds for the brachiopod genera extirpated from the Ozarks (Fig. 3A). Again, using the global occurrences stored in the Paleobiology Database, the paleolatitudinal ranges of the extirpated taxa were calculated for the Mississippian and the Pennsylvanian. Ranges for each genus are calculated as the midpoint of the paleolatitudinal range. The midpoint is used because of the mid-domain effect, which predicts that most individuals occurred at the midpoint of their latitudinal ranges and this is where they are most likely to be sampled (Willig and Lyons 1998). The temporal binning was made at the subsystem level rather than the stage level so that a reasonable number of occurrences were sampled, particularly for the Pennsylvanian. Paleolatitudinal ranges could be calculated for only 13 of the 17 extirpated genera; the four remaining genera are Lazarus taxa (Jablonski 1986) that do not have any Pennsylvanian occurrences but reappear in the post-Pennsylvanian (*Athyris*, *Eumetria*, *Schuchertella*, and *Schellwienella*). Despite the coarse temporal binning, the total number of Mississippian occurrences was much greater
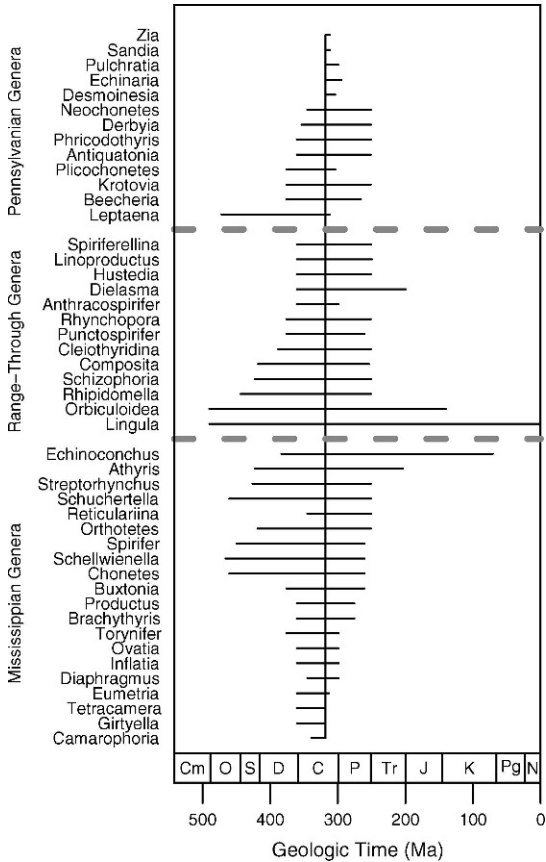

FIGURE 2. Global stratigraphic ranges of the Ozark brachiopod genera. Range data are based on genus occurrences in the Paleobiology Database on 30 September 2008. The genera in the lower group are found only in the Chesterian of the Ozarks field data set, the middle group genera are found in both the Chesterian and Morrowan of the Ozarks, and the upper-group genera are found only in the Morrowan of the Ozarks. The vertical line marks the Mississippian/Pennsylvanian boundary.

than that for the Pennsylvanian. To account for unequal sampling, a randomization routine was employed so that the Mississippian range midpoints are based on the same number of occurrences as the Pennsylvanian range midpoints. For each genus, a random sample of Mississippian occurrences was drawn that was equal to the number of Pennsylvanian occurrences. The midpoint of the paleolatitudinal range for each random sample was found, and the process repeated 10,000 times. The Mississippian ranges are represented as the mean range midpoint with 95% confidence intervals and compared with the raw Pennsylvanian range midpoints
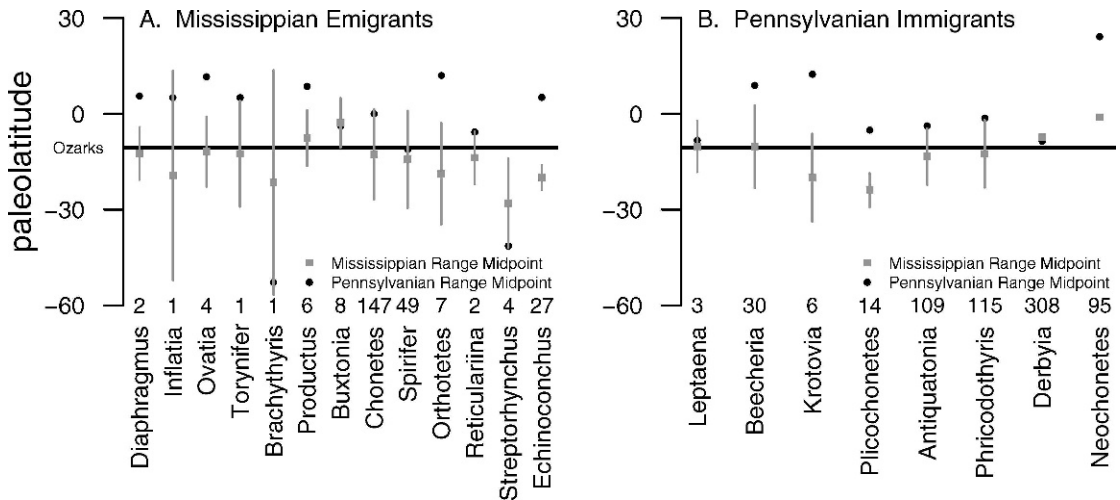
FIGURE 3. Mississippian and Pennsylvanian paleolatitudinal range midpoints for the emigrant and immigrant genera of the Ozarks. The gray squares and black dots mark the range midpoints for the Mississippian and Pennsylvanian occurrences, respectively. The Mississippian occurrences were subsampled to the number of Pennsylvanian occurrences (the numbers along the x-axis). The gray vertical lines are 95% confidence intervals about the mean midpoint based on 10,000 random subsamples of Mississippian occurrences for each genus. The horizontal line marks the mean paleolatitude of all the Ozark collections. The occurrences and paleolatitude data were downloaded from the Paleobiology Database on 30 September 2008. A, The Chesterian genera extirpated from the Ozarks. Three extirpated genera are not included because they do not have any Pennsylvanian occurrences. B, The Morrowan immigrant genera to the Ozarks. The last two genera have very small confidence intervals for their Mississippian range midpoints because there were more occurrences for the Morrowan than for the Chesterian. A randomization of the Morrowan occurrences produces 95% confidence intervals that overlap with the Chesterian range midpoints.

(Fig. 3A). Six extirpated genera show significant equatorward shifts in their range midpoints, four genera show insignificant equatorward shifts in their range midpoints, and three genera show insignificant shifts in their range midpoints toward the south pole. A similar analysis of Morrowan immigrants to the Ozarks (Fig. 3B) shows a similar trend of equatorward paleolatitudinal range shifts from the Mississippian to the Pennsylvanian.

Finally, calculations of percent global extinction and origination in brachiopod genera across the Mississippian/Pennsylvanian boundary show 11.6 ± 4.5% extinction and 21.5 ± 5.4% origination. The 95% confidence intervals were calculated using the Margin of Error software package (Holland 2008). The observed true extinctions (9%) and originations (19%) realized in the Ozarks are, within error, proportional to the global percentages. The large turnover event in the Ozarks across the Mississippian/Pennsylvanian boundary reflects a proportionally equivalent response to global macroevolu-

tionary patterns, but was primarily driven by extirpation and immigration.

Introduction to Biodiversity Methods.—Biodiversity refers to a variety of traits attributable to an assemblage of organisms. Most simply, biodiversity refers to taxonomic richness, or the number of unique taxa in an assemblage. Another aspect of biodiversity is the relative or absolute abundance of each taxon, which is used to determine how evenly individuals are distributed among the constituent taxa. By using both the richness and evenness, the biodiversity of multiple assemblages can be compared and insights gained into the underlying processes of community assembly. A combination of additive diversity partitioning, rank-abundance distributions, multivariate gradient analysis, and taxonomic similarity is used here to test the hypothesis that the regional brachiopod assemblage was restructured across the Mississippian/Pennsylvanian boundary on the Arkoma Shelf. These analytical methods can be divided into two general categories. Additive diversity partitioning and rank-abundance curves are not

sensitive to taxon identity whereas gradient analysis and similarity analysis are. The importance of this is that the taxon insensitive methods identify gross patterns in the way diversity is structured whereas the taxonomically sensitive methods show the details of how taxa are arranged within the larger structure.

Additive Diversity Partitioning.—Spatial complexities of the richness and turnover structure become apparent when diversity is divided into alpha and beta components. Such a partitioning of diversity allows several hypotheses to be tested. First, the hypothesis that there was a drop in total diversity from the Chesterian to the Morrowan, as seen in global data (Raymond et al. 1990), can be tested. Second, the hypothesis that such a drop in diversity was caused by a drop in local richness, or alpha diversity, can be tested. Finally, the hypothesis that evenness increased from the Chesterian to Morrowan in response to drop in sea level can also be tested.

Alpha diversity is defined as the diversity (simple richness or some other diversity measure) of a local sample taken from a homogeneous habitat, gamma diversity is the diversity of a regional sample that includes multiple habitats, and beta diversity describes how diversity increases from the alpha level to the gamma level as samples are pooled. Whittaker (1960, 1972) originally defined beta multiplicatively as the ratio of gamma to alpha. The major drawback to using the multiplicative form of beta diversity is that it is a unitless index, which is not directly comparable with either alpha or gamma. Lande (1996) reintroduced the idea of additive diversity partitioning (ADP), which defines beta diversity as the difference between gamma and alpha rather than their ratio. Additive diversity partitioning has three main advantages over multiplicative partitioning. First, beta diversity is directly comparable with alpha and gamma because all three measures have the same units. Second, ADP permits total diversity to be partitioned within a spatial hierarchy containing as many or as few levels needed to test a particular hypothesis (Wagner et al. 2000). Third, ADP

can be used with a variety of diversity metrics, not just richness (Lande 1996). The general ADP formula for a sampling hierarchy with n total alpha-level collections taken from k hierarchical levels is

$$\lambda = \overline{\overline{\alpha}} + \sum_{i=1}^{k} \beta_i \qquad (1)$$

where γ is total diversity, $\overline{\overline{\alpha}}$ is the mean diversity of all n collections, and $\overline{\beta}_i$ is the mean beta diversity within the ith level. Beta diversity at the ith level of the sampling hierarchy is

$$\beta_i = \alpha_{i+1} + \overline{\alpha}_i \qquad (2)$$

where $\overline{\alpha}_i$ is mean of all alpha values at the ith level. Taking the average of all alpha values at the ith level prevents pseduoreplication (Srivastava 1999), where many interdependent data points are generated from comparisons with a single value (i.e., α_{i+1}). A graphical representation of a sampling hierarchy and the various alpha and beta components is provided by Patzkowsky and Holland (2007: Fig. 3).

The data in this study are partitioned into three levels: collections, beds, and stages. In order for the additive partitions to sum to total diversity, each bed must contain the same number of collections and each stage must contain the same number of beds. Because it was not always possible to collect the ideal number of samples at each locality, the final data set was subsampled 1000 times with two collections within each bed and eight beds within each of the two stages. Subsampling the data also allows the computation of 95% confidence intervals for total diversity and for each partition. The suite of diversity, dominance, and evenness measures used comprise simple richness (S), Shannon's entropy (H), Simpson's D $(1-\lambda)$, Hurlburt's probability of interspecific encounter (PIE), and the Peters (2004) evenness metric (E_{ssmin}). These metrics were chosen because they reflect a variety of ways to measure diversity with presence/absence and quantitative data. They are also chosen for ADP analysis because they are strictly concave (Lande 1996). Strict concavity occurs when the total diversity of pooled collections is always

TABLE 1. Additive diversity partitioning of richness and several metrics of evenness and dominance for the Chesterian. a_c: mean alpha diversity of all collections, b_w: beta diversity within beds, b_a: beta diversity among beds, g: total diversity, S: simple taxonomic richness, H: Shannon's information index, D: Simpson's D, PIE: Hurlburt's probability of interspecific encounter, E_{ssmin}: Peters' (2004) metric of evenness.

	S	H	D	PIE	E_{ssmin}
g	27.47 ± 5.14	2.47 ± 0.26	0.87 ± 0.04	0.87 ± 0.04	0.87 ± 0.04
b_a	18.93 ± 4.39	0.90 ± 0.24	0.18 ± 0.09	0.17 ± 0.09	0.21 ± 0.08
b_w	2.27 ± 0.81	0.24 ± 0.12	0.06 ± 0.04	0.05 ± 0.04	0.12 ± 0.05
a_c	6.28 ± 1.07	1.33 ± 0.19	0.63 ± 0.08	0.66 ± 0.09	0.54 ± 0.08

greater than or equal to the sum of the weighted diversity of the individual collections. Applying ADP to a diversity metric that violates strict concavity will result in the constituent diversity components summing to more than total diversity. Other evenness measures such as E of Hayek and Buzas (1997) and D/D_{max} based on Simpson's index (Smith and Wilson 1996) are not strictly concave. Simpson's D, PIE, and E_{ssmin} have the added advantage of being sample-size independent (Hurlburt 1971; Lande 1996; Hayek and Buzas 1997; Peters 2004). The ADP results for richness and the evenness and dominance metrics provide a test of the hypothesis that total richness dropped from the Chesterian to the Morrowan, as predicted by global trends (Raymond et al. 1990; Kelley and Raymond 1991; Stanley and Powell 2003) and that there was an accompanying change in the spatial partitioning of richness and evenness among alpha and beta components.

The ADP results for taxonomic richness (Tables 1, 2, Fig. 4) show that total subsampled richness for the Chesterian and Morrowan was 27.5 and 25.0 genera, respectively. For both stages, the greatest contribution to total diversity came from the among-bed component (β_a), which contributed approximately 69% and 60% of the genera to Chesterian and Morrowan diversity, respectively. The next largest contribution to total diversity comes from the within collection components ($\bar{\bar{\alpha}}_c$), which constitute approximately 23% and 30% of Chesterian and Morrowan diversity, respectively. Finally, the within-bed component ($\bar{\beta}_w$) contributes approximately 9% of the total number of genera to total diversity for both stages. Neither total richness, nor any of the additive components show a statistically significant change from the Chesterian to the Morrowan (Tables 1, 2, Fig. 4). In summary, individual fossil collections in the Chesterian and Morrowan of the southern Ozarks are moderately diverse, but most of the taxonomic richness is generated by differences in taxonomic compositions among beds. Replicate sampling within beds adds little to total richness; on average, taking two collections from a bed rather than one will increase the number of genera encountered by two (<25%).

The ADP results for H, D, PIE, and E_{ssmin} (Tables 1, 2) all show the same qualitative patterns, which is relatively high total evenness that is partitioned such that the alpha component accounts for the most evenness and the within bed beta component accounts for the least. For illustrative purposes, only the E_{ssmin} results are presented graphically (Fig. 5). Evenness was generally high during both the Chesterian and Morrowan with total E_{ssmin} at approximately 0.9 with overlapping 95% confidence intervals for both stages. Like taxonomic richness, all three pairwise comparisons of Chesterian and Morrowan parti-

TABLE 2. Additive diversity partitioning of richness and several metrics of evenness and dominance for the Morrowan. Row and columns headers are the same as in Table 1.

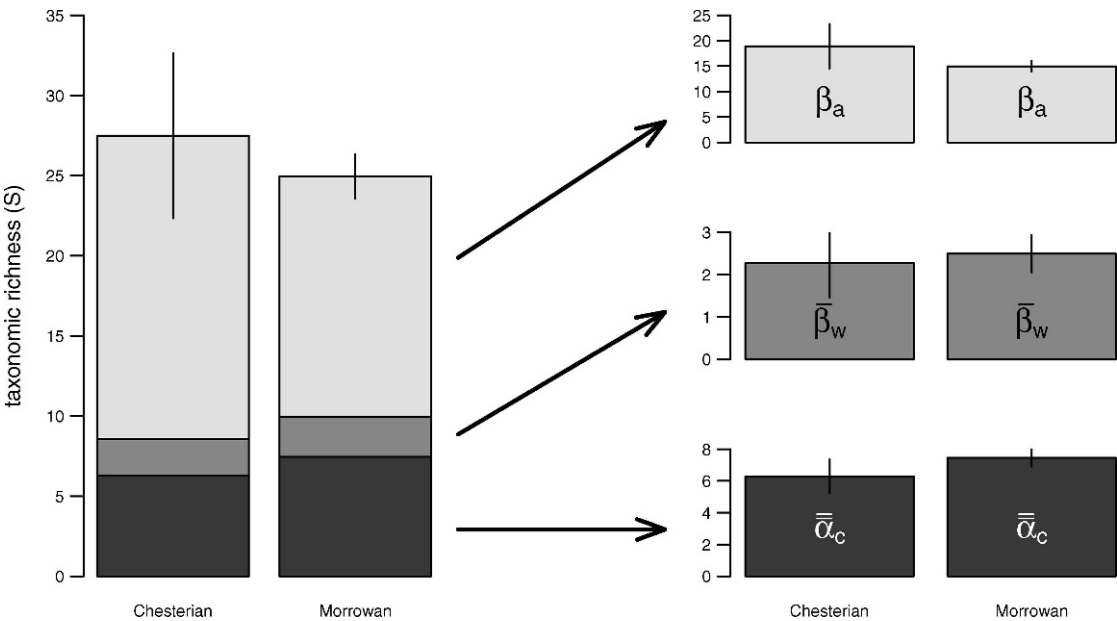|	S	H	D	PIE	E_{ssmin}
g	24.94 ± 1.40	2.51 ± 0.06	0.88 ± 0.01	0.89 ± 0.01	0.88 ± 0.01
b_a	14.99 ± 1.09	0.80 ± 0.05	0.16 ± 0.02	0.14 ± 0.02	0.20 ± 0.02
b_w	2.49 ± 0.44	0.16 ± 0.04	0.02 ± 0.01	0.01 ± 0.01	0.10 ± 0.01
a_c	7.46 ± 0.56	1.55 ± 0.07	0.70 ± 0.02	0.73 ± 0.02	0.59 ± 0.03

FIGURE 4. Additive diversity partitioning of taxonomic richness for the Chesterian and Morrowan. From bottom to top (dark gray to light gray) the partitions are among collection diversity($\bar{\bar{\alpha}}_c$), within bed diversity ($\bar{\beta}_w$), and among bed diversity (β_a). The left side shows the relative contributions of each partition to total diversity. The error bars are 95% confidence intervals for total diversity based on 1000 subsamples. The right column shows each partition with 95% confidence intervals so that Chesterian and Morrowan partitions can be compared. Note that the plots on the right are at different scales.

tions have overlapping 95% confidence intervals. Unlike taxonomic richness, greater than 50% of the evenness is contributed by the within-collection components ($\bar{\bar{\alpha}}_c$). Approximately 20% of the evenness is contributed by the among-bed component (β_a) and approximately 10% is contributed by the within-bed component ($\bar{\beta}_w$).
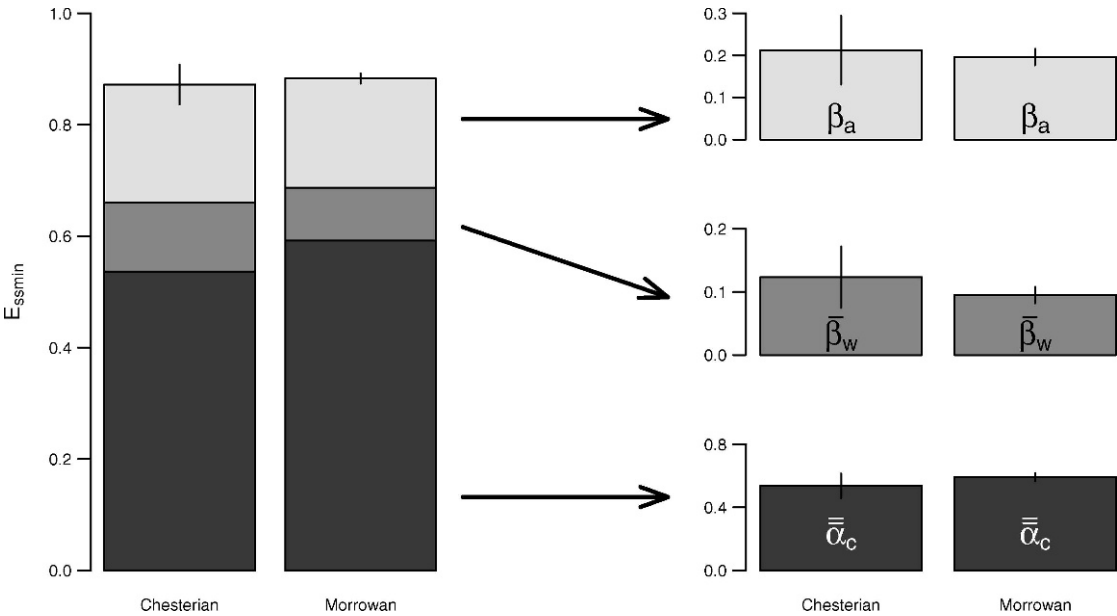

FIGURE 5. Additive diversity partitioning of E_{ssmin} (Peters 2004) for the Chesterian and Morrowan. Plotting conventions same as Figure 4.

The ADP results indicate that turnover in the paleotropics of Laurentia did not produce statistically significant changes in diversity. There were no statistically significant changes in gamma or any of the alpha or beta components of taxonomic richness from the Chesterian to the Morrowan. Likewise, there was no change in evenness at any of the hierarchical levels. Although the taxonomic composition changed in the Ozarks from the Chesterian to the Morrowan, there was no detectable change in the spatiotemporal richness or evenness structure.

Rank-Abundance Patterns.—Rank-abundance curves, on which the percent abundance of each taxon within an assemblage is plotted against its rank in abundance, graphically display the evenness of an assemblage and allow easy comparisons of multiple assemblages (Magurran 2004). A steep curve indicates a low evenness/high dominance assemblage whereas curves with a shallow slope have high evenness/low dominance. Rank-abundance curves are used here to test the hypothesis that dominance structure changed from the Chesterian to the Morrowan with the changes in taxonomic composition. The percent abundance for each genus was calculated from data in which all the collections from each stage were aggregated. To test for differences between the Chesterian and Morrowan rank-abundance distributions, the data were bootstrapped and 95% confidence intervals computed. The taxon count data for each stage was resampled with replacement 10,000 times. From the resampled data, the mean percent abundance and 95% confidence intervals were calculated for each genus. An additional test of difference was made with a two-sample Kolmogorov-Smirnov test. Finally, a Spearman rank correlation was performed on the abundances of the 13 range-through genera to see if the rank-order of range-through genera was preserved.

The shape of the Chesterian and Morrowan plots are similar (Fig. 6). In the rank-abundance plots for both stages, there are two distinct segments separated by an abrupt change in slope. The first segment is composed of the six most abundant genera and has a steep slope. The second segment contains the remaining genera and has a comparatively shallow slope. This curve morphology indicates high dominance among the most abundant taxa and relatively higher evenness among the moderately abundant and rare genera. The confidence intervals for the Chesterian and Morrowan data overlap for all genera (Fig. 6C), suggesting they are derived from the same distribution. The Kolmogorov-Smirnov test corroborates this finding with a D-statistic of 0.2923 (p-value: 0.1227). The overall abundance structure of Chesterian and Morrowan brachiopods from the Ozarks was preserved, but the rank abundance of the 13 range-through genera was not. A Spearman rank correlation on the range-through genera was not significant (r: 0.21; p-value: 0.49). The abundance of a range-through genus during the Chesterian did not predict the abundance of that genus during the Morrowan.

Gradient Analysis.—Multivariate gradient analysis is a tool for exploring the role of environmental variables in structuring communities. Gradient analysis was used here to detect underlying structure to the field data that cannot be detected with ADP or rank-abundance curves. One of the fundamental differences between gradient analysis and the previous methods used here is the importance of taxon identity. ADP and rank-abundance curves take into consideration only the number and abundances of taxa, whereas gradient analysis will potentially find differences between two assemblages with the same richness and relative abundances if those assemblages have different taxonomic compositions. Gradient analysis was used to detect the arrangement of collections along temporal, spatial, and diversity gradients. For taxa, gradients in time, abundance, and higher taxonomic groupings were sought. Two gradients expected to emerge from the Ozark data a priori. The first is an environmental gradient associated with the deltaic system to the northeast. This gradient should be seen most strongly in longitude; the system as a whole becomes less sandy to the west. The second gradient is a temporal gradient, resulting from the change
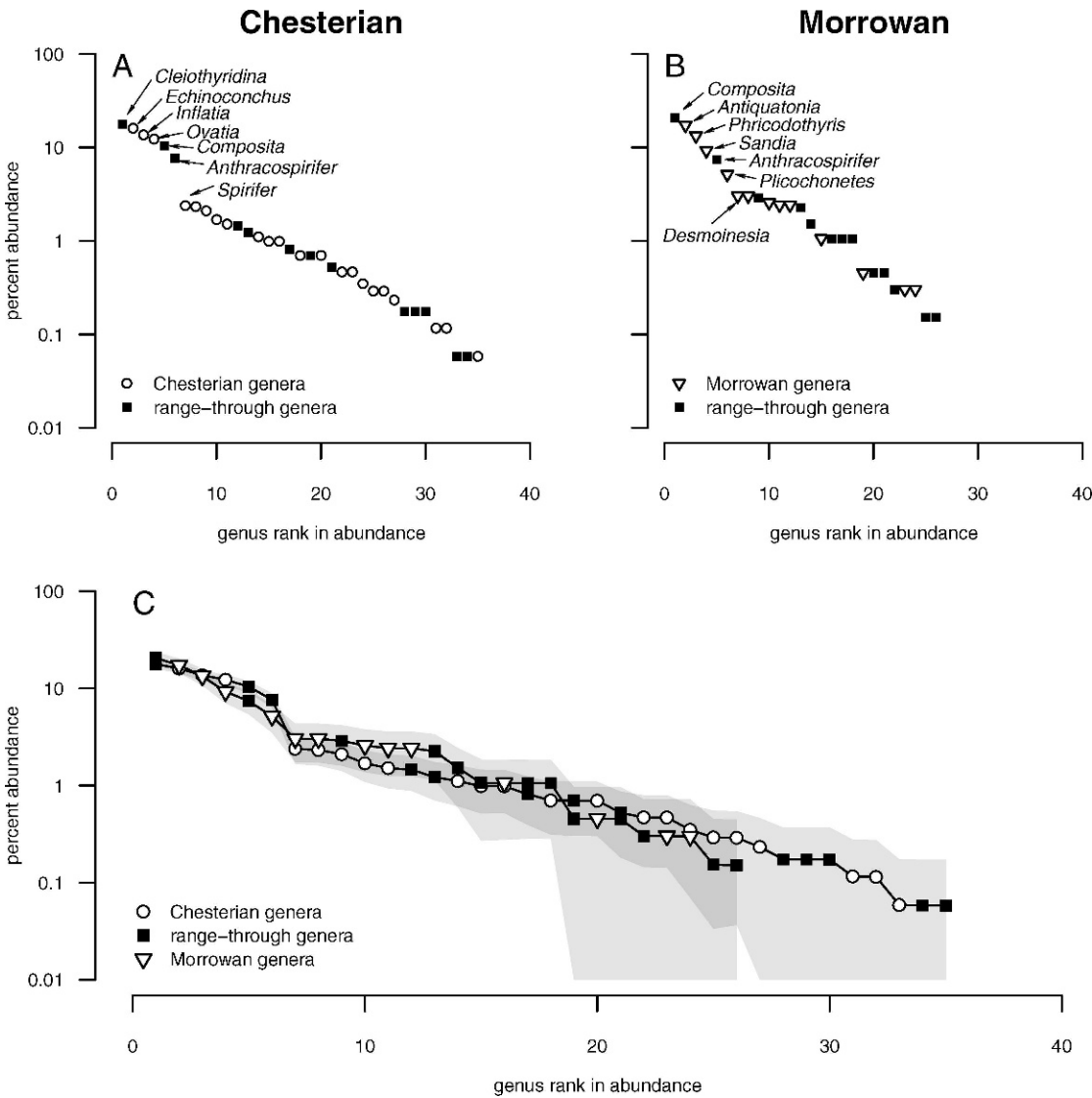
FIGURE 6. Plots of genus rank versus percent abundance, on a semi-log scale, for the Chesterian (A) and Morrowan (B). The two top plots are the raw data with the seven most abundant genera identified for each stage. The bottom plot (C) compares the two rank-abundance distributions. The gray envelopes are 95% confidence intervals based on 10,000 bootstraps. Dark-gray regions indicate overlapping confidence intervals. Open symbols are genera that occur only in the Chesterian (circles) or Morrowan (triangles); closed symbols are genera that occur in both stages.

in taxonomic composition from the Chesterian to the Morrowan.

Detrended correspondence analysis (DCA) and nonmetric multidimensional scaling (NMDS) were performed to explore underlying community gradients. Both DCA and NMDS produce gradients for collections and taxa, and both methods produce multiple orthogonal axes that explain decreasing percentages of the variance. The results from the two ordination techniques were similar, as indicated by the high degree of correlation between corresponding axes of the two methods. Because there was better separation of collection scores along axis 1 for DCA than for NMDS, only the DCA results will be discussed here. The ordinations were performed using the decorana function from the vegan package (Oksanen et al. 2007) for the R statistical software (R Core Development
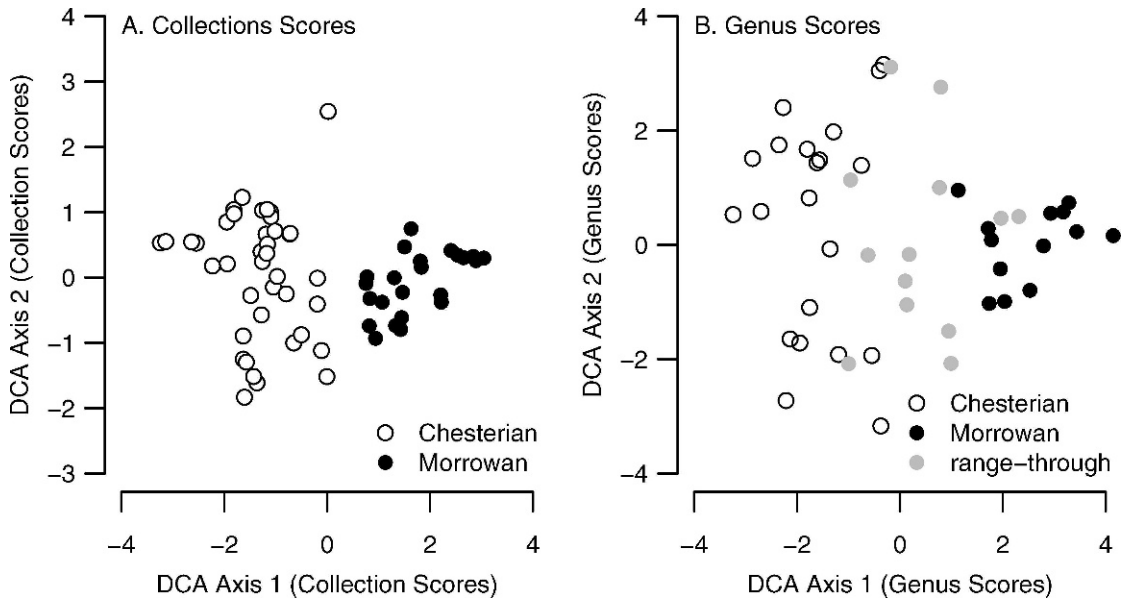
FIGURE 7. Detrended correspondence analysis (DCA) results for the full data set: DCA axis 1 scores versus DCA axis 2 scores. A, Collection scores coded by stage. B, Genus scores coded by stage. Gray symbols indicate range-through genera that are present in both the Chesterian and the Morrowan. Note the strong gradients along DCA axis 1 that correspond to time for both collection and genus scores.

Team 2008) following the data transform methodology of Holland and Patzkowsky (2007). The input data are a collection-by-genus matrix filled with raw genus abundance values. Before analysis, the data were transformed with a within-sample percent transformation. The data were then transformed again using a within-taxon percent maximum transformation. These transformations prevent the ordinations from being dominated by the most abundant taxa. To avoid gradient distortions from the least abundant taxa, rare species were downweighted within the decorana function.

An ordination of the entire data set indicates strong temporal separation along DCA axis 1 (DCA1) with no overlap in collections scores (Fig. 7A). DCA1 genus scores also indicate a temporal gradient in which genera found only in the Chesterian have low scores, range-through genera have intermediate scores, and genera found only in the Morrowan have high scores (Fig. 7B). Further exploration of the DCA results was made by calculating Pearson product-moment correlation coefficients between the first three DCA axes and a suite of collection and taxonomic

variables (Tables 3, 4). Correlation coefficients for DCA collection scores were calculated for longitude, collection abundance, collection richness, Simpson's D, and E_{ssmin} (Table 3). Longitude was chosen because of the longitudinal gradient in lithology observed in the field. Latitude was not used because there is little latitudinal variation among the sample localities. Collection richness, Simpson's D, and E_{ssmin} are significantly correlated with DCA1 (Table 3). However, the correlations are relatively weak with r^2 values less than 0.25. DCA2 is correlated with collection abundance and DCA3 is significantly correlated with Simpson's D and E_{ssmin}, again with r^2 values less than 0.5. Correlation coefficients between the DCA genus scores were calculated for genus abundance and the number of collections in which a genus occurs (Table 4). None of the correlations were significant.

Because the primary gradient observed from the DCA on the whole data set is time (Fig. 7), these same analyses were also applied to the Chesterian and Morrowan data separately. For the Chesterian collection scores, DCA1 is correlated with Simpson's D and DCA3 with longitude, richness, Simp-

TABLE 3. Pearson product-moment correlation coefficients among DCA collection scores and collection variables for full data set. Collection data were not pooled by bed in this analysis. The longitude is the present day longitude of the collection localities, not paleolongitude. Longitude is potentially important because of a large deltaic system located to the northeast of the field area, which created an east-to-west gradient of decreasing terrigenous sediments and increasing carbonate sediments. Asterisks indicate statistically significant correlations ($p \leq 0.05$).

	DCA1	DCA2	DCA3
Longitude	−0.19	0.02	0.24
Collection abundance	−0.17	0.38*	0.3
Collection richness	0.27*	0.14	0.14
Simpson's D	0.41*	−0.15	0.29*
E_{ssmin}	0.37*	0.19	0.29*

son's D, and E_{ssmin}. As with the correlations on the full data set, none of the significant correlations explain more than 25% of the data's variation (Table 5). There was a significant correlation between the Morrowan DCA collection scores and E_{ssmin} (Table 6). There were no significant correlations for either Chesterian or Morrowan genus scores (Tables 7, 8). To further explore possible gradients within genus scores, the DCA1 genus scores for the Chesterian range-through genera were plotted against the DCA1 scores for the same genera from the Morrowan (Fig. 8). Of the 13 range-through genera all but four (*Hustedia*, *Lingula*, *Rhipidomella*, *Rhynchopoda*) plot near the one-to-one line. This suggests that, with the exception of these four genera, the range-through genera are aligned along a similar gradient in the Chesterian and Morrowan. Indeed, the Spearman rank-correlation coefficient for DCA1 genus scores for those nine genera is 0.9 with a *p*-value of 0.0009. Including the four outliers makes the correlation much weaker and insignificant (*r* = 0.18, *p*-value = 0.55).

TABLE 4. Pearson product-moment correlation coefficients among DCA genus scores and genus variables for the full data set. Genus variables are the total number of occurrences for each genus and the total number of collections a genus is found. None of the correlations are statistically significant ($p \leq 0.05$).

	DCA1	DCA2	DCA3
No. of occurrences	−0.05	−0.08	−0.04
No. of collections	−0.18	0.05	0.03

TABLE 5. Pearson product-moment correlation coefficients among DCA collection scores and collection variables for the Chesterian data set. Table conventions same as in Table 3.

	DCA1	DCA2	DCA3
Longitude	−0.52	0.32*	0.44*
Collection abundance	0.14	−0.01	0.09
Collection richness	−0.07	0.27	0.45*
Simpson's D	−0.41*	0.23	−0.49*
E_{ssmin}	−0.18	0.24	−0.42*

From all these correlations, two stand out as particularly important. First is the relationship between time and DCA1 for the full data set (Fig. 7). This relationship indicates a fundamental change in the composition of the brachiopod fauna across the Mississippian/Pennsylvanian boundary. The second is the correlation between the DCA1 scores of the range-through genera for the Chesterian and the Morrowan (Fig. 8), which once again demonstrates a degree of continuity in the ecological structure across the Mississippian/Pennsylvanian boundary. However, further ecological and possibly morphological analyses are needed to explain the four outliers (Fig. 8).

Taxonomic Similarity.—The taxonomic similarity between two assemblages indicates taxonomic connectedness and implies the degree of migration or faunal exchange between those two assemblages (Heim 2008). The average similarity among beds within a stage indicates the degree of connectedness among beds and reflects environmental patchiness or the lengths of environmental gradients. Taxonomic similarity is used to test the hypothesis that regional environmental gradients and patchiness broke down across the Mississippian/Pennsylvanian boundary. The total flooded area of

TABLE 6. Pearson product-moment correlation coefficients among DCA collection scores and collection variables for Morrowan data set. Table conventions same as Table 3.

	DCA1	DCA2	DCA3
Longitude	−0.12	0.03	0.26
Collection abundance	−0.16	0.16	−0.01
Collection richness	−0.33	−0.11	0.24
Simpson's D	−0.41	−0.14	0.27
E_{ssmin}	0.46*	0.21	0.28

TABLE 7. Pearson product-moment correlation coefficients among DCA genus scores and genus variables for Chesterian data set. Genus variables are the total number of occurrences for each genus and the total number of collections a genus is found. None of the correlations are statistically significant ($p \leq 0.05$).

	DCA1	DCA2	DCA3
No. of occurrences	0.04	−0.18	0.06
No. of collections	0.08	−0.25	0.13

the Arkoma shelf was reduced in the aftermath of the middle Carboniferous eustatic drop in sea level (Scotese 2001), presumably leading to decreased habitat heterogeneity and a corresponding decrease in taxonomic heterogeneity.

The modified Morisita-Horn index (Wolda 1983) is used here to measure taxonomic similarity between the Chesterian and Morrowan because it is sample-size independent (Wolda 1981) and takes into account both taxonomic richness and abundance. Other common metrics, such as the Jaccard coefficient, only use presence-absence data and others, like the Bray-Curtis index, are biased when two collections of different sizes are compared (Wolda 1981). The Morisita-Horn index varies between zero and one, with higher values indicating a higher degree of similarity. The Morisita-Horn index (C_{MH}) is given by

$$C_{MH} = 2/[(d_a + d_b)N_aN_b] \sum_{i=1}^{S} a_ib_i \quad (3)$$

where d_a (and d_b) is given by:

$$d_a = 1/N_a^2 \sum_{i=0}^{S} a_i^2 \quad (4)$$

where S is the total number of taxa, N_a (and N_b) is the total number of individuals in

TABLE 8. Pearson product-moment correlation coefficients among DCA genus scores and genus variables for Morrowan data set. Genus variables are the total number of occurrences for each genus and the total number of collections a genus is found. None of the correlations are statistically significant ($p \leq 0.05$).

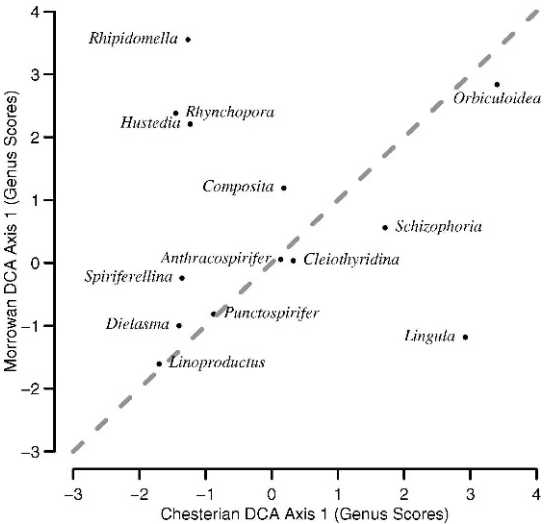|	DCA1	DCA2	DCA3
No. of occurrences	−0.05	0.07	−0.17
No. of collections	−0.03	0.08	−0.06

FIGURE 8. A plot of DCA axis 1 scores for the range-through genera for the Chesterian and Morrowan. The gray dashed line is the one-to-one line. Except for four outliers (*Hustedia*, *Lingula*, *Rhipidomella*, *Rhynchopoda*), most genera lie near the one-to-one line, indicating that a large portion of the axis 1 gradient was present in both stages.

assemblage *a* (and *b*), and a_i (and b_i) is the abundance of the ith taxon.

Before calculating similarity, collections within each bed were merged so that similarity comparisons were measured only among beds. The Morisita-Horn index was measured for each pairwise combination of beds within each stage. The mean similarity of all the pairwise indices is compared for the Chesterian and Morrowan (Fig. 9A). Ninety-five percent confidence intervals are calculated by bootstrapping the data 1000 times. The range in variation of similarity of beds for the two stages is compared by using box-and-whisker plots, with outliers defined as being more than 1.5 times the interquartile range from the box (Fig. 9B) (Sokal and Rohlf 1995).

Mean similarity was significantly lower during the Chesterian than the Morrowan. This indicates a decrease in patchiness across the interval. The range of variation is similar for the two stages, but the Chesterian has more outliers than the Morrowan. The two Chesterian outliers with exceptionally high similarity are comparisons of beds from the same outcrop, suggesting short-term temporal stability at a single location. There are four
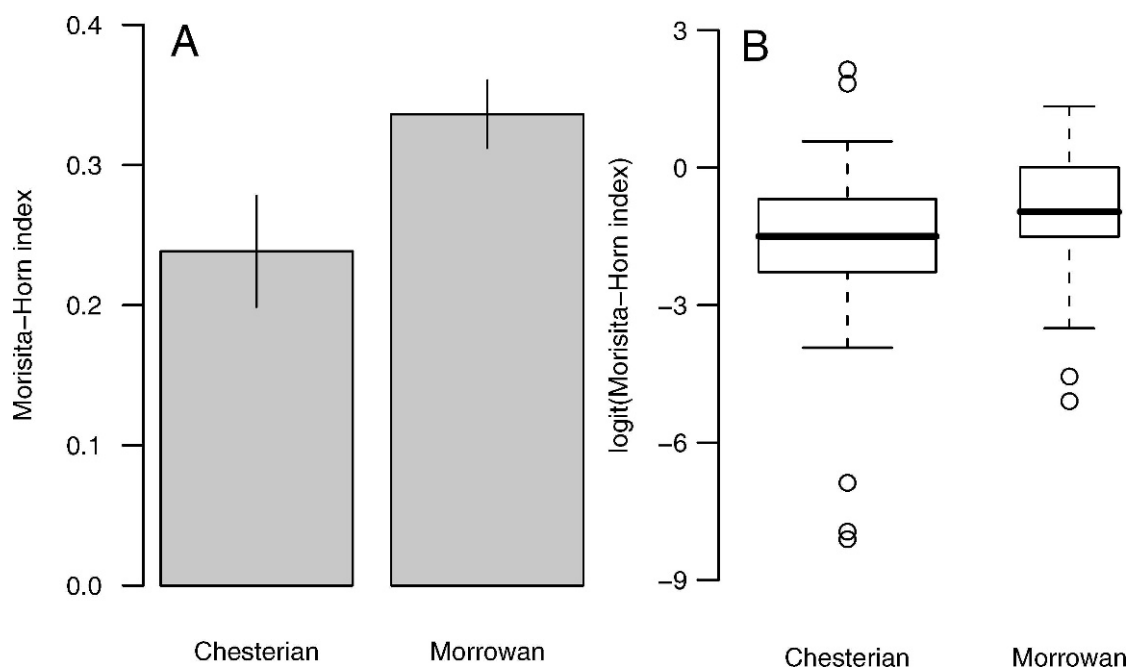
FIGURE 9. A, Mean similarity of all pairwise comparisons, based on the Morisita-Horn index, of Chesterian and Morrowan beds with 95% confidence intervals. B, Box-and-whisker plots showing the distribution of pairwise similarities of the logit transformation of the Morisita-Horn index. The logit transformation $[\ln(x/(1-x))]$ is used to linearize data that have both upper and lower bounds and highlights the variation among points that are close to the upper or lower bounds. The open symbols are outliers that lie 1.5 times the interquartile range from the box. The box widths are proportional to sample size. There is one outlier below the Chesterian box that is not shown. It has a similarity of zero, which is undefined on the logit scale.

Chesterian outliers with exceptionally low similarity, all of which are associated with the same bed from the Pitkin Formation at Braggs Mountain, Oklahoma. This suggests that this particular bed is distinct from the other beds. The Morrowan has only two outliers, both of which have anomalously low similarity. These two pairs contain the same bed from the Hale Formation near Greenland, Arkansas, again suggesting that this bed is distinct from the others in the stage. The mean similarity does not change appreciably for either the Chesterian or the Morrowan when the counts from the beds from the same outcrop are merged and the dissimilar beds are removed. The turnover in taxonomic composition between the Chesterian and Morrowan was accompanied by a significant increase in the spatiotemporal homogeneity among beds, suggesting a reduction in habitat patchiness or a shortening of an environmental gradient on the Arkoma Shelf during the Morrowan.

Discussion

A variety of geological and paleoclimate proxy data indicate that the Mississippian/Pennsylvanian boundary marked a major climatic transition, including a drop in global sea level (Saunders and Ramsbottom 1986), increased frequency of glacial deposits (Frakes et al. 1992), and positive shifts in both $\delta^{13}C$ and $\delta^{18}O$ values recorded in brachiopod shells of the North American mid-continent (Mii et al. 1999). The global middle Carboniferous brachiopod fauna responded to the climate change with an extinction event (Raymond et al. 1990), equatorward migrations (Raymond et al. 1990; Kelley and Raymond 1991), depressed rates of origination and extinction (Stanley and Powell 2003), and a depressed latitudinal diversity gradient (Powell 2005, 2007). Given the changes observed globally, it is not surprising that the tropical brachiopod fauna of the Arkoma Shelf also changed across the Mississippian/Pennsylvanian boundary. The region experi-

enced a major taxonomic turnover event that was driven primarily by brachiopod taxa shifting their latitudinal ranges. There was also a component of extinction in the Arkoma Shelf turnover event that was proportional to the extinction of brachiopods globally, but there was no statistically detectable drop in total diversity from the Chesterian to the Morrowan. Overall, extinctions and extirpations in the Chesterian were balanced by originations and immigrations in the Morrowan. This is in contrast to a 9% reduction in total generic richness across the same interval seen globally. Raymond et al. (1990) observed a greater degree of global brachiopod extinction, 26%, across the same interval (Namurian A/B boundary of their timescale), but results cannot be directly compared because the temporal bin size used by Raymond et al. (1990) was much finer than the bins used here. More interesting, though, than the regional turnover event itself is that no change in the spatiotemporal partitioning of richness and evenness, the rank-abundance structure, or the multivariate gradient structure is observed. The only two differences between the Chesterian and Morrowan are an increase in interbed homogeneity (i.e., a decrease in patchiness) and a reorganization the relative abundances of range-through taxa.

The key to linking the turnover in taxonomic composition to climate change is observation that most of the apparent regional extinctions of Chesterian genera were in fact extirpations. Approximately 51% of the Chesterian genera were extirpated from the region (Fig. 2), and the extirpations were accompanied by equatorward shifts in paleolatitudinal range in most cases (Fig. 3A). As glaciation progressed in the Southern Hemisphere, the latitudinal temperature gradient steepened and forced those taxa with narrow temperature tolerances toward the equator. Interestingly, the Morrowan immigrant genera also show an equatorward shift (Fig. 3B), but these genera generally shifted from a paleolatitudinal position near that of the Ozarks in the Chesterian to a position north of the Ozarks in the Morrowan. If these patterns in range shifts are real and not

sampling artifacts, they suggest that the Chesterian emigrants were relatively sensitive to temperature as they shifted the midpoints of their latitudinal ranges away from the Ozarks. The Morrowan immigrants also appear to have responded to changes in temperature, but they also appear to have been much less sensitive than the Chesterian emigrants. The Morrowan immigrants were generally centered at the latitude of the Ozarks during the Chesterian but did not appear in the region until their latitudinal ranges had shifted farther away in the Morrowan. Perhaps this suggests that the Morrowan immigrants were generalists that were not able to occupy the region until the Chesterian emigrants had been extirpated. Alternatively, the Morrowan immigrants may have been responding to some cryptic environmental change that is not obvious from field observations. Further paleoecological analyses of individual genera are needed to test these hypotheses.

The most striking aspect of these data is the consistency in diversity structure from the Chesterian to the Morrowan. The consistency is even more remarkable given the >50% turnover in taxonomic composition and the magnitude of the Mississippian/Pennsylvanian unconformity, at which nearly two full conodont zones are missing (Manger and Sutherland 1992). It should be emphasized again that because of the unconformity, rates of change between the Chesterian and the Morrowan cannot be inferred. Although the Ozark section is relatively complete compared to other locations in the North American mid-continent, it does not record sedimentation continuously across the interval. Further study in more complete Mississippian/Pennsylvanian boundary sections is needed to determine the exact timing of the turnover event and whether it was gradual or abrupt. The similarities in rank-abundance structure and additive diversity partitioning of richness and evenness suggest that some control exists on how brachiopod genera were organized regionally during the middle Carboniferous. However, this factor is not related to the particular identities of constituent genera or competitive interactions between

those genera. If specific competitive interactions, or niche partitioning, were responsible for organizing assemblages, then a strong rank-abundance correlation between the Chesterian and Morrowan range-through genera would be expected. To the contrary, taxa that were numerically abundant during the Chesterian were not necessarily abundant during the Morrowan, and those that were rare during the Chesterian were not necessarily rare during the Morrowan. Despite this reorganization of abundant Chesterian taxa, the Morrowan assemblage maintained the same rank-abundance and diversity structure. Given the overall persistence of environmental conditions and the steep decline in relative abundances (Fig. 6), it is likely that brachiopods were partitioning resources, but that the identities of the most successful, i.e., most abundant, genera are the result of ecological contingency (e.g., Hubbell 2001). The unconformity at the Mississippian/Boundary in the Ozarks is a surface of subaerial exposure (Handford 1995), which means that the brachiopod fauna was completely eliminated in the region and subsequently reestablished. During the repopulation of the Arkoma Shelf, many of the same brachiopod genera returned along with newcomers. As recolonization proceeded, the Chesterian success of range-through genera did not influence their subsequent success. However, the large degree of correspondence between the Chesterian and Morrowan DCA1 genus scores (Fig. 8) suggests that the range-through genera were reestablished in the same relative positions along an as yet to be recognized environmental gradient, albeit with different relative abundances.

The ecological structure analyses taken as a whole suggest that the partitioning of resources is neither random nor taxon specific. These data are consistent with Gleasonian dynamics whereby the taxa that arrive in an area first become abundant and the competition among taxa for resources plays a secondary role (Gleason 1926). Further support of this hypothesis was garnered by Patzkowsky and Holland (2007), who found the same bipartite rank-abundance structure with temporal persistence in Late Ordovician

assemblages of the Cincinnati Arch (their Fig. 10). Additionally, it appears that the overall diversity structure observed in the Ozarks is analogous to the paleocommunity types identified by Bennington and Bambach (1996) in the Middle Pennsylvanian Breathitt Formation of the Appalachian Basin. Their paleocommunity types are recurring suites of taxa that are drawn from a similar species pool but in which the exact taxonomic composition and, more importantly, the relative abundances of the constituent taxa are not preserved.

In theory, competing taxa within a saturated local community consume most of one or more limiting resources thus excluding immigrant taxa, and thus rendering local richness independent of regional richness (Cornell and Lawton 1992). Patzkowsky and Holland (2003), in a study of Upper Ordovician (Mohawkian and Cincinnatian) assemblages from central Tennessee, found that local communities were neither saturated nor strongly influenced by interspecific competition. They found that local richness increased linearly with regional richness, suggesting that local assemblages are limited only by the regional species pool. Furthermore, they found that immigrant taxa could become incorporated into the local and regional faunas, which would not have occurred if local communities were saturated. In a study of Middle Ordovician faunas from central Kentucky Holland and Patzkowsky (2004) also found that paleocommunities were not structured by intense interspecific interactions. Using biofacies analysis (Q-mode by r-mode cluster analysis) and detrended correspondence analysis, they could detect a large degree of ecological stability through the Middle Ordovician. However, it was also found that certain aspects of the paleoecology were volatile. Within certain biofacies, the rank-abundance distributions of taxa changed through time. The Ordovician findings (Patzkowsky and Holland 2003; Holland and Patzkowsky 2004) are largely consistent with this study. The richness and evenness structure at multiple spatial scales and the overall rank-abundance distributions are preserved even though there is a taxonomic turnover

event in which the relative abundances of surviving taxa are not preserved. These data suggest that interspecific competition is not the dominant means of determining brachiopod richness and abundance.

However, other studies have shown that interspecific competition in Paleozoic brachiopod assemblages is important. In particular Hermoyian et al. (2002) compared the morphology of four coexisting Late Ordovician brachiopod species and found that each species occupied a different region of morphospace. According to the law of competitive exclusion, competition among brachiopods for either space or food resources will prevent competing taxa from occupying the same morphospace. Hermoyian et al. (2002) followed this morphological approach to the question of paleocommunity competition rather than the abundance approach. Their data were collected from a single stratigraphic section, which is approximately nine meters thick, from a single locality. The results presented by Hermoyian et al. (2002) are in apparent conflict with those presented here as well as the other Ordovician studies mentioned above, but the spatial and temporal scales are not comparable. Future tests of paleocommunity saturation and interspecific competition may benefit from incorporating both abundance and morphological data on a regional scale. Although individual localities may show evidence of strong competition, those interactions may not be strong enough to maintain constant relative abundance relationships across regional spatial scales through geologic time.

The hypothesis that communities are not governed by strong taxon interactions is consistent with the unified neutral theory of biodiversity and biogeography (UNTB) put forth by Hubbell (2001), where the abundances of individual taxa are determined by stochastic processes. The UNTB predicts that communities that have the same rate of speciation and the same rate of immigration from the larger metacommunity will have approximately the same structure and will be fit by the zero-sum multinomial distribution (Hubbell 2001). Although the zero-sum multinomial does not fit the Chesterian and Morrowan data, neutral dynamics seem to be operating here. There are overarching rules that determine assemblage structure (Figs. 4–6), but individual taxa are equal in their ability of compete for resources, and which taxa become abundant during any given time interval is not predictable.

The other interesting result here is that the overall degree of similarity among beds increased from the Chesterian to the Morrowan. This suggests an increase in the ability of taxa from the regional species pool to establish themselves locally. There are three potential explanations for this observation. First, the overall environment became more homogenous during the Morrowan, which meant that certain taxa with relatively narrow environmental tolerances could become more widespread geographically. However, the increase in taxonomic homogeneity may be a sampling artifact. The total longitudinal range of the Morrowan collections is less than that of the Chesterian collections, and the Morrowan collections are primarily from the western portion of the outcrop belt. This is largely due to the paucity of Morrowan carbonate units in the east, where more Chesterian-age sandy carbonates were sampled than Morrowan-age ones. In an effort to maintain a large degree of environmental homogeneity, the Morrowan sandstones, which dominate in the east, were not sampled. Second, the Morrowan could be considered a recovery interval where the fauna was recolonizing the Arkoma Shelf after a major sea-level change, and whatever competitive interactions were taking place during the Chesterian were reduced during the Morrowan reorganization. This option, however, is not likely. If the Chesterian fauna was a late stage of ecological succession and the Morrowan an early stage, then a difference in the overall abundance structure would surely exist (e.g., Dean and Connell 1987). Third, the increase in homogeneity could be the result of increased numbers of widespread generalist taxa. However, this does not appear to be the case either. An analysis (not shown) of all the occurrences of the Ozark genera during the Chesterian and Morrowan, again based on the Paleobiology

Database, shows that the modal distance from the Ozarks decreases from the Chesterian to the Morrowan; the genera found in the Ozarks during the Morrowan appear to be somewhat more narrowly distributed than those that occur in the Chesterian. However, a detailed ecological analysis of individual taxa to determine their degree of specialization or generalization has yet to be performed.

Finally, this study reiterates the importance of regional studies of paleodiversity. Abundance data are easily collected over regional scales and can provide a more nuanced picture of diversity over presence/absence data. For example, the ADP results for richness show that there is no difference in the among-bed component (β_a, Fig. 4). A decrease in beta would indicate an increase in the overall taxonomic similarity. The stability in ADP is in contrast to the modified Morisita-Horn index findings (Fig. 7), which show an increase in the taxonomic similarity among beds. This contrast does not imply that one or both of the measures are incorrect, just that the abundance and richness components of regional diversity respond to environmental changes differently. The incorporation of abundance data provides more detailed diversity information than presence absence data alone.

The importance of regional studies is also highlighted because changes in regional diversity through time do not always parallel global patterns. The global drop in diversity at the Mississippian/Pennsylvanian boundary was not manifested in the Ozarks as a decline in richness or evenness, but rather as a taxonomic turnover event driven by extirpation and immigration associated with latitudinal range shifts. Future regional studies of the middle Carboniferous are likely to reveal complex dynamics that involve both regional extirpation and extinction.

Conclusions

1. A combination of taxonomically sensitive and insensitive techniques has proved useful for analyzing ecological structure in fossil assemblages. Insensitive methods like additive diversity partitioning and rank-abundance curves highlight the gross ecological structure of assemblages whereas multivariate gradient analysis and similarity analysis reveal the specific roles of particular taxa in shaping the details of an assemblage. In tandem these analyses can provide insight into the mechanisms of community assembly, including the roles of interspecific competition and saturation.

2. The Chesterian and Morrowan units of the southern Ozarks in Arkansas and Oklahoma show remarkable continuity of biodiversity structure. From the Chesterian to the Morrowan there are no statistically significant changes in taxonomic richness, dominance, and rank-abundance distribution. This stability is maintained despite a >50% turnover in taxonomic composition associated with a global drop in sea level caused by rapid growth of Gondwanan ice sheets. Stability in diversity structure was accompanied by a reshuffling of the abundances of genera that persisted from the Chesterian to the Morrowan. All of these observations suggest that communities living on shallow tropical carbonate platforms during the middle Carboniferous were structured by non-competitive processes that appear to be neutral with respect to taxon identity. Despite a major shift toward a cooler global climate, there was comparatively little change in tropical biodiversity.

3. A significant increase in similarity indicates greater spatial homogeneity during the Morrowan relative to the Chesterian. Although its causes remain uncertain, the increased similarity likely indicates that there was more intraregional migration of taxa during the Morrowan than during the Chesterian.

4. Regional studies provide important information on how biotas respond to global changes in climate that is obscured by global studies. Of critical importance is that regional field studies are much more likely to incorporate critical abundance data that are often lacking from global databases compiled from the literature. Furthermore, as has been demonstrated here, global extinctions are not experienced equally everywhere.

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