THE SPATIAL STRUCTURE OF BIODIVERSITY IN THE FOSSIL RECORD: CONTRASTING GLOBAL, CONTINENTAL AND REGIONAL RESPONSES TO CLIMATE CHANGE

by

NOEL ALEXANDER HEIM

(Under the Direction of Steven Holland)

ABSTRACT

Global, continental, and regional scales of diversity are examined in the context of past global climate change. A null model of global diversity highlights the importance of migration as an evolutionary process that can influence not only global, but continental diversity as well. The model also highlights extinction as a scale-dependent process that has differing effects on diversity depending on the scale of observation. The model results are confirmed by a global-scale data set of Ordovician invertebrates. A continental scale examination of the latitudinal diversity gradient in the tropical regions of western Pangea (Laurentia and South America) during the Carboniferous further highlight the differences between continental and global diversity. Previous global-scale studies produced simple symmetrical latitudinal diversity gradients. The data for western Pangea suggest a more complex and potentially asymmetric gradient during the Carboniferous. The data do support, however, a previously recognized global shallowing of the latitudinal diversity gradient with the onset of Gondwanan glaciation in the middle Carboniferous. A regional field study of middle Carboniferous paleocommunities was conducted in the southern Ozark highlands of Arkansas and Oklahoma. This study incorporated presence-absence and abundance information for brachiopod genera on the tropical shallow-water Arkoma Shelf. These data do not show the extinction event previously recognized at the global scale. Additionally, the field data show remarkable stability in the overall diversity structure of the latest Mississippian (Chesterian) and earliest Pennsylvanian (Morrowan) paleocommunities. Additive diversity partitioning of taxonomic richness and evenness show no differences between the Chesterian and Morrowan in among-collection diversity, within-bed diversity, and among-bed diversity. Likewise the overall shape of the rank-abundance distribution is preserved, although the rank-order of taxonomic membership is not. These data suggest that tropical carbonate platforms were relatively stable and recovered quickly from major environmental perturbations, like a fall in sea level. They also suggest that strong interspecific interactions were not persistent at the stage level. All of these analyses highlight the spatial complexities that are masked when diversity is measured at the global scale.

INDEX WORDS: Paleozoic, Ordovician, Carboniferous, Mississippian, Pennsylvanian, Chesterian, Morrowan, Hindsville Formation, Pitkin Formation, Hale Formation, Bloyd Formation, Sausbee Formation, McCully Formation, Ozarks, Arkansas, Oklahoma, biogeography, paleontology, paleoecology, Brachiopoda, latitudinal diversity gradient, additive diversity partitioning

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INTRODUCTION AND LITERATURE REVIEW

Introduction and Objectives

Studies of global diversity are a mainstay in paleobiological research (e.g., Sepkoski 1981; Sepkoski et al. 1981; Sepkoski 1988; Miller 1997; Westrop and Adrain 1998; Alroy et al. 2001; Peters and Foote 2001; Stanley and Powell 2003). Such studies of global diversity have led to a greater understanding of the history of life on Earth, but global diversity is an average of diversity patterns at local, regional, and continental scales. Furthermore, global patterns are not always, if ever, reflected at smaller spatial scales (e.g., Miller and Mao 1998). Although there is a growing focus on regional paleobiology (e.g., Ziegler 1965; Patzkowsky and Holland 1993; 1996; Layou 2007), there are few explicit comparisons of diversity at multiple spatiotemporal scales. An obvious exception is the latitudinal diversity gradient, which shows increasing diversity with decreasing latitude and is much studied by neontologists and paleontologists alike. The latitudinal diversity gradient likely has an important effect on global diversity patterns. However, the causal mechanisms of the latitudinal diversity gradient are not well understood (Hillebrand 2004) and it is certainly not known how the latitudinal diversity gradient changes from continent to continent or through geologic time. The purpose of this research is to dissect previously established patterns of global diversity into smaller continental and regional components, including the latitudinal diversity gradient. This dissection will provide a more spatially comprehensive understating of how diversity changes over geologic time.

This research will largely, but not exclusively, focus on the transition between the Mississippian, a time of greenhouse climate, and the Pennsylvanian, a time of icehouse climate, (Veevers and Powell 1987; Frakes et al. 1992; Mii et al. 1999; Batt et al. 2007). Focusing on an interval of global climate change is particularly important if the latitudinal diversity gradient is a major factor in determining global diversity, regardless of whether the gradient is the result of the species-area effect (Rosenzweig 1995), the mid-domain effect where taxa are concentrated in the middle of a range that has hard boundaries, i.e., the poles, (Colwell & Hurtt 1994; Lyons & Willig 1997), the energy-diversity hypothesis (Currie 1991; Chase and Leibold 2002), or higher speciation rates in the tropics (Buzas et al. 2002; Jablonski et al. 2006). All of these factors are likely influenced by the onset of glaciation, which reduced global temperatures, lowered sea level, and reduced available habitat area, especially at high latitudes.

Scientists and society at large are increasingly concerned with the impacts that human society has had, and will continue to have, on natural systems. The fossil record from intervals of global climate change has much to contribute to a more comprehensive understanding of how ecosystems have responded to past global change across a wide range of temporal and spatial scales. For instance, have fluctuations between even and uneven communities or between high and low spatial heterogeneity of taxonomic composition been associated with past climatic changes? Understanding these dynamics may have important implications for understanding how global environmental changes influence regional ecology. Although the fossil record of Paleozoic climate change is not likely to lead to predictions of future biological changes, it can provide a more comprehensive understanding of the long-term impacts of global climate change and the resilience of biological systems.

Dissertation Structure

The research focus of the dissertation progresses from larger to smaller spatial scales. A null model of global diversity and its responses to origination, extinction, and migration is presented first (Chapter 2). The model simulates diversity on three paleocontinents in response to continuous faunal exchange, origination and extinction. The model highlights the importance of dissecting global diversity by showing that extinction is a scale-dependent process. The interplay of origination, extinction, and migration are confirmed by a data set of global genus occurrences of Ordovician invertebrates. The scale dependance of extinction is also confirmed in these data. Next, the latitudinal diversity gradient is examined for Laurentia and South America during the Carboniferous (Chapter 3). The latitudinal diversity patterns observed in the tropical regions of Laurentia and South America differ from previously recognized global patterns. The continental patterns are complex and dynamic across the interval of climate change at the Mississippian/Pennsylvanian boundary, while the global patterns have a regular distribution and are likely the result of many regional averages. Finally, a field study is presented that examines the regional faunal changes across the Mississippian/Pennsylvanian boundary in the southern Ozarks (Chapter 4). Once again, the regional study highlights differences between patterns observed at different spatial scales. A summary of the conclusions drawn from this research is presented in Chapter 5.

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CHAPTER 2

A NULL BIOGEOGRAPHIC MODEL FOR QUANTIFYING THE ROLE OF MIGRATION IN SHAPING PATTERNS OF GLOBAL TAXONOMIC RICHNESS AND DIFFERENTIATION DIVERSITY, WITH IMPLICATIONS FOR ORDOVICIAN BIOGEOGRAPHY[1]

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Abstract

Biodiversity patterns in the fossil record are often interpreted as functions of only origination and extinction whereas the migration of taxa among regions or paleocontinents is rarely considered. A null biogeographic model is presented that evaluates the role of migration in shaping global biodiversity patterns across evolutionary time scales. As taxa are allowed to originate, go extinct, and migrate among continents, the model keeps track of global richness and differentiation diversity (the diversity gained by pooling continents). The model's results highlight the difference between global-scale and continental-scale origination and extinction rates. Intuitively, origination and extinction have opposite effects on global richness at the global scale, but they interact with migration at the continental scale to influence differentiation diversity and global richness in surprising ways. The model shows that the migration of taxa among paleocontinents can facilitate an increase in global richness, even when continental extinction is greater than continental origination. Additionally, the model shows that differentiation diversity reaches a dynamic equilibrium that is dictated by the combination of migration, origination, and extinction rates. A test of the model with Ordovician macroinvertebrate data indicates that migration rates were low during the Ordovician and that differentiation diversity was high and varied little. Overall, the Ordovician was an interval of high provinciality. It also shown that widespread genera were less prone to global extinction, even though extinction of genera on individual paleocontinents was common.

Introduction

Understanding the history of Phanerozoic biodiversity is a major goal of paleobiology. To this end, many studies of Phanerozoic biodiversity have focused on the dynamics of origination and extinction (e.g., Gilinsky and Bambach 1987; Gilinsky 1994; Patzkowsky 1995; Foote 2000, 2003; Jablonski 2001; Stanley and Powell 2003; Bambach et al. 2004). However, the migration of taxa from the regions in which they originate to other regions plays a key role in shaping regional and global biodiversity. Knowing the role migration plays in shaping biodiversity over evolutionary time scales is necessary for a complete understanding of diversity patterns observed in the fossil record. Such an understanding may also be useful to conservation biologists who need to predict the long-term evolutionary impacts of invasive species, whose migration potential is increased by anthropogenic activities (e.g., Elton 1958; Stachowicz et al. 1999; Mooney and Cleland 2001). Null models provide simple hypotheses that require a minimum number of parameters to explain observations (Gotelli and Graves 1996) and in the past, null models have been used to evaluate migration and local extinction (MacArthur and Wilson 1967). A null biogeographic model is presented here that examines how migration interacts with origination and extinction to affect changes in differentiation diversity and global richness.

Many studies of biodiversity at the global scale (e.g., Sepkoski 1981; Sepkoski et al. 1981) have not fully considered the role of migration (for an exception, see Jablonski et al. 2006). This is likely because origination and extinction have typically been viewed as sufficient to explain global richness patterns. However, global richness is not the simple sum of its paleogeographic regions (Sepkoski 1988; Miller and Mao 1998). The proportion of widespread taxa exerts an important control on global diversity, and taxa typically become widespread through migration. Thus, when collecting data for more than one discrete region, it is necessary to address differentiation diversity (Whittaker 1977), which is a measure of the diversity gained by pooling samples. The present model simulates biodiversity on three continents as a function of migration, origination, and continental extinction. It is important here to distinguish between different levels of extinction. This model is concerned primarily with continental extinction, which is the loss of all populations of a taxon on a continent. Continental extinction is distinguished from the loss of all populations (global extinction) and the loss of a single population (localized extirpation). Examining combinations of the model parameters allows the effects of each parameter on global richness and differentiation diversity to be isolated from the others.

Methods

Differentiation Diversity. — To help better understand the scales of biodiversity, Whittaker (1977) outlined two broad categories of diversity metrics that can be applied to multiple spatial scales: inventory diversity and differentiation diversity. Inventory diversity measures diversity at a single spatial scale whereas differentiation diversity measures diversity between two spatial scales. The most commonly used level of differentiation diversity in the paleontological literature is beta, which is the difference among environmentally homogenous local communities (alpha) within a single landscape (gamma). Beta diversity is the diversity gained by pooling multiple local samples to form a single regional sample. However, the scales of interest for the present study are continental and global; the model presented below simulates delta diversity (Whittaker

1977), rather than beta diversity. The reintroduction of delta diversity here is warranted. Previous studies of differentiation diversity of the Phanerozoic fossil record have focused on local fossil collections (Kowalewski et al. 2002; Layou 2007; Patzkowsky and Holland 2007), even when they are pooled over continental or global scales (Sepkoski 1988; Miller and Mao 1998). Beta and delta are both forms of differentiation diversity; the difference between the two is the spatial scale to which they are applied. Although the computations of beta and delta are identical, ecological and evolutionary processes operate differently at different spatial scales (Okuda et al. 2004), and beta and delta may vary independently. This study focuses on genus lists compiled for entire paleocontinents, not local collections. Therefore, delta diversity is the measure of differentiation diversity used here. The specific measure of delta diversity used in the model is based on the Jaccard coefficient of similarity. In order for greater values of delta diversity to reflect greater differences, delta is calculated as one minus the Jaccard coefficient,

$$\delta = 1 - S_c / (S_1 + S_2 - S_c) \tag{1}$$

where S_1 is the number of taxa in assemblage one, $\underline{S_2}$ is the number of taxa in assemblage two, and S_c is the number of taxa in common to both assemblages. Delta varies from a maximum of one, when no taxa are shared, to a minimum of zero, when both assemblages are identical.

The Jaccard coefficient has a long history as a diversity metric in the paleontological literature (e.g., Cheetham and Hazel 1969; Sepkoski 1974, 1988; Miller and Mao 1998; Shen and Shi 2004). The advantages to using the Jaccard coefficient are that it is a simple and direct measure of similarity (i.e., percentage of shared taxa), and it relies on presence/absence data rather than abundance data. One problem with the Jaccard coefficient is that it is sensitive to differences in the sizes of the samples being compared. However, sample-size dependence cannot be avoided with many commonly used metrics that do not consider abundances (Wolda 1981). The sample sizes (i.e., number of genera) for the model are approximately equal for all continents, and no sample-size bias is imposed on the results.

The Model. — The model presented here tracks changes through time in global richness and delta diversity among continents as taxa are randomly allowed to undergo origination, extinction, and migration among three continents. The fundamental evolutionary unit considered here is the denizen, used in the general sense as a taxon that occupies a region or continent. Each taxon on each continent represents a single denizen. At each time step, the action of each denizen is determined by three model parameters: the probability of migration to another continent (p_m), the probability of origination (p_o), and the probability of extinction on a continent (p_e). The latter two parameters correspond to continental, not global, rates of origination and extinction. The three parameters do not necessarily sum to one, allowing the possibility of no change during a time step. An important quantity in the model is the ratio of the probability of origination to the probability of extinction, called inflation (p_o/p_e). Inflation indicates how the richness of a continent will change in the absence of migration. When inflation is equal to one ($p_o=p_e$), continental origination and continental extinction balance each other and any net changes in continental richness is the result of migration. When inflation is less than one ($p_o<p_e$), the net richness of a continent will decrease unless migration replaces extinct taxa with immigrants. When inflation is greater than one ($p_o>p_e$), migration will combine with origination to induce a net increase in the richness of a continent.

For the purposes of this model, migration is defined as the dispersal to, and successful establishment of, a taxon on a new continent while remaining present on the original continent. Migrating taxa are increasing their geographic range. In this null model, all denizens are equal with respect to the model parameters. Additionally, the model parameters are not independent. If a denizen undergoes a change during a time step, the probability of the other two parameters automatically becomes zero for that denizen during that time step; a denizen will undergo not more than one change during a single time step. This is an oversimplification of real-world possibilities because all three pairwise parameter combinations are theoretically possible within a single time step. For example, a denizen could migrate to establish that taxon elsewhere and go extinct locally during the same time step. However, allowing for such scenarios increases the model's complexity, possibly beyond our current ability to accurately document them in nature. For example, if simultaneous migration and extinction are allowed, should simultaneous origination and extinction be allowed? Allowing for the complete independence of all three parameters introduces unwieldy complexities, particularly with respect to extinction. In this model there are continental and global rates of extinction. Continental extinction is explicitly defined in the model, and global extinction results from one or more random continental extinction events. If simultaneous origination and extinction, potentially interpretable as phyletic extinction, is allowed, then four levels of extinction need to be tracked—continental and global for both phyletic and non-phyletic extinction. Tracking phyletic extinctions in the fossil record at global and continental scales requires detailed phylogenies that are presently not available for most taxa. For the time being, the most useful model has dependence among the three parameters rather than selective independence among some pairs and dependence among others. As more data for testing this new approach to biodiversity dynamics become available, more sophisticated models will certainly be developed. For now the simple null hypotheses generated by this model are most appropriate for the available data.

Each model run consists of 15,000 time steps of 10 Kyr each; the total duration of each run is 150 Myr. The model includes 405 trials covering all combinations of the discrete values of p_m, p_o and p_e used in the model (see Appendix A, also online at http://dx.doi.org/10.1666/07043.s1). Model parameters are fixed within each run, but they vary among runs with continental rates of 0.0001 per Myr to 1.0 per Myr. Continental origination and extinction rates are calculated for a data set of Ordovician marine invertebrates (see "Application of Null Model"), which bracket the rates used here.

Global diversity at the beginning of each model run (t_0) is 100 taxa. These taxa are assigned to continents by scrolling through the taxon list and randomly assigning each taxon to exactly one of the three continents. This ensures that each continent contains a unique, endemic fauna at t_0. The model was also run with initial conditions of three identical continental faunas at t_0; there was no difference in results, which are not shown here. At each time step, each denizen will do one of the following: (1) expand its range to include another continent, (2) go extinct on the continent on which it is being evaluated, (3) generate a new taxon (origination) on the continent on which it is being evaluated, or (4) remain unchanged. A key aspect of the model is that taxon occurrences on each continent (i.e., denizens) are evaluated independently. For example, a single taxon could migrate from one continent to a second and be extirpated from a third in the same time step.

At the end of each model run, global richness and the richness of each continent are tabulated. Also, delta diversity is calculated for each combination of two continents and the mean pairwise delta diversity of all three is computed. The mean delta diversity is one at t_0 because each continent starts with a unique set of endemic taxa. In approximately 73% of the runs, the average delta diversity reaches a dynamic equilibrium (see "Model Results"). The equilibrium delta diversity (δ_{eq}) and equilibrium time, the time it takes to reach equilibrium, are estimated for each run by fitting a logistic curve to a time series plot of global average delta. The logistic curve is fit using the *SSlogis* function in the software package R (R Core Development Team 2006). The fit logistic function has the following form:

$$f(t) = A / (1 + e^{(m-t)/r}), \tag{2}$$

where A is the asymptote, $\underline{m}$ is the location of the inflection point, and $\underline{r}$ is a fit constant. The equation parameters are fit to the data by using the least squares method. The equilibrium delta diversity (δ_{eq}) is the asymptote of the fit logistic curve, and the equilibrium time is designated as the first time step in which the global average delta is within two standard errors of the asymptote. See the Appendix A (also online at http://dx.doi.org/10.1666/07043.s2) for δ_{eq} values with standard errors.

Model Results

Migration and Global Richness. — Migration of taxa among continents has an important impact on global richness. A critical quantity that emerges from the model is inflation (p_o / p_e). If migration is set to zero, global richness is always less than or equal to the initial richness when inflation is less than one (i.e., $p_o < p_e$), and global richness is always greater than or equal to the initial richness when inflation is greater than one (i.e., $\underline{p_o} > \underline{p_e}$). However, if migration is non-zero, there are instances when inflation is less than one and global richness is greater than the initial richness, especially as the fauna ages (Fig. 2.1A, Fig. 2.2). Keep in mind that p_o and p_e are continental, not global, rates. When continental extinction outpaces continental origination and the migration rate is the maximum considered here (1 Myr^{-1}), global richness begins to increase within 10 Myr. Over a duration of up to 150 Myr, migration rates as low as 0.01 Myr^{-1} may induce an increase in global richness under similar conditions of continental origination and extinction. Increasing global richness when continental extinction outpaces continental origination highlights the difference between continental and global rates. The difference between continental and global rates arises because the denizens of a single taxon on separate continents are evaluated independently. In order for a taxon that occurs on more than one continent to go extinct globally, it must go extinct independently on all continents. Thus, the probability of global extinction is less than that of continental extinction and is given by

$$p_{e\,global} = p_e^{\,n}, \tag{3}$$

where p_e is the probability of continental extinction and $\underline{n}$ is the number of continents on which the taxon occurs. It is true that $p_{e\,global} \leq p_e$ for all possible values of p_e (Fig 1B).

Extinction must be less than or equal to one, otherwise there would be more extinction events than available denizens. The probability of global origination for a taxon occurring on multiple continents is greater than that for continental origination because there are multiple independent chances to produce a daughter taxon. The global origination probability is given by

$$p_{o\,global} = p_o \times n, \tag{4}$$

where p_o is the probability of continental origination. It is always true that $p_{o\,global}$ is greater than or equal to p_o (Fig 2.1C). As a taxon becomes more widespread with increasing migration rate, the chance of global extinction is reduced, and the chance of origination is increased, allowing global richness to increase despite continental extinction being greater than continental origination (Fig 2.2).

Migration and Delta Diversity. — The migration of taxa among continents also influences delta diversity. Because the model begins with three continents containing endemic faunas, delta diversity will remain at one (δ_o) if there is no migration. The null expectation is maximal differentiation, so delta diversity can only decrease from δ_o as migration is allowed to vary, and it does so in several ways. The best way to visualize the influence of migration, origination, and extinction on delta diversity is through bivariate plots of delta diversity versus the probability of continental extinction for each level of continental origination (Fig. 2.3). Several general patterns emerge from the modeled delta diversity. First, increasing migration reduces delta diversity relative to δ_o. As increased migration makes the taxonomic composition of the continents more similar, delta decreases for any given combination of continental origination and extinction. Second, increasing the rate of continental origination counteracts the influence of migration by adding new endemics, thus increasing delta diversity. Third, negative inflation (i.e., $p_o < p_e$) also counteracts migration for any given combination of migration and origination. Because continental extinction is greater than continental origination, the world will be populated with older, widespread taxa. The extinction of denizens belonging to widespread taxa will increase delta diversity. Fourth, delta diversity reaches a steady state for all values of migration when the rate of continental origination is greater than the rate of continental extinction. The steady state in delta diversity is generated by a balance between origination and migration. Because continental origination is greater than continental extinction, new endemic taxa have time to migrate to other continents before becoming locally extinct. In this situation, continental extinction is neutral with respect to delta diversity. Because there is a mixture of widespread and endemic taxa, the continental extinction of the former increases delta diversity while the extinction of the latter decreases delta diversity. These patterns emphasize the fundamental difference between continental origination and extinction as evolutionary processes. All originations increase delta diversity, whereas the extinction of a denizen may increase or decrease delta diversity. Similarly, all originations increase global richness, whereas the extinction of a denizen may or may not decrease global richness.

Approximately 27% of the 405 model runs fail to reach a dynamic equilibrium in delta diversity within 150 Myr (Fig. 2.4). Equilibrium is not reached for the full range of migration when inflation is less than one ($p_o < p_e$) and extinction is greater than about 0.1 Myr^{-1}. When extinction greatly outpaces origination, the residence time of immigrant taxa is too short for an equilibrium to be reached quickly. Also, equilibrium is not reached within 150 Myr for low levels of migration when inflation is greater than one (p_o

$> p_e$). With low rates of migration, it is expected that an equilibrium will be reached slowly, even with high origination. Delta diversity remains maximal when the rate of extinction is high and the rate of migration is low, except for the highest levels of origination. Combining the highest extinction and lowest migration rates inhibits taxa from spreading to new continents.

An important aspect of this model is the equilibrium time. Equilibrium times are determined primarily by continental origination and migration; extinction has little effect on the equilibrium time in most cases (Fig. 2.5). As with δ_{eq}, continental extinction appears to be neutral, and a balance between continental origination and migration is reached. Lower levels of migration produce longer equilibrium times. As the level of origination increases, the equilibrium time tends to decrease. For nearly all runs with continental origination rates greater than 0.1 Myr^{-1}, the equilibrium time is less than 10 Myr (Fig. 2.5).

Discussion of the Model

Migration and Global Diversity. — The results of this model show that the migration of taxa among continents influences global richness. Because of this, explicitly including migration as an evolutionary parameter in future studies of evolutionary rates is warranted. The typical data set from which global Phanerozoic origination and extinction rates are calculated contains a list of genera with some estimate of the timing of global first and last appearances (e.g., Sepkoski et al. 2002). However, this type of data set excludes vital geographic information that is necessary for estimating migration rates and continental rates of origination and extinction. These model results highlight a fundamental difference between global and smaller-scale, in this case continental, rates of origination and extinction. Under conditions of non-zero migration, global richness may increase, while continental rates of extinction are higher than those of continental origination. Although Miller and Mao (1998) did not calculate origination and extinction rates, this result corroborates their conclusion that continental dynamics need not exhibit a one-to-one correspondence with global dynamics. Furthermore, the model results suggest that migration can play a role in increasing global richness. The nature of the model does not allow for a direct assessment of the relationship between global richness and migration, but there is an inferred positive relationship based on the influence of migration on global origination and extinction rates (eqs. 3 and 4). However, the positive relationship at this point is speculative. Migration could also decrease global diversity. If three continents each have 100 taxa and delta diversity is high because of high migration, global richness will be greater than if delta diversity and migration are low. Despite the ambiguity of migration's role in determining global richness, the model results suggest that global richness is driven primarily by origination. Migration is likely to have an important influence on global richness only when continental extinction rates are low relative to origination and migration rates are high.

Migration and Delta Diversity. — The model results for delta diversity (Fig. 2.3) highlight migration as a process that reduces delta diversity, continental origination as a process that increases delta diversity by counteracting migration, and extinction as a process that can either increase or maintain differentiation diversity, depending on inflation. Migration reduces delta diversity by increasing the taxonomic similarity among continents, an unsurprising result. The immigration of a new taxon will increase the richness of that continent while making the difference between the continents less. This suggests that intervals of high provinciality should be characterized by low rates of migration. This is consistent with an increase in late Paleozoic provinciality (Bambach 1990), which has been attributed to reduced geographic range of taxa (possibly from reduced migration) rather than increased endemism (possibly from increased origination). The role of continental extinction in determining delta diversity is more ambiguous than that of migration and origination. The ambiguous role of continental extinction in diversity dynamics is manifest in the response of δ_{eq} to inflation; delta diversity remains at a steady state while extinction is less than origination, but rapidly approaches δ_o as extinction becomes greater than origination, especially for the highest rates of migration (Fig. 2.3). This result is somewhat surprising, particularly the stability of δ_{eq} when inflation is less than one. Because the extinction of a continental denizen will decrease delta diversity if the denizen is endemic and will increase delta diversity if the denizen is of a widespread taxon, the overall effect of extinction depends on the proportion of endemic and non-endemic taxa on a continent. If there is a mix of widespread and endemic taxa then continental extinction is neutral with respect to delta diversity. But, if most taxa are widespread, then continental extinction increases delta diversity. The interpretation of these extinction dynamics is surprising, but preliminary. Further theoretical and empirical exploration of how extinction influences biodiversity dynamics at multiple spatial scales should yield interesting and more definite results.

The time it takes the model to reach an equilibrium in delta diversity ranges from less than 1 Myr to more than 150 Myr. For the range of origination rates in this model, many of the equilibrium times are between 1 and 10 Myr. Many paleontological data sets are binned chronologically by stages. The average post-Cambrian stage has a duration of 5.7 Myr (Gradstein et al. 2004), which means that calculations of delta diversity for individual stages potentially reflect equilibrium values, especially if rates of continental origination and migration are greater than about 0.1 Myr^{-1} (Fig. 2.5). The assumption of equilibrium at the stage level will not necessarily be easy to verify. High-resolution stratigraphic information is required to observe an asymptotic, logistic increase in delta diversity through a stage. Such data may be available from detailed regional field studies, but the correlation of individual collections across continents is not likely for any substantial portion of the Phanerozoic record. Although the demonstration of equilibrium in delta diversity is unattainable for large spatial scales across intervals of geologic time, the assumption of equilibrium may be reasonable if observed rates are large enough.

Delta Diversity and Mass Extinctions. — The steady state in delta diversity when origination is greater than extinction and the increase in delta diversity as origination becomes greater than extinction (Fig. 2.3) may have important implications for understanding Phanerozoic extinction events. Indeed, Jablonski (1998) found that the proportion of invasive (i.e., migrating) genera immediately following the end-Cretaceous extinction varied among continents. Bambach et al. (2004) recognized two categories of mass extinction events: true mass extinctions characterized by elevated extinction rates and mass depletions characterized by reduced origination rates. The model results suggest that delta diversity will change differently for each type of extinction. Consider a hypothetical situation where the rates of origination and extinction are equal and migration is at a high level but constant. During a mass extinction event where the continental extinction rate is elevated above the continental origination rate, delta diversity will increase precipitously. However, during a mass depletion where the origination rate drops below the extinction rate, delta diversity will decrease. Continuing with the same hypothetical system with initially equal continental origination and extinction rates and constant migration, changes in delta diversity can also be predicted for radiation events. If origination increases from its initial state, delta diversity should increase. Finally, if the rate of extinction drops below the rate of origination, no change in delta diversity is expected. This last scenario generates exponential diversification with constant origination that is not balanced by extinction. These hypotheses have yet to be tested, but they represent a potentially fruitful new direction in paleoecological research.

With the emergence of high-quality paleogeographic maps (Scotese 2001) and global-scale databases, such as the Paleobiology Database (paleodb.org), that contain paleogeographic and paleoenvironmental information, it is now possible to track not only global richness and global origination and extinction rates through time, but also migration and continental origination and extinction rates. With paleogeographic information for each taxon occurrence in a database, migration rates can be calculated by comparing the timing of a taxon's global first occurrence with each of its continental first occurrences. Continental extinctions can be calculated by comparing global last occurrences with continental last occurrences. Origination, of course, is not scale dependent; the continental origination of a taxon is also its first global occurrence. Understanding the macroevolutionary role of migration in the history of Phanerozoic biodiversity represents a new and important direction for paleobiological research.

Application of Null Model

Ordovician Data. — This biogeographic model of migration is applied to a data set of Ordovician benthic macro-invertebrates extracted from the Paleobiology Database (PBDB). The full data set consists of 9187 genus occurrences, 1147 unique genera, and 1993 collections (Appendix B). Following Miller and Mao (1998), the data set is composed of the Trilobita, Brachiopoda, and the molluscan classes Monoplacophora, Bivalvia, and Gastropoda. Using only benthic groups standardizes the ecological and life history traits by excluding groups such as nektonic cephalopods that spend the entirety of their life in the water column above the sediment-water interface and are largely viviparous (Ruppert and Barnes 1994). Additionally, these taxa are chosen because they represent a cross section of Ordovician marine invertebrates and all three evolutionary faunas (Sepkoski 1981). The data are stratigraphically binned into the PBDB's five default bins for the Ordovician, corresponding to the Tremadocian, Arenigian, combined Llanvirnian and Llandeilian, Caradocian, and Ashgillian stages of the standard British time scale. Additionally, data from the youngest Cambrian and oldest Silurian bins are included so evolutionary rates can be calculated for all Ordovician bins. The data for each bin are subdivided into three paleogeographic regions: Laurentia, South China, and all other Ordovician paleocontinents. Laurentia and South China have sufficient numbers of collections in the PBDB to be analyzed separately. The remaining data are combined so that more accurate rates of origination, extinction, and migration can be calculated. As more data become available from other paleocontinents, a more realistic paleogeographic division of the data can be applied. In order to standardize the stratigraphic scale of the collections used, only collections made at the levels of bed or group of beds are included. This prevents a bias from long formation-level species lists that are common for Laurentia, but rare for South China. The other paleocontinent data from the Ashgillian has the smallest number of collections; diversity is calibrated to this level.

Ordovician Biodiversity. — Simple genus richness is calculated for each time bin, and a subsampling routine is used to account for differences in sampling intensity among time bins and paleocontinents. The data are subsampled using the by-list unweighted method (Alroy 2000; Bush et al. 2004) whereby the same number of collections (i.e., taxon lists) are randomly drawn without replacement from the pool of all collections, and the number of unique genera is tabulated. The unweighted method is used here because it assumes that differences in list length are real and not an artifact of sampling intensity (Bush et al. 2004). Because long formation-level lists were excluded from the data set, a weighted subsampling method would obscure real differences in list lengths.

Genus richness curves are generated for Laurentia, South China, and the pool of all other paleocontinents (Fig. 2.6). Genus diversity in South China increased through the Llanvirnian/Llandeilian then remained constant through the Ashgillian. The major feature of the Laurentian curve is a marked decrease in richness in the Llanvirnian/Llandeilian that interrupts an overall increase in richness. This large drop in diversity in the Llanvirnian/Llandeilian is likely due to the Knox unconformity seen throughout eastern and central North America (Mussman and Read 1986). The curve for the other paleocontinents is volatile and shows no trend. This is likely due to the lumping of geographically disparate regions that are variably sampled within the PBDB. Presently, controlling for depositional environment is not possible because none of the Llanvirnian/ Llandeilian collections from Laurentia have diagnostic environmental information.

Origination and Extinction Rates. — As described above, origination and extinction rates can be calculated at the global or continental level. Both levels of origination and extinction are calculated for the Ordovician data (Fig. 2.7). In calculating global rates, all stratigraphic gaps between first and last global occurrences are filled. For continental rates, it is assumed that each taxon has a continuous range on any given paleocontinent; all gaps between the first and last occurrences are filled on each paleocontinent. This assumption is parsimonious and avoids complicated histories wherein a genus is present on a paleocontinent, migrates to another paleocontinent, is extirpated from the original paleocontinent, and finally migrates back to the original paleocontinent.

Per-interval extinction rates are calculated as the ratio of the number of genera with their last occurrence in a bin to the total number of genera in that bin. Per-interval origination (and migration) rates are calculated as the ratio of the number of originations (or migrations) within a bin to the number of genera that crossed the lower boundary of that bin. Both continental and global origination rates (Table 2.1, Fig. 2.7) are maximal during the Tremadocian and decrease though the Llanvirnian/Llandeilian. Following an increase in the Caradocian, origination rates reach their minimum during the Ashgillian. Continental and global extinction rates are constant during the early Ordovician, drop to their minimum in the Llanvirnian/Llandeilian, then increase to their maximum in the Ashgillian. Origination rates are higher than extinction rates during the Tremadocian through the Caradocian. Origination and extinction rates diverge in the Ashgillian, and extinction outpaces origination. The high rates of origination in the early Ordovician account for the Ordovician radiation, and the elevated extinction in the Ashgillian is likely a response to the end-Ordovician mass extinction.

The global and continental rates are nearly parallel for both origination and extinction. As predicted by equations (3) and (4), the global extinction rate is always less than the continental extinction rate, and the global origination rate is always greater than the continental origination rate (Fig. 2.7). The difference between the two extinction curves represents the difference between the extinction of denizens on paleocontinents and the global extinction of genera. However, the global and continental extinction curves may not be directly comparable and may reflect an artifact of comparing global extinctions per genus with continental extinctions per denizen. To confirm that there are real differences between global and continental extinction rates, global extinctions per genus are compared with continental extinctions per genus (not shown). For all five Ordovician bins, the number of continental extinctions per genus is greater than the global extinctions per genus. This indicates that, on average, a genus will experience at least one continental extinction before it becomes globally extinct, suggesting that widespread taxa are less prone to global extinction. The interpretation of the origination curves is less straightforward. Because an origination event is the same whether it is being counted globally or within discrete geographic regions, the difference between global origination rates and continental origination rates is, at least partially, a mathematical artifact. The same number of originations is divided by either the total number of genera or the total number of continental denizens. Despite the artifactual nature of the offset, the difference between global and continental origination rates is biologically meaningful. If allopatric speciation is a common, if not the predominant, mode of speciation, then it is expected that for a single genus present on two distant paleocontinents separated by a deep ocean basin thousands of kilometers wide, as Laurentia and South China were during the Ordovician (Scotese 2001), independent divergence between the isolated denizens is expected. Although a phylogenetic analysis is needed to confirm this hypothesis, these results suggest that allopatric speciation may be a normal mode of speciation, whereby a single parent genus can give rise to multiple daughter genera through isolation on multiple paleocontinents. Although phylogenetics often considers polytomies unsatisfactory in solutions to evolutionary relationships, they may be real consequences of paleobiogeography.

Migration Rate and Delta Diversity. — Migration rate and global average delta diversity among the three paleogeographic regions are calculated for the Ordovician data (Fig. 2.7). Delta diversity is calculated for the Ordovician data in the same way as in the model, one minus the global average Jaccard. The migration rate is roughly parallel to origination rate through the Ordovician. Overall, delta diversity is high throughout the Ordovician and varies between 0.87 and 0.93 (Fig. 2.7). The Ordovician data are largely consistent with the model. The model results indicate that when origination and extinction rates are greater than about 0.05 Myr^{-1} and migration is less than about 0.01 Myr^{-1}, then delta diversity will be greater than about 0.9 (Fig. 2.3). This is the case for the Ordovician. Because origination is consistently greater than extinction, the variations in extinction should have no effect on delta diversity, and continental origination is fast enough to generate delta diversity values above 0.8. This is consistent with observations that the Ordovician, particularly the late Ordovician, was an interval of high provinciality

(Sheehan and Coorough 1990; Jin 2001) and that provinciality was driven by high rates of origination and low rates of intercontinental migration.

In order for the model to be applied to the Ordovician data, the measured values of delta diversity need to be either shown or assumed to represent equilibrium conditions. Given the relatively low rates of per-stage migration, it is possible that observed delta diversity does not reflect equilibrium conditions. Non-equilibrium is even more likely given that the durations of the Llanvirnian/Llandeilian and Ashgillian are shorter than the other Ordovician bins. Data with high stratigraphic resolution are needed to test for equilibrium. And, even if equilibrium was reached, only the data from the stratigraphic intervals that have reached equilibrium should be used. Questions related to equilibrium certainly need to be answered before any definite conclusions can be drawn. What proportion of the Phanerozoic record is characterized by equilibrium conditions with respect to delta diversity? Is delta diversity partially or fully reset at stage boundaries or mass extinctions? As mentioned above, answering these questions at the global scale is not tractable for the time being. However, at the sub-continental and regional scales, these questions can be investigated with detailed field studies.

Miller and Mao (1998) observed a decline in beta diversity through the Ordovician, especially in South China. As indicated above, beta and delta diversities are fundamentally different and there is no reason to assume that trends in beta diversity will have any bearing on trends in delta diversity. A pattern of scale-independence within biodiversity dynamics has emerged in recent years with the increasing number of studies using additive diversity partitioning to measure differentiation diversity at multiple spatial scales (Lande 1996; Veech et al. 2002). Although conducted at sub-continental spatial scales, several studies of differentiation diversity indicate that biodiversity dynamics at one scale are independent of those at larger or smaller scales (Gering and Crist 2002; Okuda et al. 2004; Layou 2007; Patzkowsky and Holland 2007).

Miller (1997) found that the fauna aged through the Ordovician and that older genera were widespread. Taxon ages were calculated (data not shown) for the Ordovician data used here, and the percentage of endemic genera decreases from the Llanvirnian/ Llandeilian through the Ashgillian. As indicated above, if origination and extinction operate randomly on denizens at the continental level, then widespread genera will be less prone to global extinction than their endemic counterparts. This suggests that being widespread is more important for avoiding global extinction than being a good competitor with other taxa for resources. This hypothesis corroborates a finding by Jablonski and Hunt (2006) that geographic range, at least for Cretaceous mollusks, is the most important factor in species survivorship. Jablonski and Hunt also found that the mode of larval development is much less important in survivorship than geographic range. If larval mode is important for long-distance dispersal and the expansion of geographic range, then it appears that the equality among taxa with respect to migration used in the model may be an accurate representation of nature.

Despite coarse temporal constraints and possible non-equilibrium conditions, the ability of the model to explain observations in the Ordovician data is remarkable. Clearly, the migration of taxa among paleogeographic regions is an important factor in the biodiversity dynamics of ancient systems. More importantly, the quantification of migration in the fossil record is tractable, even at coarse paleogeographic and temporal scales. Additionally, these results highlight the importance of analyzing rates of origination and extinction at the regional or paleocontinental levels. If origination and extinction operate on isolated denizens, and migration generates some degree of taxonomic similarity among isolated continents, then measures of global origination and extinction rates will be different from continental rates. The difference between global and continental rates, particularly for extinction, allows a more nuanced understanding of biodiversity dynamics. Of course, these results are preliminary and likely to be modified as better data become available. This new approach to studying the Phanerozoic history of evolution and biodiversity has potential to generate a more refined understanding of how macroevolution operates over large and intermediate spatial scales.

Conclusions

1. Migration is an important evolutionary process that can facilitate an increase in global richness, even when continental extinction rates are greater than continental origination rates. Migration exerts this influence on richness by increasing the global origination rate above the continental origination rate and depressing the global extinction rate below the continental extinction rate.
2. When taxa migrate among continents, delta diversity tends to reach a dynamic equilibrium, generally within 100 Myr. However, in cases where origination <u>or</u> migration rates are high (greater than about 0.1 Myr^{-1}), equilibrium is reached between 1 and 10 Myr, which brackets the average duration of a Phanerozoic stage. The equilibrium delta diversity is determined by the combination of migration, continental origination, and continental extinction rates.

3. Migration has complex interactions with continental origination and extinction to produce delta diversity. Migration reduces delta diversity and continental origination increases delta diversity. Continental extinction increases delta diversity only when there is net extinction ($p_o < p_e$). For any given combination of migration and continental origination, delta diversity reaches a steady state with respect to continental extinction rate when there is net origination ($p_o > p_e$).
4. An examination of Ordovician data parsed by paleocontinent shows that the high rates of continental origination and low rates of migration were important factors in determining delta diversity during the Ordovician. Delta diversity was relatively high during the entirety of the period, indicating consistently high provinciality.

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Figure 2.1 — Schematic representations of the relationships among continental extinction (p_e), continental origination (p_o), and global richness. In all plots the shaded regions represent impossible values. (A) The relationships between inflation (p_o/p_e) and increases in global richness. S_0 is the initial global richness. The vertical line marks where the rate of origination equals the rate of extinction. The horizontal line represents global richness at t_0, 100 taxa. (B) Differences between continental and global extinction rates as taxa become more and more widespread. n = the number of continents on which a taxon exists. When n = 1, global extinction equals continental extinction. Global extinction is always less than or equal to continental extinction. Note that the rate of extinction can never be greater than one. (C) Differences between continental and global origination rates as taxa become more and more widespread. When $n = 1$, global origination equals continental origination. Global origination is always greater than or equal to continental origination, and rates greater than one are possible.

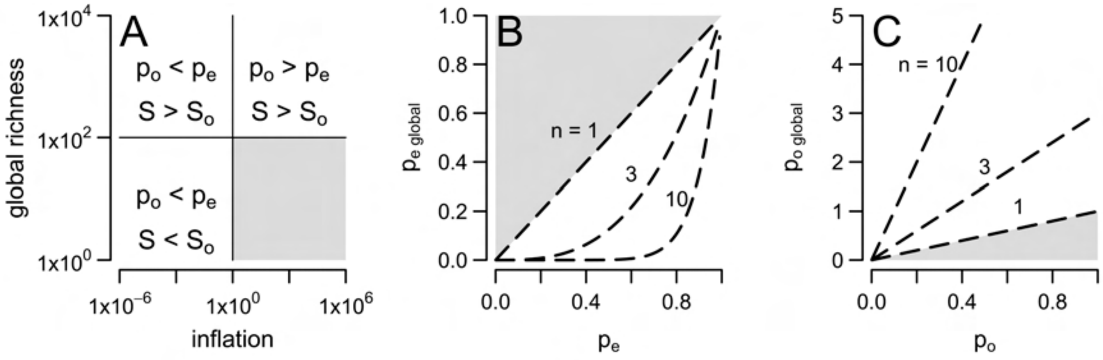

Figure 2.2 — Global richness plotted against inflation (p_o / p_e) for all 405 runs of the model at six time intervals after t_0. These plots are set up as in Figure 2.1A. The points are shaded so that overlapping points are darker. In all panels, the rate of migration is non-zero. Note that when inflation is greater than one, global richness is always greater than or equal to the initial richness of 100, but when inflation is less than one, global richness is sometimes greater than 100 because migration increases the global origination rate above p_o and decreases global extinction blow p_e.

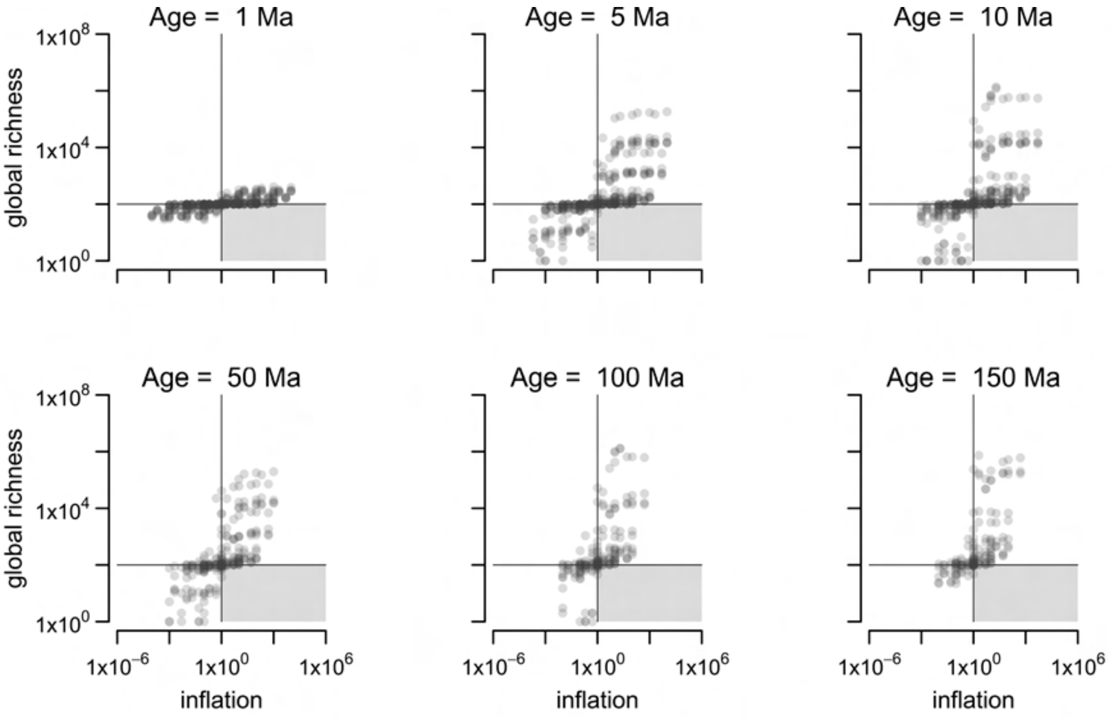

Figure 2.3 — Bivariate plots of delta diversity versus extinction rate. Delta is computed as one minus the Jaccard coefficient. Each plot area is for a different continental origination rate (*p_o*) and the symbols represent different migration rates. All rates have units of Myr^{-1}. The vertical line marks where the rate of origination equals the rate of extinction.

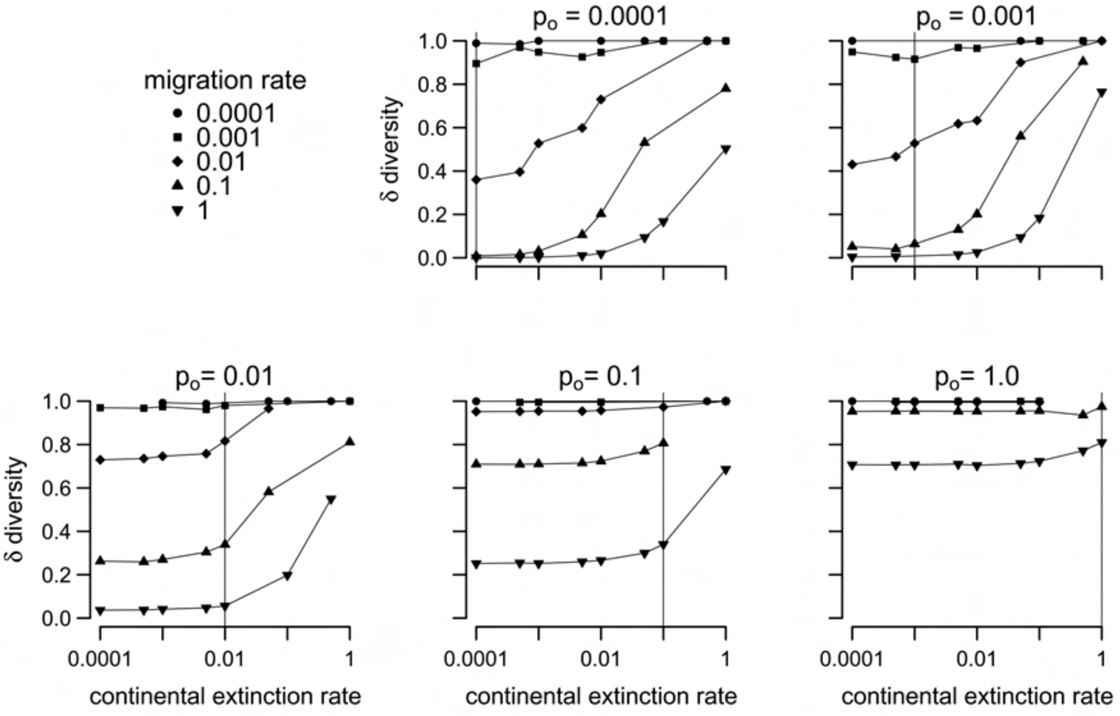

Figure 2.4 — Bivariate plots of the migration rates versus continental extinction rate for those model runs whose δ_{eq} value is one (circles) or δ_{eq} is never reached (triangles). Each plot area is for a different continental origination rate (p_o).

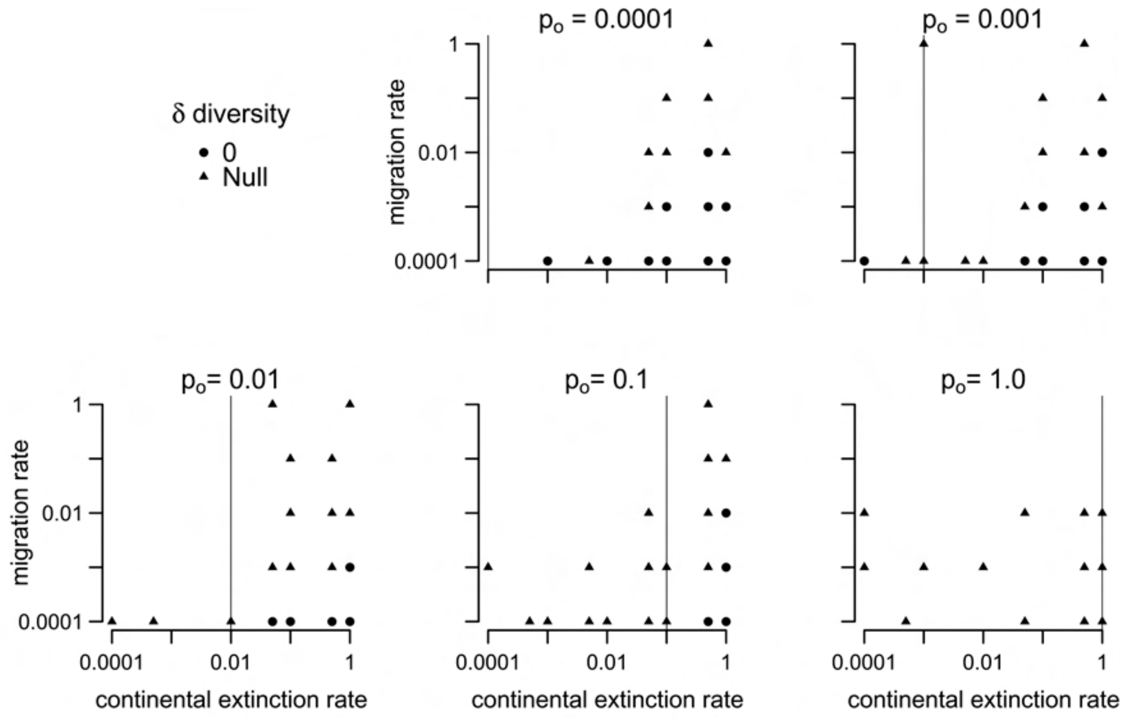

Figure 2.5 — Bivariate plots of the equilibrium time versus continental extinction rate. Each plot area is for a different continental origination rate (*p_o*) and the symbols represent migration rates. The vertical line is the same as in Figure 2.3. The horizontal line is at 150 Myr, the maximum time the model can simulate. The shaded regions indicate equilibrium times between 1 Myr and 10 Myr, which bracket the average Phanerozoic stage duration.

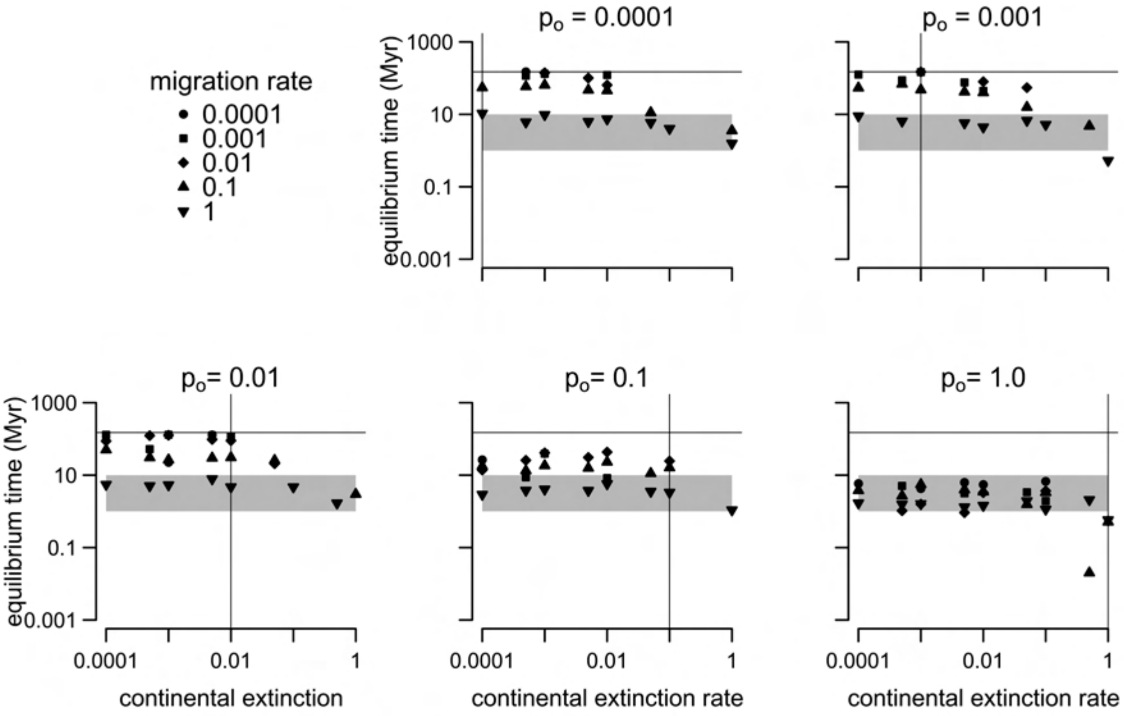

Figure 2.6 — Subsampled Ordovician generic richness. Richness is calculated within each bin from 100 subsamples drawn by the by-list unweighted method (Alroy 2000; Bush et al. 2004). The time bins are the default Paleobiology Database bins for the Ordovician and correspond to the standard British time stages: T, Tremadocian; Ar, Arenigian; L, combined Llanvirnian and Llandeilian; C, Caradocian; As, Ashgillian. Each curve is for a different paleogeographic region: Laurentia (dot-dash), South China (dotted), and the combination of all other paleocontinents (solid). Vertical bars are 95% confidence intervals about the means of 100 subsamples.

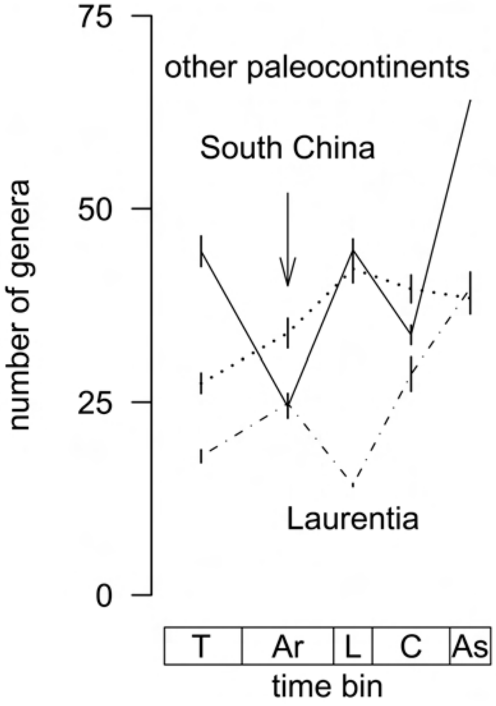

Figure 2.7 — Per-time-bin origination, extinction, and migration rates for the Ordovician data. Closed symbols are global rates and the open symbols are continental rates. Also plotted is delta diversity, which is computed as the global average Jaccard among the three paleogeographic regions: South China, Laurentia, and all other paleocontinents. The time bins are the same as in Figure 2.6. All curves are based on means of 1000 bootstraps. Vertical bars are 95% confidence intervals.

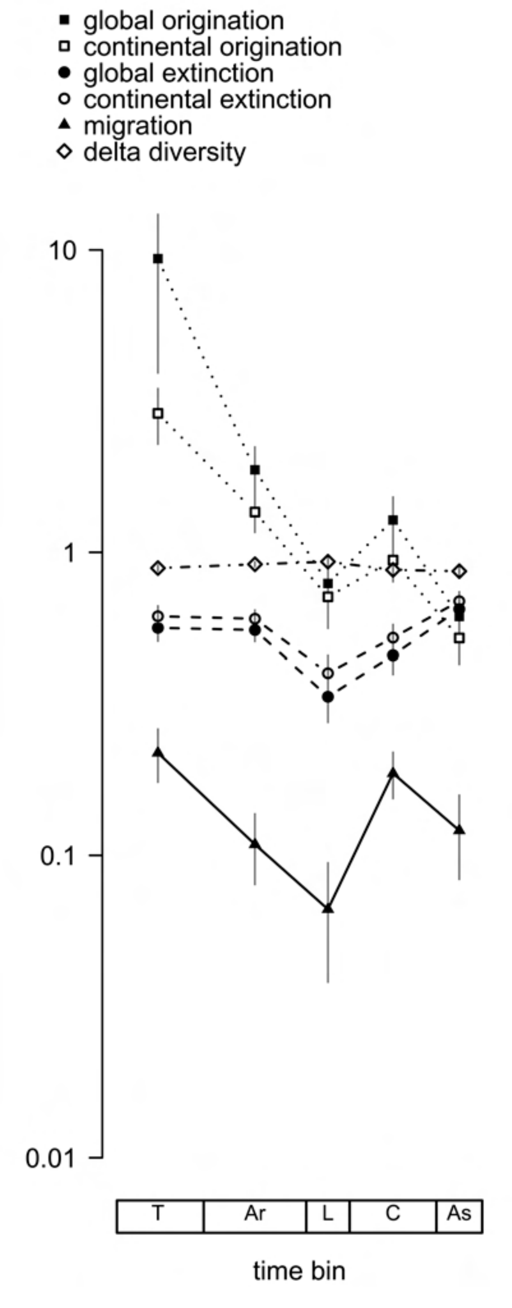

Table 2.1 — Per-time-bin origination, extinction, and migration rates for the Ordovician. Origination and migration rates are calculated as the ratio of the number of new genera (newly originated or immigrants) in a time bin to the number of genera that cross the lower boundary of that bin. Extinctions are calculated as the ratio of the number of extinctions in a bin to the total number of genera in that bin. See the text for the distinctions between continental and global rates. All rates are mean values based on 1000 bootstraps.

	Tremadocian	Arenigian	Llanvirnian/ Llandeilian	Caradocian	Ashgillian
Migration	0.22 ± 0.044	0.11 ± 0.029	0.07 ± 0.028	0.19 ± 0.033	0.12 ± 0.038
Global origination	9.35 ± 5.448	1.87 ± 0.364	0.79 ± 0.183	1.28 ± 0.250	0.61 ± 0.129
Continental origination	2.88 ± 0.609	1.36 ± 0.198	0.71 ± 0.153	0.94 ± 0.146	0.52 ± 0.095
Global extinction	0.56 ± 0.056	0.55 ± 0.048	0.33 ± 0.060	0.46 ± 0.063	0.65 ± 0.050
Continental extinction	0.61 ± 0.052	0.60 ± 0.040	0.40 ± 0.058	0.52 ± 0.057	0.69 ± 0.043

CHAPTER 3

THE LATITUDINAL DIVERSITY GRADIENT AND MIDDLE CARBONIFEROUS CLIMATE CHANGE[1]

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[1] Heim, N.A. Submitted to *Paleobiology.* 5 July 2008

Abstract

An analysis of 2447 collections of Mississippian and Pennsylvanian macroinvertebrates extracted from the Paleobiology Database show that the latitudinal diversity gradient in the paleotropical regions (within 20° of the paleoequator) of Laurentia and South America was dynamic and different from most observed modern latitudinal diversity gradients. In the early and middle Mississippian, taxonomic richness was at a minimum just north of the equator and increased towards higher latitudes to the south. In the middle Mississippian, diversity in the higher southern latitudes decreased so that diversity was highest at about 10°S. Finally, in the Pennsylvanian the latitudinal diversity gradient disappeared, and diversity was equal across all latitudes examined. The changes in the shape of the latitudinal diversity gradient are attributed to paleogeography and the development of the late Paleozoic Ice age. Additionally, a tropical Laurentian and South American extinction event is seen in the late Pennsylvanian that was not detected in previous studies of global Carboniferous diversity. This extinction event was caused by a drop in the latitudinal component of beta diversity as narrowly distributed genera were replaced by those with a wider latitudinal range.

Introduction

The latitudinal diversity gradient, which is the pattern of decreasing taxonomic richness with increasing latitude, is a prevalent pattern in modern terrestrial and marine systems (Hillebrand 2004a, 2004b). Several processes have been invoked to explain the modern latitudinal diversity gradient, including greater area in the topics (Rosenzweig 1995), the mid-domain effect where taxa are concentrated in the middle of a range that has hard boundaries, i.e., the poles, (Colwell & Hurtt 1994; Lyons & Willig 1997; Willig & Lyons 1998), more available energy in the tropics (Currie 1991; Chase and Leibold 2002), and higher speciation rates in the tropics (Buzas et al. 2002; Jablonski et al. 2006). As ecologists attempt to understand the processes that shape the modern latitudinal diversity gradient, paleobiologists have taken an interest in the history of ancient latitudinal diversity gradients. Understanding the long-term dynamics of the latitudinal diversity gradient is important for understanding how biodiversity will continue to be altered as a result of natural and anthropogenic activities. Much of the work on ancient latitudinal diversity gradients has focused on Cenozoic molluscs (Roy et al. 1998, 2000; Jablonski et al. 2000, 2006; Crame 2001; Roy and Martien 2001). However, as the effects on diversity from modern climate change are being realized (Parmesan 2006), the macroevolution and biogeography of the late Paleozoic has sparked an interest among paleobiologists (Raymond et al. 1989, 1990; Kelley et al. 1991; Stanley and Powell 2003; Shen and Shi 2004; Powell 2005, 2007a, 2007b; Heim in review). The late Paleozoic is important because it was an interval that experienced major climatic fluctuations related to an ice age that was of the same magnitude as the Pleistocene glaciation (Frakes et al. 1992). The goal of this study is to test the hypothesis that the latitudinal diversity gradient of benthic macroinvertebrates on the paleocontinents of Laurentia and South America steepened within the tropics from the Mississippian to the Pennsylvanian coincident with the transition from a global greenhouse climate to an icehouse climate (Veevers and Powell 1987; Mii et al. 1999; Batt et al. 2007).

The Carboniferous latitudinal diversity gradient is examined with a literature-based data set extracted from the Paleobiology Database (paleodb.org). The Paleobiology Database generates paleocoordinates for each collection, and taxonomic richness was tallied for 10° latitudinal bins for the duration of the Carboniferous. Diversity was also calculated in terms of alpha, beta, and gamma (Whittaker 1960, 1972). This spatial analysis tests whether changes in total diversity are the result of changes in diversity within latitudinal bins or changes in the taxonomic heterogeneity among latitudinal bins. Previous studies of Carboniferous diversity, conducted at the global scale, indicate an extinction event that started in the latest Mississippian and continued across the Mississippian/Pennsylvanian boundary (Raymond et al. 1990; Stanley and Powell 2003). During the extinction, genera typically migrated towards the paleoequator (Raymond et al. 1990), and the slope of the latitudinal diversity gradient shallowed (Powell 2007a). These diversity patterns were presumably in response to Gondwanan glaciation. If the global patterns are representative of regional patterns, which is not always the case (e.g., Miller and Mao 1998; Heim in press), it is expected that total diversity in western Laurentia and South America declined at the Mississippian/Pennsylvanian boundary and that the slope of the latitudinal diversity gradient shallowed.

Data and Methods

The data for this study were extracted from the Paleobiology Database. The Paleobiology Database does include abundance data, but because those data are relatively rare for the Carboniferous, only presence-absence information is used. Data in the Paleobiology Database are entered as collections, which are fossil assemblages collected at a particular place at a particular time. Each taxon within a collection is an occurrence, such that if *Punctospirifer*, for example, is present in five collections, there are five occurrences of that genus. The data set used here consists of 17830 occurrences of 921 genera from 2447 collections (Appendix). The data set is comprised of common late Paleozoic benthic taxa: Trilobita, Brachiopoda, Bryozoa, Bivalvia, Gastropoda, Echinodermata, and Anthozoa. Using only benthic groups standardizes the ecological and life history traits by excluding groups such as nektonic cephalopods.

Additionally, these taxa are chosen because they represent a cross section of Carboniferous marine invertebrates and all three evolutionary faunas (Sepkoski 1981). The data are restricted to collections from Laurentia and South America, because these paleocontinents contain a continuous latitudinal distribution of collections for the Carboniferous. The data are stratigraphically binned into the Paleobiology Database's five default bins for the Carboniferous, corresponding to the Tournaisian, lower to middle Visean, combined upper Visean and Serpukhovian, combined Bashkirian and Moscovian, and combined Kasimovian and Gzhelian Stages of the global Carboniferous time scale (Gradstein et al. 2004; Heckel and Clayton 2006). These bins will be referred to in the text as Mississippian 1 through 3 and Pennsylvanian 1 and 2, which are ordered from oldest to youngest (Fig. 3.1). Before analysis, some collections that were not assigned to a time bin by the Paleobiology Database were assigned to one of the five bins after reviewing the original literature sources. Most of these collections are in the Mississippian 2 and 3 bins, which split the Visean. The Paleobiology Database rotates and translates modern latitude and longitude coordinates for each collection to appropriate paleolocations (Fig. 3.2) using paleogeographic reconstructions from the PALEOMAP Project (Scotese 2002). The paleolatitude information provides the basis for analyzing the Carboniferous latitudinal gradient. For each time interval, the collections are divided into five bins: paleolatitudes greater than 20°S, paleolatitudes between 20°S and 10°S, paleolatitudes between 10°S and the paleoequator, paleolatitudes between the paleoequator and 10°N, and all paleolatitudes greater than 10°N (Fig. 3.2).

The latitudinal and temporal distributions of collections are uneven (Figs. 3.2 and 3.3). To account for this, most analyses are performed with the raw data and subsampled data. Subsampling ensures that each latitudinal bin during each time interval is represented equally.

Subsampling was done using the unweighted by-list (i.e., taxonomic list or Paleobiology Database collection) method and the by-list occurrence weighted method (Alroy et al. 2001). For the unweighted subsampling, the same number of collections are drawn at random from each latitudinal bin for each time interval. For the occurrence weighted subsampling, collections are drawn at random until a certain number of genus occurrences is reached; each latitudinal bin in each time interval has the same number of occurrences. The subsampling routine was executed 1000 times, and mean values with 95% confidence intervals are presented. The results of the two subsampling methods are comparable, so only the unweighted results are shown. The disadvantage of subsampling is that although it reduces biases imparted by uneven sampling intensity, it also reduces the number of collections in each spatiotemporal bin. Thus, diversity is undersampled, and the results may change as more collections become available within each bin. The subsampled results are generally comparable to the raw data for the Mississippian, but there are enough differences in the Pennsylvanian data that both are shown.

The concepts of alpha, beta, and gamma were originally championed by Whittaker (1960, 1972) and are defined as the diversity within a local habitat (alpha), the diversity gained by pooling multiple local habitats across a landscape (beta), and the diversity of a heterogeneous landscape (gamma). 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 that is not directly comparable to either alpha or gamma. Lande (1996) reintroduced the idea of additive diversity partitioning, which defines beta diversity as the difference between gamma and alpha, rather than their ratio. The main advantage of the additive form of beta diversity for the present study is that beta diversity is directly comparable to alpha and gamma because all three measures have the same units, number of genera. For the present study, alpha diversity is defined as the taxonomic richness of a spatiotemporal bin, gamma is defined as the total continental richness (Laurentia plus South America) during a time interval, and beta is the difference between gamma and mean alpha. Within each time interval, there are up to five measurements of alpha, one for each latitudinal bin. The mean of these alpha values is used in order to avoid pseudoreplication (Srivastava 1999). The final equation for computing beta diversity for each time interval is:

$$\beta = \gamma - \frac{1}{n}\sum_{i=1}^{n}\alpha_i \tag{1}$$

where *n* is the number of latitudinal bins.

Results

Latitudinal Diversity. – Across the entire data set, collection richness varies from 1 to 68 genera (Fig. 3.3). Although the data set contains collections that were originally collected from stratigraphic scales ranging from a single bed to a group of formations, the collections with the greatest richness were collected at the levels of bed or group of beds. During the Mississippian, the most taxonomically rich collections were centered at about 20°S, but shift northward to within 10°S during the Pennsylvanian. The pattern of an equatorward shift is mirrored in the genus richness of each latitudinal bin through time (Fig. 3.4).

Mississippian 1 shows a steep monotonic decline in latitudinal diversity from a maximum south of 20°S and a minimum north of 10°N. Likewise, Mississippian 2 shows a diversity maximum in the higher southern latitudes followed by a steep decline northwards to a minimum north of 10°N (Fig. 3.4A). Mississippian 3 appears to be transitional between the early Mississippian monoclines and the more symmetrical latitudinal diversity gradient of the

Pennsylvanian. Mississippian 3 shows diversity minima at the extreme northern and southern latitudes and a diversity plateau in the middle thee latitudinal bins. Note, however, that the low richness in the southernmost bin is the result of having only one collection in that bin (Table 3.1). The symmetrical latitudinal diversity gradient is fully developed in Pennsylvanian 1 with diversity maxima in the 0° to 10°S bin. This pattern persists into Pennsylvanian 2 (Fig. 3.4B). A possible source of bias in these results is the uneven sampling intensity (Table 3.1) of the spatiotemporal bins. Such a bias is tested for with correlations of richness and the number of collections within each latitudinal bin.

Correlation between the taxonomic richness of each spatiotemporal bin and the log of the number of collections in each bin (Table 3.2) reveals a strong positive significant relationship for the full data set. The correlations for each time interval show a relatively weak and insignificant relationship for Mississippian 1, but the strength of the correlation and the statistical significance increases sequentially through the remaining time intervals. This suggests that the latitudinal diversity patterns observed from the raw data for Mississippian 1 and 2, and possibly Mississippian 3, are not the result of sampling intensity. A sample size bias can not be ruled out for the two Pennsylvanian intervals.

To account for a sampling intensity bias, a subsampling routine was employed whereby 10 collections were randomly drawn from each spatiotemporal bin, and the taxonomic richness was calculated for each bin. The subsampling routine was executed 1000 times, and 95% confidence intervals were computed. Five of the 25 spatiotemporal bins have fewer than 10 collections (Table 3.1). These spatiotemporal bins were dropped from the analyses. The subsampled data show a nearly continuous decrease in diversity from south to north for Mississippian 1 and a monotonic decrease in the same direction for Mississippian 2 (Fig. 3.5A). These are the same patterns observed from the raw data. Mississippian 3 could not be subsampled at the two extreme latitudinal bins, but it shows a large increase in taxonomic richness in the 0° to 10°S bin. The spike in Mississippian 3 richness is significantly greater than the richness in the adjacent Mississippian 3 latitudinal bins and the richness in the same latitudinal bin for Mississippian 2 and Pennsylvanian 1. Pennsylvanian 1 and 2 have flat latitudinal diversity trends, and the diversity for the two time intervals is equal (Fig. 3.5B).

Alpha, Beta, and Gamma Diversities. – Diversity decreases at the alpha and gamma levels through the Carboniferous (Fig. 3.6). Continental richness (gamma) decreases primarily because of a reduction in latitudinal richness (alpha). Alpha, beta, gamma were also calculated for the subsamples discussed above (Fig. 3.7). At the sampling level of 10 collections per spatiotemporal bin, gamma diversity is constant from Mississippian 1 through Pennsylvanian 1. Pennsylvanian 2 shows a significantly lower gamma diversity than the rest of the Carboniferous. Alpha diversity is constant for Mississippian 1 and 2 and Pennsylvanian 1 and 2. Alpha increases significantly in Mississippian 3. This increase is likely due to the increase in richness in the 0° to 10°S bin (Fig. 3.5). Beta diversity is constant from the Mississippian 1 through the Pennsylvanian 1 and drops, along with gamma diversity, during the Pennsylvanian 2. The taxonomic compositions of the latitudinal bins were more similar in Pennsylvanian 2 than during other time intervals.

Discussion

The subsampled and raw data confirm an unusual latitudinal diversity pattern during the early and middle Mississippian. There are two prominent differences between the Mississippian and the prototypical modern latitudinal diversity gradient. First, the Mississippian latitudinal gradient is not symmetrical about the equator, or any other paraequatorial latitude; it declines continuously from 20ºS to 10ºN. Second, the Mississippian gradient is reversed relative to the modern gradient; the maximum diversity is located at the highest latitudes and the equatorial latitudes harbor the least diversity. Despite the peculiarity of the Mississippian latitudinal pattern, it is not unique. A paraequatorial diversity minimum has been documented in living shallow-water molluscs along the Pacific coast of South America, which is correlated with available shelf area (Valdovinos et al. 2003). A reversed latitudinal diversity gradient was also found in Tithonian (Late Jurassic) molluscs, but only at the lowest latitudes (Crame 2002). This particular inverse relationship was attributed to under-sampling of the paraequatorial region. However, the diversity of the two regions between the paleoequator and 20ºN had a diversity that was lower than all of the regions between 20ºN and 60ºN. At least anecdotally, it appears that some equatorial regions during the Tithonian had low diversity. Shen and Shi (2004) found a latitudinal diversity cline that was continuously decreasing from a maximum at about 60ºN to a minimum at 70ºS during the Capitanian (Late Guadalupian, Permian). This cline in diversity was driven by low tropical diversity in western Laurentia, while the Paleotethys exhibited a symmetrical latitudinal diversity gradient with a tropical maximum. The low tropical diversity was attributed to oceanographic conditions during the Permian.

The interpretation of the latitudinal diversity gradient during the Pennsylvanian is less straightforward. The raw data indicate a strong latitudinal diversity gradient that is symmetrical about the southern paraequatorial latitudes, but the subsampled data suggests that diversity did not vary with latitude during the Pennsylvanian. This latter observation is consistent with the global distributions of Mississippian through Permian brachiopods (Powell 2007a), which show a weaker latitudinal diversity gradient coincident with the onset of the late Paleozoic Ice age.

Perhaps, if more collections were available within each spatiotemporal bin for subsampling, a weak rather than flat diversity cline would emerge.

The Laurentian latitudinal diversity cline gradually transitions from continuously declining from the southern paleolatitudes towards the equator, to symmetrical and declining from a position in the southern paraequatorial region, to a flat distribution. This is in contrast to the global latitudinal diversity gradient in late Paleozoic brachiopods that is consistently symmetric with a maximum in the southern paraequatorial latitudes (Powell 2007a). There are several possible explanations of the divergence between the global and continental patterns. First, the data used here include all major macroinvertebrate taxa while Powell's data are restricted to brachiopods. Second, the data used here span a shorter latitudinal range; Powell has 10° latitudinal bins from 60°S to 60°N while the exactly 10° latitudinal bins used for this study span 20°S to 10°N. A difference in latitudinal scale could be expected to produce less pronounced latitudinal clines, but the clines are not expected to disappear all together. Indeed, Roy et al. (1998) found a steep latitudinal diversity gradient in modern molluscs from the eastern Pacific which show a change in diversity between the equator and 20°N latitude.

Although speculative, it is plausible that the early steep cline in latitudinal diversity during Mississippian 1 and 2 was the product of paleogeography. Laurentia was positioned over the equator during the early and middle Mississippian with most of the present-day mid-continent situated south of the equator and flooded by an epeiric sea. North of the equator, only a narrow strip of active margin on the western edge of Laurentia was submerged. The highest diversity at about 20°S may be attributed to the fact that a greater area of the shelf and slope habitats were available at that latitude. As glaciation began in Gondwana and the ice sheets began expanding north, many taxa either went extinct or adapted by shifting their ranges equatorward. As

Gondwanan glaciation became fully developed in the Pennsylvanian, global climate and oceanic circulation changed (Mii et al. 1999), the available submerged habitat on Laurentia decreased and tropical diversity dropped to produce equal diversity across approximately 40° of Latitude about the equator.

An alternative interpretation is that the full latitudinal diversity gradient is modal and asymmetric, which resulted from the combination of northward rotation of Laurentia and variable area of flooded continental crust during the Carboniferous. Living prosobranch gastropods in the eastern Pacific show a complex latitudinal diversity gradient that is modal and asymmetric, and maximum diversity is not centered on the equator (Valdovinos et al. 2003, their Fig. 3.5). The increase in diversity towards the south pole is attributed to the increased habitat area (Valdovinos et al. 2003), presumably because of the increased area provided by embayments and fjords in southern Chile. The offset in maximum latitudinal diversity from the equator is correlated with sea surface temperature (Roy et al. 1998; Valdovinos et al. 2003). It is possible that such a complex latitudinal diversity gradient existed during the Carboniferous and was volatile in response to continental movements and glacio-eustatic fluctuations in sea level. Perhaps the data here are capturing small segments of a complex and dynamic latitudinal diversity gradient. To further test this hypothesis more data are needed from detailed paleogeographic maps so that the area of flooded continental shelves can be calculated.

The extinction event observed at the global scale (Raymond et al. 1990; Stanley and Powell 2003) does not appear in the Laurentian and South American tropical data. Although there is a drop in gamma diversity between Mississippian 2 and 3 in the raw data (Fig. 3.6), it does not show up in the subsampled data (Fig. 3.7). Surprisingly, there appears to be an extinction between Pennsylvanian 1 and 2, which is apparent in both the raw and subsampled data. This extinction event in the late Pennsylvanian is not correlated with shifts in carbon or oxygen isotope fractionation (Mii et al. 1999), which would indicate changes in ocean circulation and paleotemperature, respectively. As indicated by the drop in beta diversity (Fig. 3.6 and 3.7), this extinction event was driven by taxonomic similarity among the latitudinal bins. Genera that had narrow latitudinal ranges were replaced by those with longer ranges. Thus, the diversity within each latitudinal bin remained constant from Pennsylvanian 1 to 2, but the similarity among latitudinal bins increased. This may represent a previously unrecognized type of extinction, but further tests with more complete data are required before any definite conclusions can be drawn.

Conclusions

1. The early and middle Mississippian of Laurentia and South America was characterized by a latitudinal diversity gradient within the tropics (i.e., within 20° of the paleoequator) that was the inverse of most modern gradients; minimum diversity was at the equator and increased towards higher latitudes. This gradient is likely due to the increased area available on the flooded continental interior of Laurentia, which was situated at about 20°S. During the late Mississippian, diversity south of 20°S dropped drastically, producing a more symmetrical latitudinal diversity cline with a diversity plateau across the middle range of latitudes considered. This was likely driven by the onset of glaciation on Gondwana, which caused the extinction of some taxa and forced the migration of others northward. Finally, the Pennsylvanian was characterized by constant diversity across the tropical latitudes. As glaciation at the paleosouth pole hit its maximum, tropical diversity leveled out.

2. The tropics of Laurentia and South America did not experience an extinction event until the late Pennsylvanian. This is in contrast to global studies of the Carboniferous that have

indicated an extinction event from the late Mississippian into the early Pennsylvanian. Furthermore, the late Pennsylvanian extinction event was driven by a drop in beta diversity rather than a drop in alpha diversity. During the late Pennsylvanian the number of widespread genera increased as the number of narrowly distributed genera decreased.

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Figure 3.1 — Carboniferous time scale showing ages (in mega-annums), global and North America stage names, and Paleobiology Database bins. Figure is modified from the Time Scale Creator software (Ogg and Lugowski 2007), which is based on Gradstein et al. (2004). The broken lines separating the Mississippian Paleobiology Database bins indicate uncertainty in the exact placement of collections from the Osagean, Chesterian, and Visean Stages. Also, the age of the boundary between Mississippian 2 and 3 (dotted line) is uncertain.

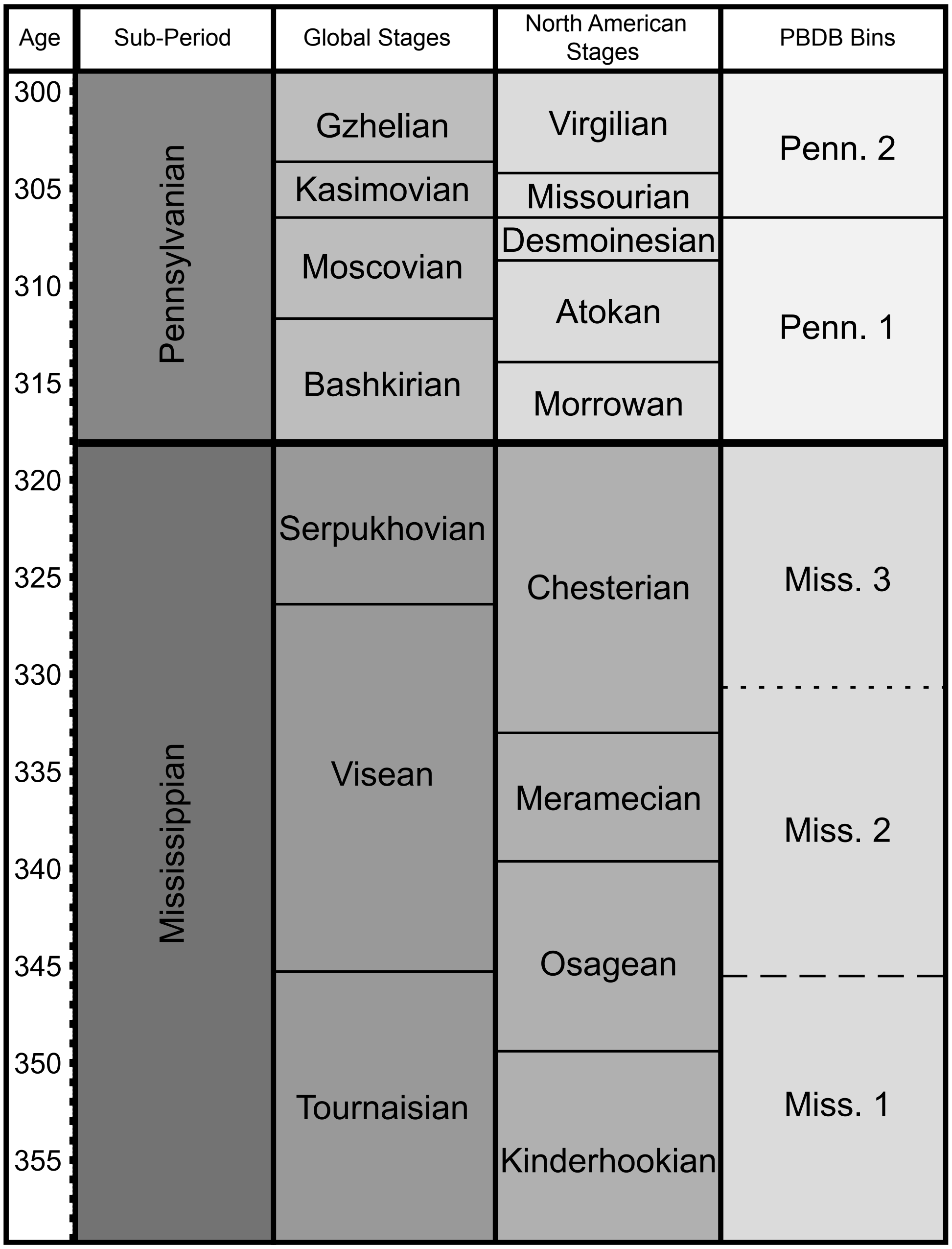
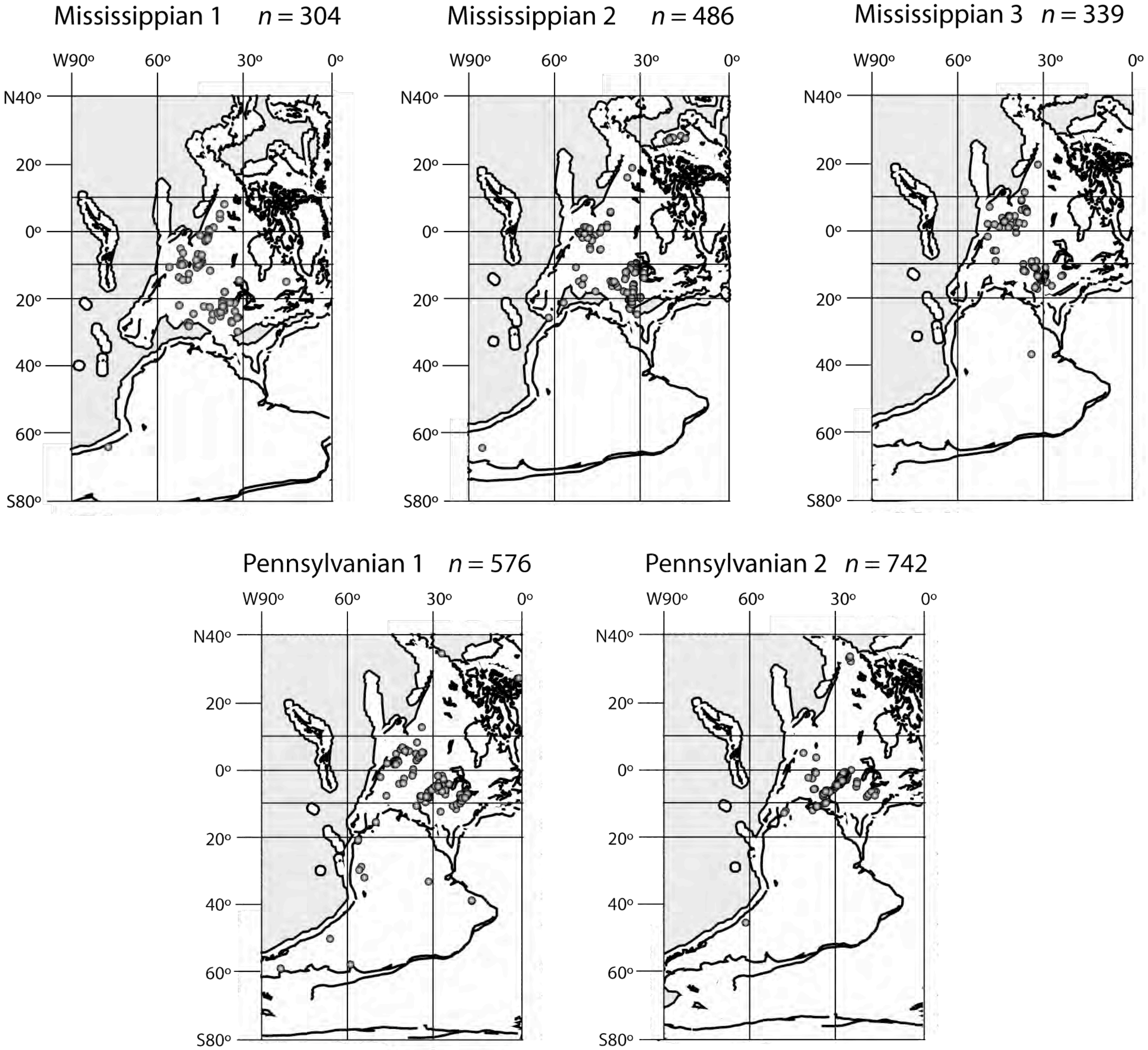


Figure 3.2 — Paleogeographic maps of the 2447 collections included in this study. Each map is for the time interval indicated. The horizontal lines demarcate the paleolatitudinal bins used in the analyses. *n* refers to the number of collections. The gray region represents oceanic crust, and the white region represents continental crust. The lines on the continental interiors represent present-day coastlines, which allow easy recognition of Laurentia and South America. Note that flooding of continental interiors is not included. The paleotectonic reconstructions for Mississippian 1 through Pennsylvanian 2 are for 353 Ma, 339 Ma, 326 Ma, 313 Ma, and 303 Ma, respectively. Maps are based on PALEOMAP Project data (Scotese 2002) and were modified from the Paleobiology Database downloads.



Mississippian 1 *n* = 304

Mississippian 2 *n* = 486

Mississippian 3 *n* = 339

Pennsylvanian 1 *n* = 576

Pennsylvanian 2 *n* = 742

Figure 3.3 — Genus richness of the 2447 collections included in this study plotted against paleolatitude. The first plot is the entire data set and the other plots show collection richness for the time intervals indicated. Negative values on the x-axis indicate south paleolatitudes. *n* refers to the number of collections. The points are shaded so that overlapping points appear darker.

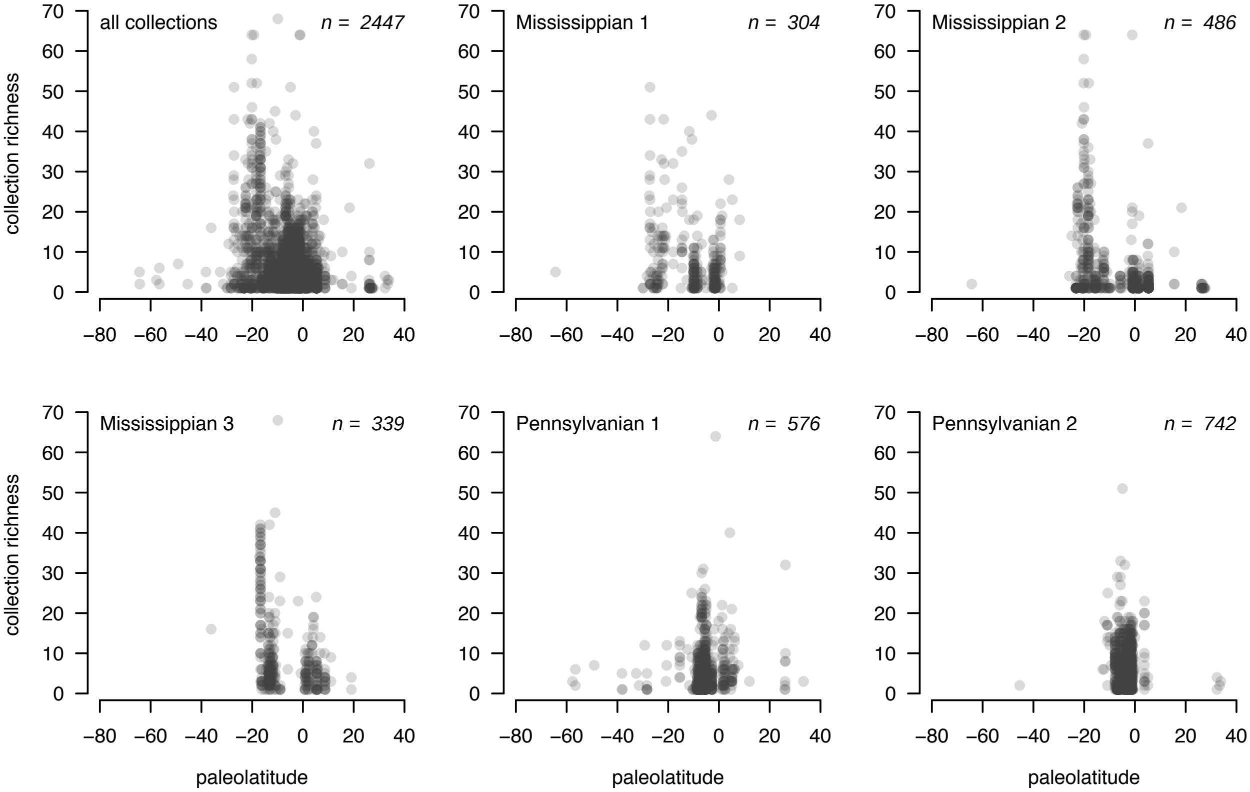


Figure 3.4 — Plots of raw richness versus paleolatitude. Latitude is divided into five bins, the middle three bins are exactly 10° of latitude while the northernmost and southernmost bins, indicated by a dashed axis, include all collections greater than the latitude indicated. Negative values on the x-axis indicate south paleolatitudes. The number of collections in each spatiotemporal bin is given in Table 3.1. Closed and open symbols are for Mississippian and Pennsylvanian spatiotemporal bins, respectively. Vertical lines mark 95% confidence intervals based on bootstrapping the raw data 1000 times; in most instances, the confidence intervals are shorter than the plot symbols. A) Latitudinal richness continuously decreasing from south to north for Mississippian 1 and 2. Note that Mississippian 1 did not have any collections in the greater than 10°N bin. B) Symmetrical latitudinal richness for Mississippian 3, Pennsylvanian 1, and Pennsylvanian 2. The low richness in the less than 20°S bin for Mississippian 3 is due to the presence of only one collection in that spatiotemporal bin.

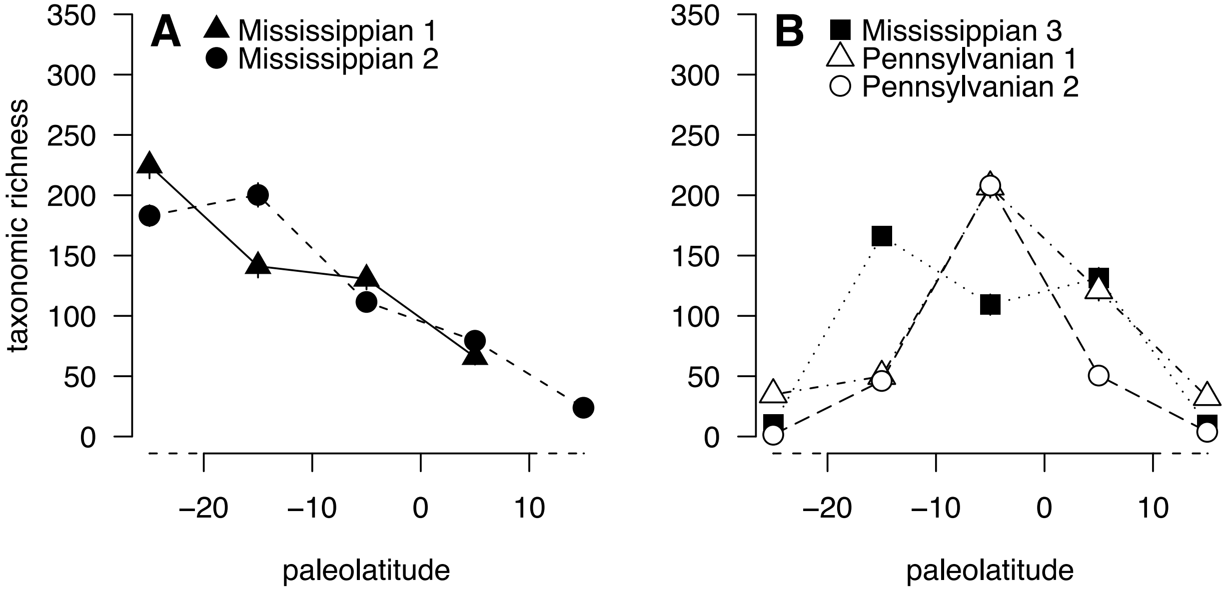


Figure 3.5 — Plots of subsampled latitudinal richness versus paleolatitude. Bin axes and symbols are the same as in Figure 3.4. Subsampling was carried out to 10 collections per spatiotemporal bin. Because there are fewer than 10 collections in every spatiotemporal bin, Mississippian 1 is missing one point and Mississippian 3 and Pennsylvanian 2 are missing two points. The vertical lines are 95% confidence intervals about the means of 1000 subsampling trials. A) Continuously decreasing latitudinal richness for Mississippian 1 and 2. B) Modal and flat latitudinal richness for Mississippian 3, Pennsylvanian 1, and Pennsylvanian 2.

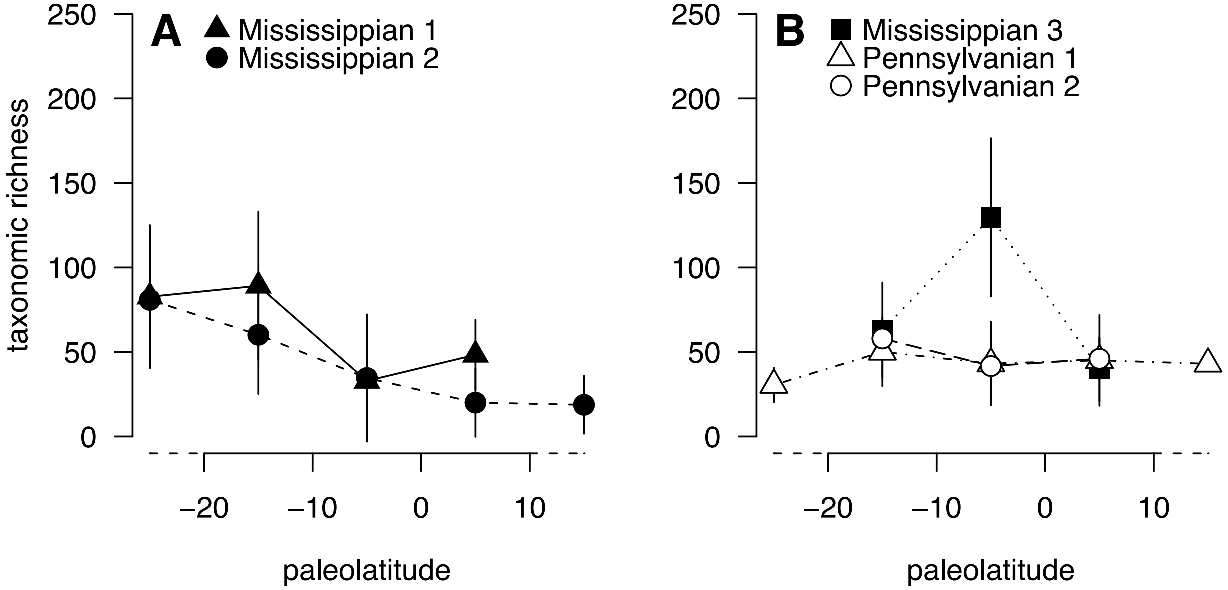


Figure 3.6 — Raw alpha, beta, and gamma diversities for each of the five time intervals. Vertical lines mark 95% confidence intervals based on bootstrapping the raw data 1000 times. A) Alpha beta, and gamma diversities plotted simultaneously. Gamma diversity is the total diversity within a time interval and is represented by the total bar height. Alpha diversity is the mean diversity of the latitudinal bins within each time interval and is represented by the dark bar heights. B) Beta diversity from A plotted on its own so that temporal changes in beta are easily recognized.

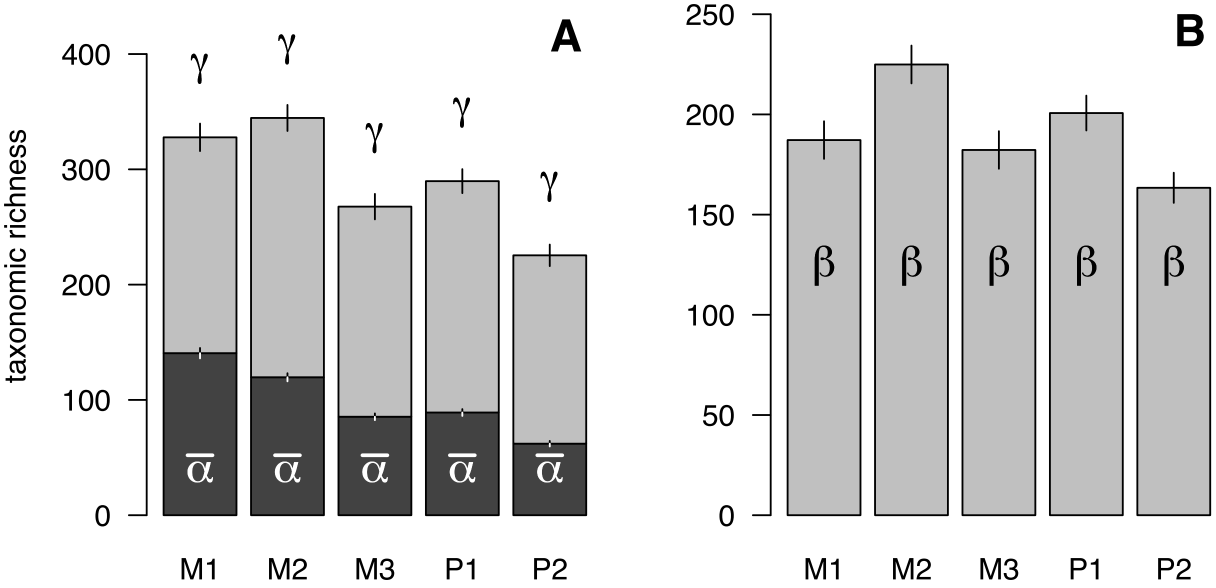


Figure 3.7 – Subsampled alpha, beta, and gamma diversities for each of the five time intervals. Subsampling was carried out to 10 collections per spatiotemporal bin. The vertical lines are 95% confidence intervals about the means of 1000 subsampling trials. The confidence intervals are large, particularly for beta and gamma, because the subsampling was conducted to only 10 collections. A) Alpha, beta, and gamma diversities plotted simultaneously. Bars are the same as in Figure 3.6A. B) Beta diversity from A plotted on its own so that temporal changes in beta are easily recognized.

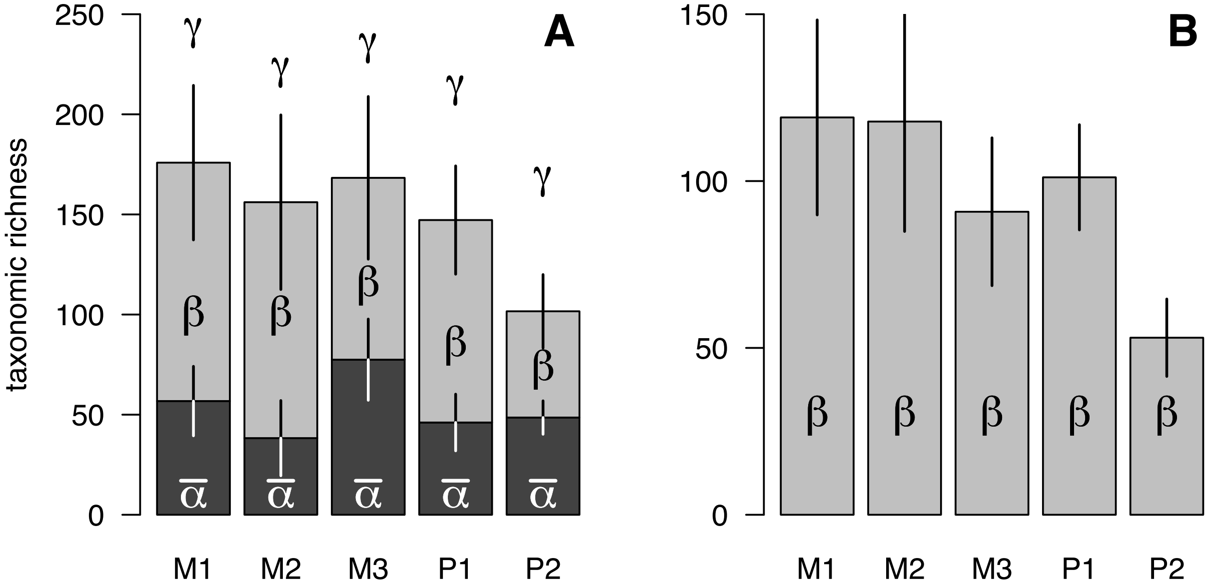


Table 3.1 — Sampling intensity of the raw data based on the number of collections in each spatiotemporal bin. South 3 is less than or equal to 20ºS; South 2 is greater than 20ºS and less than or equal to 10ºS; South 1 is greater than 10ºS and less than or equal to 0º; North 1 is greater than 0º and less than or equal to 10ºN; North 2 is greater than 10ºN.

	South 3	South 2	South 1	North 1	North 2
Mississippian 1	83	32	159	30	0
Mississippian 2	101	155	88	120	22
Mississippian 3	1	209	12	113	4
Pennsylvanian 1	19	15	452	80	10
Pennsylvanian 2	1	10	707	20	4

Table 3.2 — Pearson's product-moment correlation coefficients (ρ) and p-values between the log of the number of collections and taxonomic richness for each of the spatiotemporal bins. n is the number of spatiotemporal bins available to compute the correlation. There are no data available for the Mississippian 1 greater than 10ºN bin.

	ρ	p-value	n
all collections	0.881	< 0.0001	24
Mississippian 1	0.419	0.5811	4
Mississippian 2	0.804	0.1009	5
Mississippian 3	0.890	0.0429	5
Pennsylvanian 1	0.987	0.0018	5
Pennsylvanian 2	0.969	0.0065	5

CHAPTER 4

STABILITY OF REGIONAL BRACHIOPOD DIVERSITY STRUCTURE ACROSS THE MISSISSIPPIAN/PENNSYLVANIAN BOUNDARY[1]

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[1] Heim, N.A. Submitted to *Paleobiology.* 14 April 2008

Abstract

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 63% regional extinction of latest Mississippian genera and 50% of the earliest Pennsylvanian genera are either immigrants or newly originated. Taxonomic richness and evenness (Simpson's D) 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. Multivariate ordinations using detrended correspondence analysis show strong separation of Mississippian and Pennsylvanian collections and genera. Within each stage, DCA indicates reorganization of brachiopod orders along DCA axis 1, which may correspond to subtle changes in water depth. This rearrangement of orders in ordination space is also seen in the rank-order of genera that are found in both stages. Rank-abundance plots of genera show the same distribution for both stages, but there is no correlation between the abundance of taxa in the Mississippian and their abundance in the Pennsylvanian. An estimation of spatio-temporal heterogeneity of taxonomic composition within each stage reveals that the earliest Pennsylvanian was significantly more homogeneous (Morisita-Horn index). 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.

Introduction

The Mississippian/Pennsylvanian boundary coincides with a major change in global climate and a global shift in biodiversity dynamics, particularly of the brachiopods. The Mississippian/Pennsylvanian boundary is associated with a global extinction event (Raymond et al. 1990; Kelley et al. 1991), reduced rates of origination and extinction (Stanley and Powell 2003), and a shift from narrowly to widely distributed genera (Powell 2005), which led to 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. Diversity structure is analyzed for richness and evenness patterns as well as the processes of migration and interspecific competition. The hypothesis is tested with brachiopod assemblages from southern Ozark highlands of Arkansas and Oklahoma, USA, which were situated on a shallow carbonate platform between 8° and 13° south paleolatitude during the middle Carboniferous. The results of this study have implications for our understanding of regional biotic responses to global climate change and regional paleocommunity 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).

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. During the onset of Gondwanan glaciation in the Serpukhovian Stage of the late Mississippian, the Gondwanan ice cap was not fully developed. Truly ice house conditions were not reached until the Bashkirian, the first stage of the Pennsylvanian (Mii et al. 1999; Batt et al. 2007). 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 an 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-based data set is used here to understand the long-term regional impacts of global climate change associated with the Mississippian/Pennsylvanian boundary on the brachiopod assemblages from the southern Ozarks. Field data were collected within the regional chronostratigraphic framework for the Carboniferous of North America (i.e., latest Mississippian is the Chesterian Stage and the earliest Pennsylvanian is the Morrowan Stage). The 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 the recently accepted global Carboniferous time scale (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. 4.1). The Mississippian/Pennsylvanian boundary in the southern Ozarks, as in most of North America, is marked by an unconformity. In the Ozarks, the unconformity is bounded below and above by marine strata of the Chesterian and Morrowan Stages. The Chesterian and Morrowan strata of the southern Ozarks were deposited on the passive-margin Arkoma shelf (Sutherland 1988) between 8° and 15° 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 can be analyzed at multiple levels (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 kilometer transect trending roughly east-west across northwestern Arkansas and northeastern Oklahoma (Fig. 4.1). 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) under reference number 26838.

Biodiversity

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. 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, multivariate gradient analysis, rank–abundance distributions, and taxonomic similarity is used here to test the hypothesis that previously recognized global diversity patterns across the Mississippian/Pennsylvanian boundary are not mirrored in the regional diversity structure of the Arkoma Shelf.

Additive Diversity Partitioning. — Taxonomic turnover between the Chesterian and Morrowan is apparent from simple comparison of 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 63% extinction or extirpation. Thirteen genera persist into the Morrowan, which has a total of 26 brachiopod genera. Fifty percent of the Morrowan genera are holdovers from the Morrowan. Spatial complexities of the richness and turnover structure become apparent when diversity is divided into alpha and beta components. Such a partitioning of diversity will allow 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 the diversity drop was caused by a drop in local richness 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 homogenous 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. 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 to 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 to 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:

$$\gamma = \overline{\overline{\alpha}} + \sum_{i=1}^{k} \overline{\beta_i} \tag{1}$$

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 i^{th} level. Beta diversity at the i^{th} level of the sampling hierarchy is:

$$\beta_i = \alpha_{i+1} + \overline{\alpha_i} \tag{2}$$

where $\overline{\alpha}$ is mean of all alpha values at the i^{th} level. Taking the average of all alpha values at the i^{th} level prevents pseudoreplication (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, their 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 two diversity metrics used are simple richness and Simpson's D, which reflects evenness. These metrics are chosen for ADP analysis because they are easily interpretable and are strictly concave (Lande 1996). Strict concavity occurs when the total diversity of pooled collections is always 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. Simpson’s D has the added advantage of being sample-size independent (Lande 1996). Simpson’s D is the probability that two individuals drawn randomly from a sample belong to different taxa and is given by:

$$D = 1 - \sum_{i=1}^{S} p_i^2 \tag{3}$$

where S is the total number of taxa in a sample and p_i is the proportional abundance of the i^{th} taxon. Simpson’s D emphasizes abundant taxa by squaring the abundances. The ADP results for richness and Simpson’s D provide a test of the hypothesis that total richness dropped from the Chesterian to the Morrowan, as predicted by global trends (Raymond et al. 1989; Kelley et al.

1991; Stanley and Powell 2003), and that there was an accompanying change in the spatial partitioning of richness and evenness.

The ADP results for taxonomic richness (Fig. 4.2) 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 ($\overline{\overline{\alpha}}_c$), which constitute approximately 23% and 30% of Chesterian and Morrowan diversity, respectively. Finally, the within-bed component ($\overline{\beta}_w$) 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 (Fig. 4.2). 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 diversity; on average, taking two collections from a bed will increase the number of genera encountered over taking one collection by two (< 25%).

The ADP results for Simpson's D (Fig. 4.3) indicate that dominance was high during both the Chesterian and Morrowan with total D at approximately 0.9 with overlapping 95% confidence intervals for both stages. Like taxonomic richness, all three pairwise comparisons of Chesterian and Morrowan partitions have overlapping 95% confidence intervals. Unlike taxonomic richness, greater than 70% of the dominance is contributed by the within-collection components ($\overline{\overline{\alpha}}_c$). Approximately 20% of the dominance is contributed by the among-bed component (β_a) and approximately 5% is contributed by the within-bed component ($\overline{\beta}_w$).

The ADP results falsify the hypothesis that the global extinction event was experienced in the paleotropics of Laurentia. There was not a statistically significant reduction in total diversity. Likewise, the hypothesis of declining alpha diversity is also rejected. There were no statistically significant changes in any of the alpha or beta components of taxonomic richness. Finally, there was no change in evenness, as measured by Simpson's D, 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.

Gradient Analysis. — Gradient analysis is a tool for exploring the role of environmental variables in structuring communities. Gradient analysis was employed to detect underlying structure to the field data that can not be detected with ADP. In particular, the arrangement of collections along temporal, spatial, and diversity gradients was sought. For taxa, gradients in time, abundance, and higher taxonomic groupings were sought. There are two gradients expected *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. This should show up as a result of the change in taxonomic composition from the Chesterian to the Morrowan.

Detrended correspondence analysis (DCA) and non-metric multidimensional scaling (NMDS) were performed to explore underlying community gradients. Both DCA and NMDS produce gradients for collections and taxa. 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 one 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 Team 2007) following the data transform methodology of Holland and Patzkowsky (2007): before analysis the data were transformed with a within-sample percent transformation 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 one (DCA1) with no overlap in collections scores (Fig. 4.4A). DCA1 taxon scores also indicate a temporal gradient. Genera found only in the Chesterian have low scores, genera found in both stages have intermediate scores, and genera found only in the Morrowan have high scores (Fig. 4.4B). Further exploration of the DCA results were made by calculating Pearson product-moment correlation coefficients between the first three DCA axes and a suite of collection and taxonomic variables. Correlation coefficients for DCA collection scores were calculated for longitude, collection abundance, collection richness, and Simpson's D (Table 4.1). Longitude was chosen because there is little latitudinal variation among the sample localities and there is a longitudinal gradient in lithology observed in the field. Collection richness and Simpson's D are significantly correlated with DCA1 (Table 4.1). The complete separation of of Chesterian and Morrowan collections along DCA1 (Fig. 4.4A) and the correlations with richness and evenness suggest that the Morrowan has higher richness and evenness within collections than the Chesterian. DCA2 is correlated with collection abundance, and DCA3 is significantly correlated with abundance and Simpson's D. Correlation coefficients between the DCA genus scores were calculated for genus abundance, class, and order (Table 4.2). The class and order of each genus were assigned according the *Treatise on Invertebrate Paleontology* (Kaesler 1997, 2000, 2002, 2006).

For purposes of calculating correlations, the mean DCA axis scores of the genera within each class and order were calculated and each class and order was sequentially assigned a numerical code in order from the lowest mean to the highest. This method of scoring higher level taxonomy was also applied to families, but the number of families is so similar to the number of genera that strong correlations always result. Like collection scores, DCA1 clearly represents the temporal distribution of genera (Fig. 4.4B), and a significant correlation between DCA1 and order (Table 4.2) indicates that order membership changed over time. DCA2 and DCA3 have significant correlations with both class and order (Table 4.2). There are no significant correlations between DCA axes and genus abundance. These same analyses were also applied to the Chesterian and Morrowan data separately. The only significant correlations were for the Chesterian collection scores between DCA2 and longitude; DCA3 and longitude; DCA3 and collection richness; and DCA3 and Simpson's D. There were no significant correlations for any of the Morrowan data or the Chesterian genus scores. The correlation with longitude likely represents the environmental gradient of decreasing terrigenous sediments to the west.

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 while 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 and environmental conditions (Mii et al. 1999). 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. 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 thirteen genera present in both stages to see if the rank-order of surviving genera was preserved.

The shape of the Chesterian and Morrowan plots are similar (Fig. 4.5). In both stages, there are two easily distinguishable regions separated by an abrupt change in slope. The first segment is comprised of the six most abundant genera and has a steep slope. The second segment contains the remaining genera and has a comparatively shallow slope. There is high dominance among the most abundant taxa and relatively high evenness among the moderately abundant and rare genera. The confidence intervals for the Chesterian and Morrowan data overlap for all genera (Fig. 4.5C), suggesting they have the same distribution. The Kolmogorov–Smirnov test corroborates this finding with a D-statistic of 0.2923 (*p*-value: 0.1227). Even though the abundances of the surviving genera were not maintained from the Chesterian to the Morrowan, the overall abundance structure was conserved. However, the Spearman rank correlation coefficient is -0.08 and is not significantly different from zero. In short, the abundance of a genus during the Chesterian does not predict the abundance of that genus during the Morrowan.

Like the ADP results and much of the DAC results, the rank-abundance distributions show that the gross structure of the Chesterian and Morrowan remained unchanged. There are no changes among metrics that ignore the identity of constituent taxa. However, like the DCA correlations with order, the organization of specific taxa did change from the Chesterian to the

Morrowan. The rank abundance of the surviving genera was not preserved from one stage to the next.

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, in press). The average similarity among beds within a stage indicates the degree of connectedness among beds, which 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 the Morrowan Arkoma shelf was reduced in the aftermath of global sea level fall (Scotese 2002), presumably leading to decreased habitat heterogeneity and a corresponding increase 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:

$$C_{MH} = \frac{2}{(d_a + d_b)N_a N_b} \sum_{i=1}^{S} a_i b_i \tag{4}$$

where d_a (and d_b) is given by:

$$d_a = \frac{1}{N_a^2} \sum_{i=0}^{S} a_i^2 \tag{5}$$

where S is the total number of taxa, N_a (and N_b) is the total number of individuals in assemblage a (and b), and a_i (and b_i) is the abundance of the i^{th} 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 are compared for the Chesterian and Morrowan. 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 using box and whisker plots, with outliers defined as being more than 1.5 times the interquartile range from the box (Sokal 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 Chesterian outliers with exceptionally low similarity, all of which are associated with the same bed from Pitkin formation at the 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 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 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 & 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. 1989; Kelley and Raymond 1991), depressed rates of origination and extinction (Stanley and Powell 2003), and a depressed latitudinal diversity gradient (Powell 2005, 2007). However, none of these environmental and ecological changes observed at the global scale are manifest on the tropical Arkoma Shelf. Although there was appreciable taxonomic turnover in the region, there was no statistically detectable drop in total diversity from the Chesterian to the Morrowan. This is in contrast to a 9% reduction in total generic richness across the same interval seen globally (Raymond et al. 1990). Neither a change in the spatiotemporal partitioning of richness and evenness, nor the rank-abundance 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 of surviving taxon abundances.

With regard to the middle Carboniferous extinction event, the results of this study are largely consistent with those of Raymond et al. (1990), who examined changes in total generic richness globally and for two paleolatitudinal bins. They found a modest drop in the number of genera in the earliest Pennsylvanian (Namurian B) globally. However, there was only a small drop in diversity that was recovered quickly in the equatorial zone (± 10^{o} of the paleoequator) while the extratropical regions experienced a much more substantial drop in diversity. Given that the Ozarks were situated in the tropics during the middle Carboniferous, the lack of extinction is not surprising. However, the degree of turnover was not predicted by Raymond et al. (1990), nor was the overall stability in diversity structure observed in the Ozarks. These data suggest a regime of relative stability in the tropics, possibly in response to high primary productivity and an equable climate.

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 magnitude of the Mississippian/Pennsylvanian unconformity, at which nearly two full conodont zones are missing (Manger and Sutherland 1992) and the degree of turnover in taxonomic composition. The similarities in additive diversity partitioning of richness and evenness, and rank-abundance suggest some control on how brachiopod genera were organized regionally during the middle Carboniferous. 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 there would be a strong rank-abundance correlation between the Chesterian and Morrowan. 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 over time and the steep decline in relative abundances (Fig. 4.5), it is likely that brachiopods are partitioning resources, but that the identity of the most successful, i.e., most abundant, genera are the result of ecological contingency (e.g., Hubbell 2001). After the sea-level fall at the end of the Mississippian, many of the same brachiopod genera returned to the Arkoma Shelf along with newcomers. However, the recolonization was not influenced by previous success and new taxa became abundant without necessarily forcing extinction or extirpation of the previously abundant taxa. Despite this taxonomic reorganization, the overall abundance structure remained conserved (Fig. 4.5C), suggesting 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).

In theory, competing taxa within a saturated local community consume all of one or more limiting resources thus excluding immigrant taxa, which renders 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 not saturated and not strongly influenced by interspecific competition, based on comparisons of regional and local richness. They found that local richness increased linearly with regional richness, suggesting that local assemblages are limited only by the regional species pool. Furthermore, it was found that immigrant taxa were able to become incorporated into the local and regional faunas, something that 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, a large degree of ecological stability was detected through the Middle Ordovician. However, it was also found that certain aspects of the paleoecology were volatile. Within certain biofacies, the rank-abundance of taxa changed through time. The Ordovician findings (Patzkowsky and Holland 2003; Holland and Patzkowsky 2004) are 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 mode 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. The theory is that competition 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 the paleocommunity saturation and interspecific competition may benefit from incorporating both abundance and morphological data on a regional scale. While 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 abundance of individual taxa are determined by stochastic processes. The UNTB predicts that communities have the same rate of speciation and the same rate of migration 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, but individual taxa are equal in their ability of compete for resources, and which taxa are the best competitors 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 that ability of taxa from the regional species pool to establish themselves locally increased. There are two 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; there were more Chesterian age sandy carbonates that were sampled in the east than there were in the Morrowan. 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 drop in sea level. In this recovery interval, all taxa may be immigrants and stable local dominance has not yet been established. Whatever competitive interactions were taking place during the Chesterian were reduced. This option is, however, not likely. If the Chesterian fauna were indeed a late stage of ecological succession and the Morrowan and early stage, then a difference in the overall abundance structure would surely exist (e.g., Dean and Connell 1987).

Finally, this study reiterates the importance of regional studies of paleodiversity. Abundance data is 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. 4.2). 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. 4.6), 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 are not always parallel to global patterns. The global extinction at the Mississippian/Pennsylvanian boundary was not manifest in the Ozarks in total richness or evenness. This suggests that the majority of the extinction was taken up in the middle and high paleolatitudes. Future regional studies of the middle Carboniferous are likely to reveal complex dynamics that involve both regional extirpation and extinction.

Conclusions

1. 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 related to 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 towards a global climate, there was comparatively little change in tropical biodiversity.

2. A significant difference in similarity indicates greater spatial homogeneity during the Morrowan relative to the Chesterian. The cause the increased similarity is uncertain for the moment, but it likely indicates that there was more migration of taxa within the region during the Morrowan than during the Chesterian.

3. Regional studies provide important information on how biotas respond to global changes in climate that are obscured by global studies. Of critical importance is that regional field studies are much more likely to incorporate critical abundance data that is often lacking from global databases compiled from the literature. Furthermore, it has been demonstrated here

that global extinctions are not experienced equally everywhere. The global cooling at the end of the Mississippian did not result in a either extinction or reorganization of brachiopod communities on the tropical Arkoma Shelf.

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FIGURE 4.1 — 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.

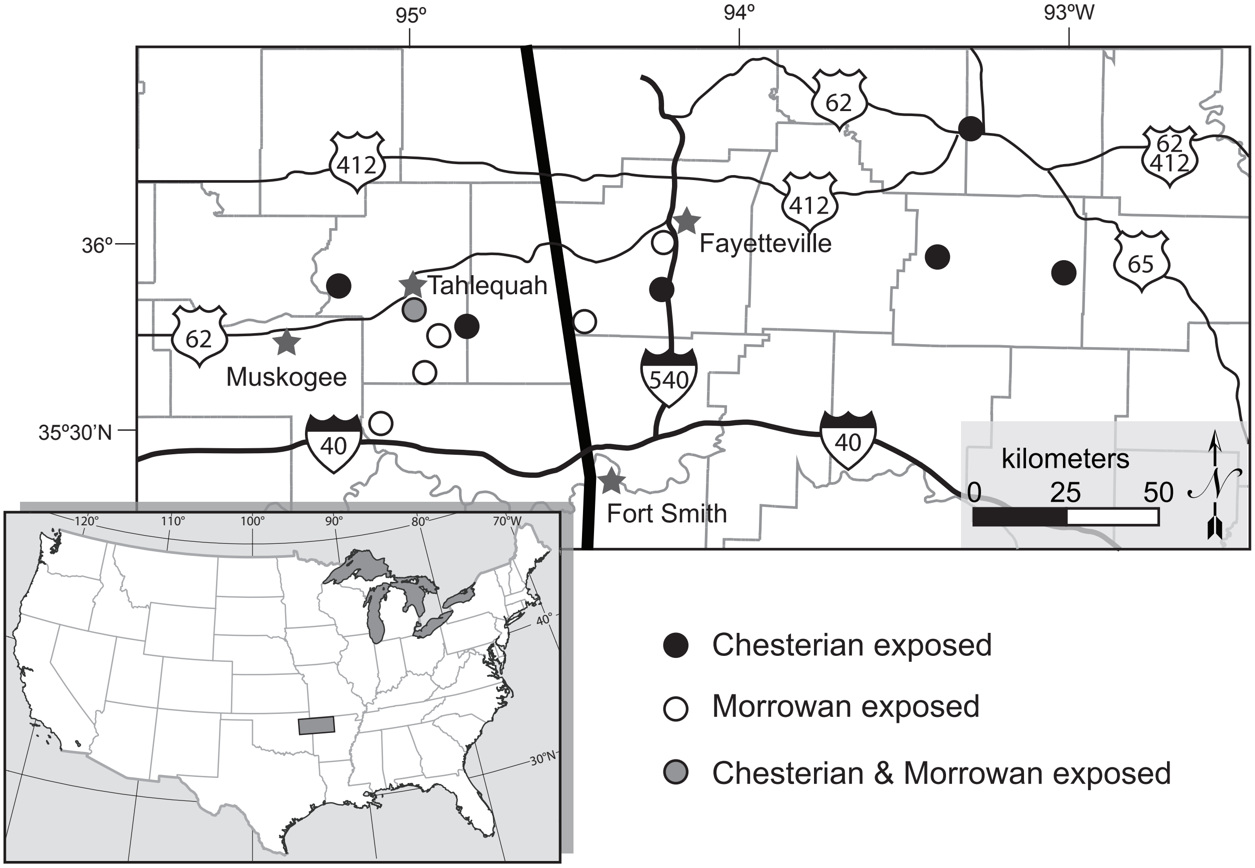

FIGURE 4.2 — Additive diversity partitioning (ADP) of taxonomic richness for the Chesterian and Morrowan. From bottom to top (dark gray to light gray) the partitions are among collection diversity($\overline{\overline{\alpha}}_c$), within bed diversity($\overline{\beta}_w$), and among bed diversity(β_a). 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 all plots are at different scales.

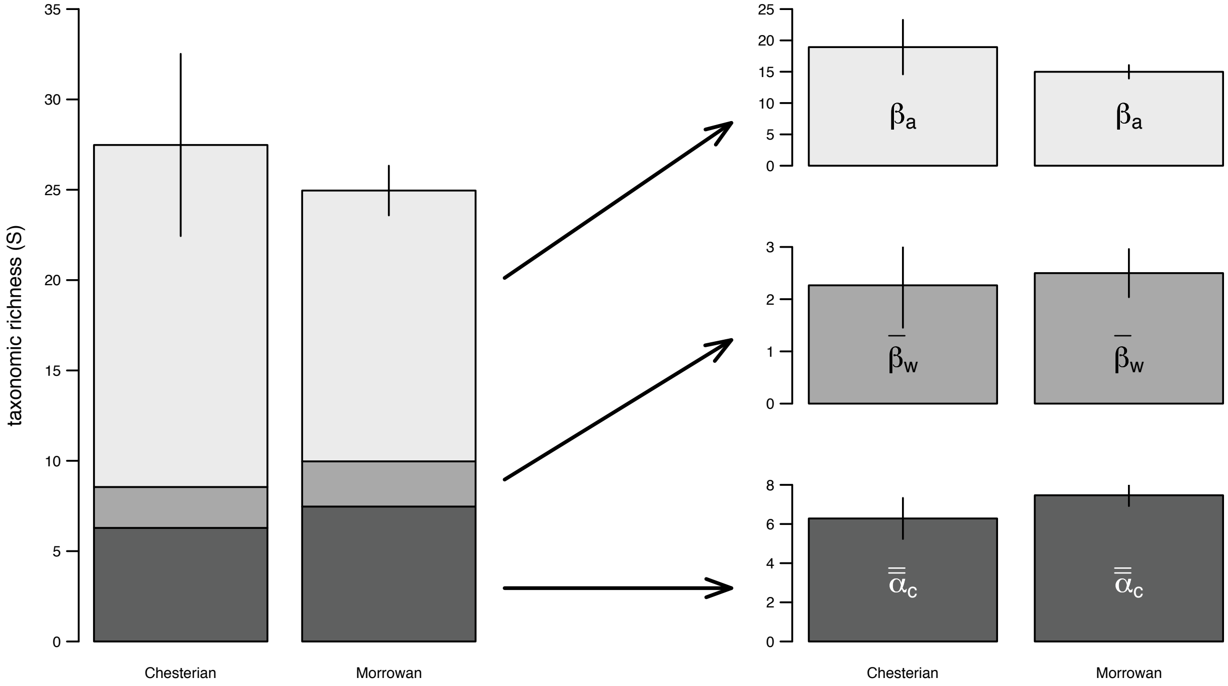

FIGURE 4.3 — Additive diversity partitioning (ADP) of Simpson's D for the Chesterian and Morrowan. Plotting conventions same as Fig. 4.2.

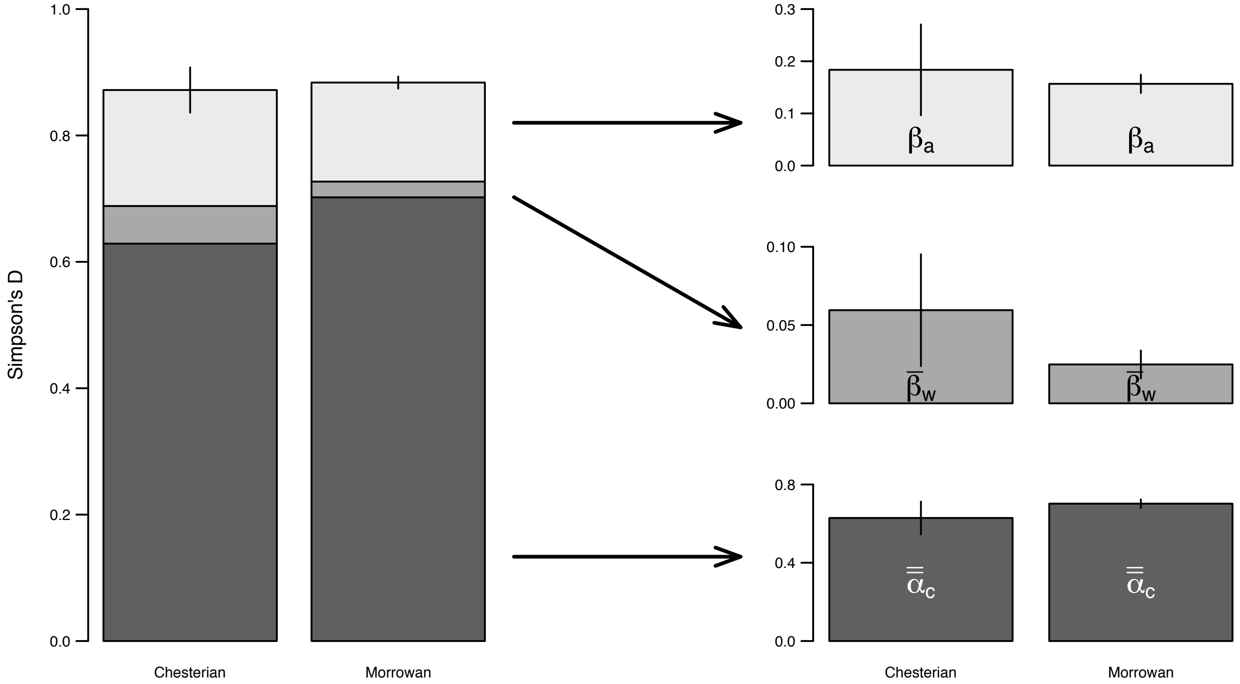

FIGURE 4.4 — Detrended correspondence analysis (DCA) results for full the data set: DCA axis 1 scores versus DCA axis 2 scores. A) Collection scores coded by stage. B) Genus scores coded by stage. Gray symbols indicate genera that are present in both the Chesterian and Morrowan. Note the strong gradients along DCA axis 1 that correspond to time for both collection and genus scores.

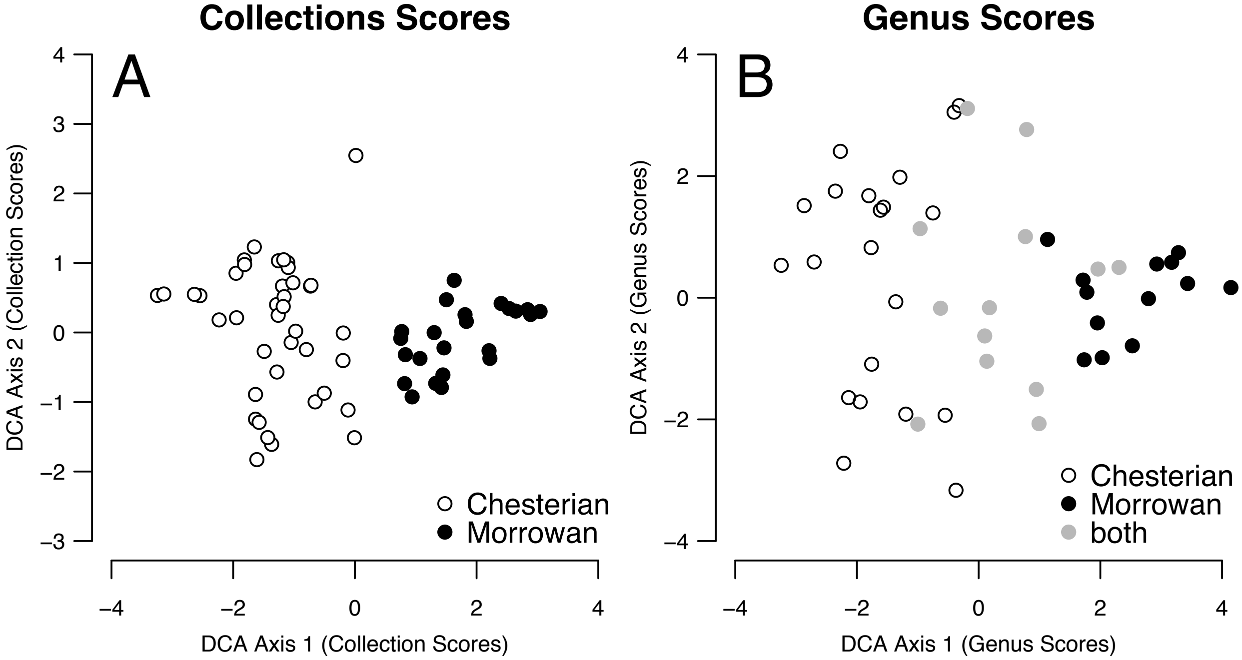

FIGURE 4.5 — Plots of genus rank versus percent abundance, on a semi-log scale, for the Chesterian (A) and Morrowan (B). The two top plots are the raw data with the seven most abundant genera identified for each stage. The bottom plot (C) compares the two rank-abundance distributions. The gray envelopes 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.

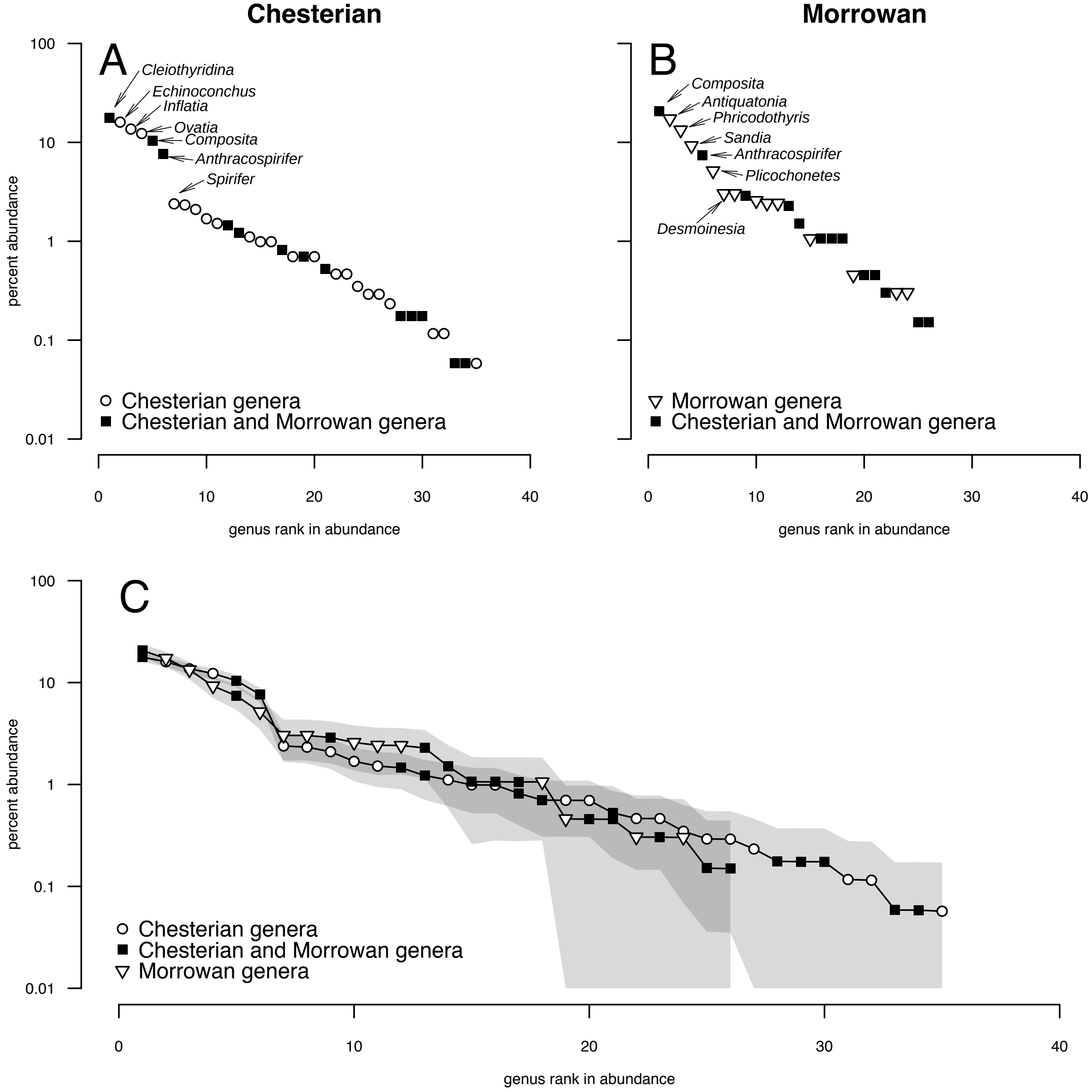

FIGURE 4.6 — A. Mean similarity of all pairwise comparisons, based on the Morisita-Horn index, of Chesterian and Morrowan beds with 95% confidence intervals. B. Box and whisker plots to show the distribution of pairwise similarities of the logit transformation of the Morisita-Horn index. The logit transformation [*ln(x/(1-x))*] is used to linearize data that has 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.

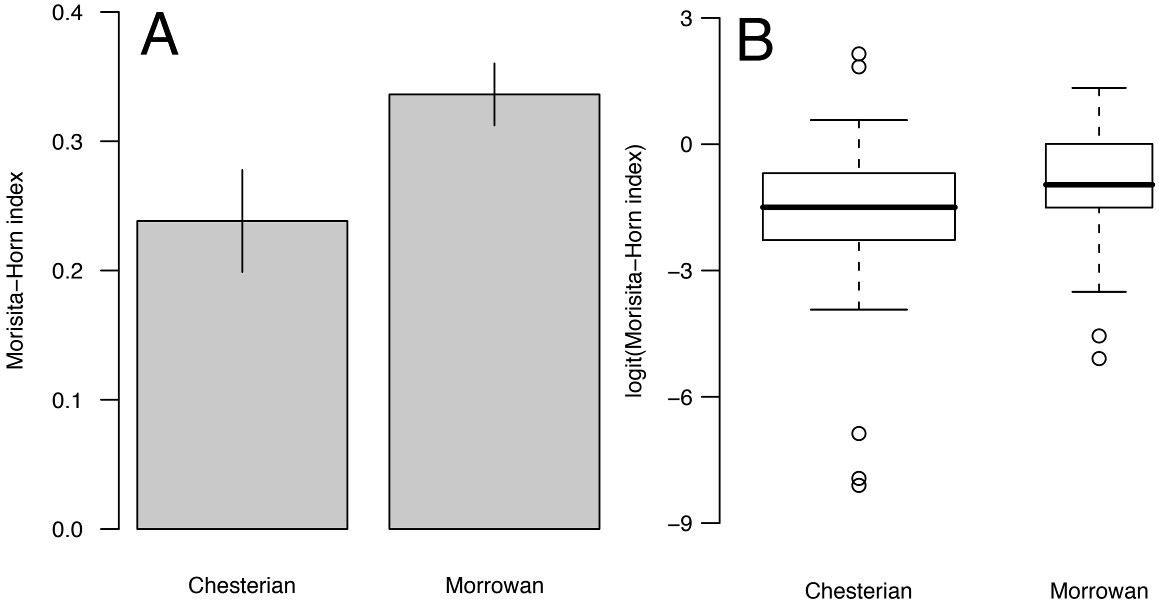

TABLE 4.1 — Pearson product-moment correlation coefficients among DCA collection scores and collection variables for full data set. Collection data were not pooled by bed in this analysis. The longitude is the present day longitude of the collection localities, not paleolongitude. Longitude is potentially 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	-0.190	0.024	0.237
collection abundance	-0.165	0.376*	0.302*
collection richness	0.267*	0.143	0.137
Simpson's D	0.418*	-0.153	0.288*

TABLE 4.2 — Pearson product-moment correlation coefficients among DCA genus scores and genus variables for full data set. The abundance variable is is the number of individuals within each genus. For purposes of calculating correlations, the mean DCA axis score of the genera within each class and order was calculated and each class and order was sequentially assigned a numerical code from the lowest mean to the highest. Asterisks indicate statistically significant correlations ($p \leq 0.05$).

	DCA1	DCA2	DCA3
abundance	-0.183	0.049	0.027
class	0.154	0.387*	0.302*
order	0.376*	0.576*	0.480*

CHAPTER 5

CONCLUSIONS

The overall conclusion to be drawn from this research is that global diversity patterns observed in the fossil record are not simply scaled up replicates of continental and regional patterns. Rather, global diversity is the average of diverse and complex patterns produced at smaller spatial scales. This realization is important for fully understanding the processes that ultimately shape diversity at all scales.

The null model highlights extinction as a scale-dependent process in which the impact of an individual extinction event is determined by the scale at which it is observed. For example, at the continental scale, the extinction of a genus from Laurentia will reduce diversity by one, but if that genus also exists in South China, global diversity remains unchanged. The model also demonstrates that migration is an important evolutionary process that can facilitate an increase in global richness, even when continental extinction rates are greater than continental origination rates. Migration does this by increasing the global origination rate above the continental origination rate and depressing the global extinction rate below the continental extinction rate. Migration is also shown to produce a dynamic equilibrium in global differentiation diversity, this is important because if migration is fast enough, differentiation diversity data collected at the stage level may reflect equilibrium conditions. Finally, global Ordovician data parsed by paleocontinent show that high rates of continental origination and low rates of migration were important factors in determining differentiation diversity during the Ordovician, and confirming other studies indicating high Ordovician provinciality.

The latitudinal diversity gradient on western Gondwana during the Mississippian was the inverse of most modern gradients; diversity was minimum at the equator and increased towards higher latitudes. Then during the Pennsylvanian the gradient flattened, at least in the tropics. This temporal pattern was probably the result of a larger area available on the flooded continental interior of Laurentia during the Mississippian. There may also have been a component driven by the onset of glaciation on Gondwana, which caused the extinction of some taxa and forced the migration of others northward. Interestingly, in contrast to global studies, the tropics of Laurentia and South America did not experience an extinction event until the late Pennsylvanian, and the regional extinction event was driven by a drop in beta diversity as the number of widespread genera increased and the number of narrowly distributed genera decreased.

The detailed regional field study of the Chesterian and Morrowan units of the southern Ozarks in Arkansas and Oklahoma show remarkable continuity of biodiversity structure, with no statistically significant changes in taxonomic richness, evenness, and rank-abundance distribution. Stability is maintained despite a large turnover in taxonomic composition. Although the gross diversity structure was stable, there was a shuffling of the abundances of genera that persisted across the Mississippian/ Pennsylvanian boundary. These results 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 towards a global climate, there was comparatively little change in tropical biodiversity. In addition to stability, a difference in taxonomic similarity demonstrates an decrease in habitat patchiness across the Mississippian/Pennsylvanian boundary. These field data once again reiterate the differences between regional and global scale patterns and processes. This is particularly apparent in the lack of extinction across the Mississippian/Pennsylvanian boundary. The global cooling at the end of the

Mississippian does not appear to have caused an extinction or a reorganization of diversity on the tropical Arkoma Shelf.

APPENDICES

Appendix A — Model output for all 405 combinations of origination, extinction, and migration. A value of "NULL" indicates that the model did not reach an equilibrium state within 15,000 time steps or 150 Myr.

migration	*origination*	*extinction*	*equilibrium delta*	*std. error*	*equilibrium time (Myr)*
1.00E-08	1.00E-08	1.00E-08	9.89E-01	4.52E-05	0.00E+00
1.00E-08	1.00E-08	5.00E-08	9.85E-01	1.92E-04	1.50E+00
1.00E-08	1.00E-08	1.00E-07	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-08	5.00E-07	NULL	NULL	NULL
1.00E-08	1.00E-08	1.00E-06	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-08	5.00E-06	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-08	1.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-08	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-08	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-08	5.00E-08	1.00E-08	9.90E-01	1.47E-05	1.42E+00
1.00E-08	5.00E-08	5.00E-08	NULL	NULL	NULL
1.00E-08	5.00E-08	1.00E-07	9.90E-01	7.72E-06	5.17E-01
1.00E-08	5.00E-08	5.00E-07	NULL	NULL	NULL
1.00E-08	5.00E-08	1.00E-06	1.00E+00	0.00E+00	0.00E+00
1.00E-08	5.00E-08	5.00E-06	1.00E+00	0.00E+00	0.00E+00
1.00E-08	5.00E-08	1.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-08	5.00E-08	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-08	5.00E-08	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-07	1.00E-08	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-07	5.00E-08	NULL	NULL	NULL
1.00E-08	1.00E-07	1.00E-07	NULL	NULL	NULL
1.00E-08	1.00E-07	5.00E-07	NULL	NULL	NULL
1.00E-08	1.00E-07	1.00E-06	NULL	NULL	NULL
1.00E-08	1.00E-07	5.00E-06	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-07	1.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-07	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-07	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-08	5.00E-07	1.00E-08	9.93E-01	9.66E-06	2.28E-01
1.00E-08	5.00E-07	5.00E-08	9.92E-01	2.47E-04	0.00E+00
1.00E-08	5.00E-07	1.00E-07	9.94E-01	3.97E-04	0.00E+00
1.00E-08	5.00E-07	5.00E-07	NULL	NULL	NULL
1.00E-08	5.00E-07	1.00E-06	NULL	NULL	NULL
1.00E-08	5.00E-07	5.00E-06	1.00E+00	0.00E+00	0.00E+00
1.00E-08	5.00E-07	1.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-08	5.00E-07	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-08	5.00E-07	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-06	1.00E-08	NULL	NULL	NULL
1.00E-08	1.00E-06	5.00E-08	NULL	NULL	NULL
1.00E-08	1.00E-06	1.00E-07	9.93E-01	1.64E-05	2.24E-01
1.00E-08	1.00E-06	5.00E-07	9.88E-01	5.19E-05	1.29E+00
1.00E-08	1.00E-06	1.00E-06	NULL	NULL	NULL
1.00E-08	1.00E-06	5.00E-06	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-06	1.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-06	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-06	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-08	5.00E-06	1.00E-08	9.99E-01	1.41E-06	6.74E-01
1.00E-08	5.00E-06	5.00E-08	NULL	NULL	NULL
1.00E-08	5.00E-06	1.00E-07	9.99E-01	1.05E-06	8.22E-01

migration	*origination*	*extinction*	*equilibrium delta*	*std. error*	*equilibrium time (Myr)*
1.00E-08	5.00E-06	5.00E-07	NULL	NULL	NULL
1.00E-08	5.00E-06	1.00E-06	NULL	NULL	NULL
1.00E-08	5.00E-06	5.00E-06	NULL	NULL	NULL
1.00E-08	5.00E-06	1.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-08	5.00E-06	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-08	5.00E-06	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-05	1.00E-08	9.99E-01	2.42E-06	2.65E-01
1.00E-08	1.00E-05	5.00E-08	NULL	NULL	NULL
1.00E-08	1.00E-05	1.00E-07	NULL	NULL	NULL
1.00E-08	1.00E-05	5.00E-07	NULL	NULL	NULL
1.00E-08	1.00E-05	1.00E-06	NULL	NULL	NULL
1.00E-08	1.00E-05	5.00E-06	NULL	NULL	NULL
1.00E-08	1.00E-05	1.00E-05	NULL	NULL	NULL
1.00E-08	1.00E-05	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-05	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-08	5.00E-05	1.00E-08	1.00E+00	5.37E-07	9.02E-02
1.00E-08	5.00E-05	5.00E-08	1.00E+00	6.96E-07	1.62E-01
1.00E-08	5.00E-05	1.00E-07	1.00E+00	3.47E-07	9.67E-02
1.00E-08	5.00E-05	5.00E-07	NULL	NULL	NULL
1.00E-08	5.00E-05	1.00E-06	NULL	NULL	NULL
1.00E-08	5.00E-05	5.00E-06	NULL	NULL	NULL
1.00E-08	5.00E-05	1.00E-05	NULL	NULL	NULL
1.00E-08	5.00E-05	5.00E-05	NULL	NULL	NULL
1.00E-08	5.00E-05	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-08	1.00E-04	1.00E-08	1.00E+00	3.80E-07	5.85E-02
1.00E-08	1.00E-04	5.00E-08	NULL	NULL	NULL
1.00E-08	1.00E-04	1.00E-07	1.00E+00	1.24E-06	4.25E-02
1.00E-08	1.00E-04	5.00E-07	1.00E+00	3.40E-07	6.30E-02
1.00E-08	1.00E-04	1.00E-06	1.00E+00	1.70E-07	5.49E-02
1.00E-08	1.00E-04	5.00E-06	NULL	NULL	NULL
1.00E-08	1.00E-04	1.00E-05	1.00E+00	1.65E-07	6.74E-02
1.00E-08	1.00E-04	5.00E-05	NULL	NULL	NULL
1.00E-08	1.00E-04	1.00E-04	NULL	NULL	NULL
1.00E-07	1.00E-08	1.00E-08	8.95E-01	2.66E-04	0.00E+00
1.00E-07	1.00E-08	5.00E-08	9.70E-01	4.52E-05	1.16E+00
1.00E-07	1.00E-08	1.00E-07	9.48E-01	7.30E-05	1.31E+00
1.00E-07	1.00E-08	5.00E-07	9.26E-01	1.09E-03	0.00E+00
1.00E-07	1.00E-08	1.00E-06	9.47E-01	4.91E-05	1.22E+00
1.00E-07	1.00E-08	5.00E-06	NULL	NULL	NULL
1.00E-07	1.00E-08	1.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-07	1.00E-08	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-07	1.00E-08	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-07	5.00E-08	1.00E-08	9.46E-01	4.88E-05	1.28E+00
1.00E-07	5.00E-08	5.00E-08	9.23E-01	1.43E-04	0.00E+00
1.00E-07	5.00E-08	1.00E-07	8.91E-01	4.92E-04	0.00E+00
1.00E-07	5.00E-08	5.00E-07	9.25E-01	1.42E-03	0.00E+00
1.00E-07	5.00E-08	1.00E-06	9.09E-01	2.98E-04	1.48E+00
1.00E-07	5.00E-08	5.00E-06	9.33E-01	6.73E-04	3.79E-01
1.00E-07	5.00E-08	1.00E-05	9.64E-01	6.60E-04	1.96E-01
1.00E-07	5.00E-08	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-07	5.00E-08	1.00E-04	NULL	NULL	NULL
1.00E-07	1.00E-07	1.00E-08	9.49E-01	1.58E-04	1.25E+00
1.00E-07	1.00E-07	5.00E-08	9.24E-01	6.55E-05	8.73E-01

migration	*origination*	*extinction*	*equilibrium delta*	*std. error*	*equilibrium time (Myr)*
1.00E-07	1.00E-07	1.00E-07	9.15E-01	1.15E-04	1.46E+00
1.00E-07	1.00E-07	5.00E-07	9.69E-01	6.55E-05	7.60E-01
1.00E-07	1.00E-07	1.00E-06	9.66E-01	1.67E-04	4.45E-01
1.00E-07	1.00E-07	5.00E-06	NULL	NULL	NULL
1.00E-07	1.00E-07	1.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-07	1.00E-07	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-07	1.00E-07	1.00E-04	NULL	NULL	NULL
1.00E-07	5.00E-07	1.00E-08	9.46E-01	1.59E-04	1.47E+00
1.00E-07	5.00E-07	5.00E-08	9.34E-01	2.81E-04	0.00E+00
1.00E-07	5.00E-07	1.00E-07	9.68E-01	7.13E-05	1.04E+00
1.00E-07	5.00E-07	5.00E-07	9.83E-01	2.46E-05	3.70E-01
1.00E-07	5.00E-07	1.00E-06	9.76E-01	3.20E-04	6.89E-01
1.00E-07	5.00E-07	5.00E-06	NULL	NULL	NULL
1.00E-07	5.00E-07	1.00E-05	NULL	NULL	NULL
1.00E-07	5.00E-07	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-07	5.00E-07	1.00E-04	NULL	NULL	NULL
1.00E-07	1.00E-06	1.00E-08	9.70E-01	4.84E-05	1.30E+00
1.00E-07	1.00E-06	5.00E-08	9.67E-01	2.48E-05	5.25E-01
1.00E-07	1.00E-06	1.00E-07	9.74E-01	1.12E-04	1.31E+00
1.00E-07	1.00E-06	5.00E-07	9.62E-01	6.56E-05	1.25E+00
1.00E-07	1.00E-06	1.00E-06	9.80E-01	1.97E-04	1.15E+00
1.00E-07	1.00E-06	5.00E-06	NULL	NULL	NULL
1.00E-07	1.00E-06	1.00E-05	NULL	NULL	NULL
1.00E-07	1.00E-06	5.00E-05	NULL	NULL	NULL
1.00E-07	1.00E-06	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-07	5.00E-06	1.00E-08	9.90E-01	1.06E-05	5.42E-01
1.00E-07	5.00E-06	5.00E-08	9.91E-01	8.15E-06	5.10E-01
1.00E-07	5.00E-06	1.00E-07	NULL	NULL	NULL
1.00E-07	5.00E-06	5.00E-07	9.90E-01	9.39E-06	4.60E-01
1.00E-07	5.00E-06	1.00E-06	9.92E-01	8.10E-06	1.96E-01
1.00E-07	5.00E-06	5.00E-06	NULL	NULL	NULL
1.00E-07	5.00E-06	1.00E-05	NULL	NULL	NULL
1.00E-07	5.00E-06	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-07	5.00E-06	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-07	1.00E-05	1.00E-08	NULL	NULL	NULL
1.00E-07	1.00E-05	5.00E-08	9.95E-01	9.40E-06	8.73E-02
1.00E-07	1.00E-05	1.00E-07	9.95E-01	6.45E-06	3.93E-01
1.00E-07	1.00E-05	5.00E-07	NULL	NULL	NULL
1.00E-07	1.00E-05	1.00E-06	9.95E-01	5.40E-06	8.31E-02
1.00E-07	1.00E-05	5.00E-06	NULL	NULL	NULL
1.00E-07	1.00E-05	1.00E-05	NULL	NULL	NULL
1.00E-07	1.00E-05	5.00E-05	NULL	NULL	NULL
1.00E-07	1.00E-05	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-07	5.00E-05	1.00E-08	NULL	NULL	NULL
1.00E-07	5.00E-05	5.00E-08	9.99E-01	1.62E-06	9.15E-02
1.00E-07	5.00E-05	1.00E-07	NULL	NULL	NULL
1.00E-07	5.00E-05	5.00E-07	NULL	NULL	NULL
1.00E-07	5.00E-05	1.00E-06	9.99E-01	3.73E-06	1.15E-01
1.00E-07	5.00E-05	5.00E-06	NULL	NULL	NULL
1.00E-07	5.00E-05	1.00E-05	9.99E-01	3.74E-06	6.98E-02
1.00E-07	5.00E-05	5.00E-05	NULL	NULL	NULL
1.00E-07	5.00E-05	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-07	1.00E-04	1.00E-08	NULL	NULL	NULL

migration	*origination*	*extinction*	*equilibrium delta*	*std. error*	*equilibrium time (Myr)*
1.00E-07	1.00E-04	5.00E-08	9.99E-01	1.80E-06	5.05E-02
1.00E-07	1.00E-04	1.00E-07	NULL	NULL	NULL
1.00E-07	1.00E-04	5.00E-07	1.00E+00	2.83E-06	3.15E-02
1.00E-07	1.00E-04	1.00E-06	NULL	NULL	NULL
1.00E-07	1.00E-04	5.00E-06	9.99E-01	3.66E-06	3.36E-02
1.00E-07	1.00E-04	1.00E-05	1.00E+00	2.16E-05	1.93E-02
1.00E-07	1.00E-04	5.00E-05	NULL	NULL	NULL
1.00E-07	1.00E-04	1.00E-04	NULL	NULL	NULL
1.00E-06	1.00E-08	1.00E-08	3.60E-01	1.50E-03	0.00E+00
1.00E-06	1.00E-08	5.00E-08	3.96E-01	1.20E-03	0.00E+00
1.00E-06	1.00E-08	1.00E-07	5.28E-01	5.67E-04	1.40E+00
1.00E-06	1.00E-08	5.00E-07	5.98E-01	3.22E-04	1.01E+00
1.00E-06	1.00E-08	1.00E-06	7.30E-01	2.92E-04	6.42E-01
1.00E-06	1.00E-08	5.00E-06	NULL	NULL	NULL
1.00E-06	1.00E-08	1.00E-05	NULL	NULL	NULL
1.00E-06	1.00E-08	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-06	1.00E-08	1.00E-04	NULL	NULL	NULL
1.00E-06	5.00E-08	1.00E-08	4.21E-01	8.84E-04	0.00E+00
1.00E-06	5.00E-08	5.00E-08	4.08E-01	5.52E-04	0.00E+00
1.00E-06	5.00E-08	1.00E-07	5.33E-01	5.89E-04	1.46E+00
1.00E-06	5.00E-08	5.00E-07	6.19E-01	3.31E-04	1.15E+00
1.00E-06	5.00E-08	1.00E-06	7.13E-01	3.22E-04	7.77E-01
1.00E-06	5.00E-08	5.00E-06	NULL	NULL	NULL
1.00E-06	5.00E-08	1.00E-05	NULL	NULL	NULL
1.00E-06	5.00E-08	5.00E-05	1.00E+00	0.00E+00	0.00E+00
1.00E-06	5.00E-08	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-06	1.00E-07	1.00E-08	4.30E-01	5.52E-04	0.00E+00
1.00E-06	1.00E-07	5.00E-08	4.67E-01	4.16E-04	0.00E+00
1.00E-06	1.00E-07	1.00E-07	5.28E-01	3.59E-04	1.49E+00
1.00E-06	1.00E-07	5.00E-07	6.18E-01	7.65E-04	0.00E+00
1.00E-06	1.00E-07	1.00E-06	6.32E-01	3.12E-04	7.98E-01
1.00E-06	1.00E-07	5.00E-06	9.01E-01	9.10E-04	5.45E-01
1.00E-06	1.00E-07	1.00E-05	NULL	NULL	NULL
1.00E-06	1.00E-07	5.00E-05	NULL	NULL	NULL
1.00E-06	1.00E-07	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-06	5.00E-07	1.00E-08	5.95E-01	4.71E-04	1.40E+00
1.00E-06	5.00E-07	5.00E-08	6.45E-01	3.50E-04	1.19E+00
1.00E-06	5.00E-07	1.00E-07	6.75E-01	3.66E-04	1.19E+00
1.00E-06	5.00E-07	5.00E-07	7.01E-01	2.08E-04	1.16E+00
1.00E-06	5.00E-07	1.00E-06	7.46E-01	3.65E-04	1.36E+00
1.00E-06	5.00E-07	5.00E-06	9.28E-01	1.08E-03	3.13E-01
1.00E-06	5.00E-07	1.00E-05	NULL	NULL	NULL
1.00E-06	5.00E-07	5.00E-05	NULL	NULL	NULL
1.00E-06	5.00E-07	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-06	1.00E-06	1.00E-08	7.30E-01	1.80E-04	8.76E-01
1.00E-06	1.00E-06	5.00E-08	7.35E-01	1.89E-04	1.24E+00
1.00E-06	1.00E-06	1.00E-07	7.46E-01	2.50E-04	1.26E+00
1.00E-06	1.00E-06	5.00E-07	7.58E-01	2.35E-04	9.68E-01
1.00E-06	1.00E-06	1.00E-06	8.16E-01	2.05E-04	8.98E-01
1.00E-06	1.00E-06	5.00E-06	9.66E-01	5.77E-04	2.07E-01
1.00E-06	1.00E-06	1.00E-05	NULL	NULL	NULL
1.00E-06	1.00E-06	5.00E-05	NULL	NULL	NULL
1.00E-06	1.00E-06	1.00E-04	NULL	NULL	NULL

migration	*origination*	*extinction*	*equilibrium delta*	*std. error*	*equilibrium time (Myr)*
1.00E-06	5.00E-06	1.00E-08	9.14E-01	3.23E-05	6.87E-01
1.00E-06	5.00E-06	5.00E-08	9.14E-01	4.48E-05	7.53E-01
1.00E-06	5.00E-06	1.00E-07	9.14E-01	4.48E-05	5.51E-01
1.00E-06	5.00E-06	5.00E-07	9.18E-01	3.00E-05	7.11E-01
1.00E-06	5.00E-06	1.00E-06	9.25E-01	4.39E-05	2.22E-01
1.00E-06	5.00E-06	5.00E-06	NULL	NULL	NULL
1.00E-06	5.00E-06	1.00E-05	NULL	NULL	NULL
1.00E-06	5.00E-06	5.00E-05	NULL	NULL	NULL
1.00E-06	5.00E-06	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-06	1.00E-05	1.00E-08	9.52E-01	2.64E-05	1.38E-01
1.00E-06	1.00E-05	5.00E-08	9.53E-01	3.36E-05	2.57E-01
1.00E-06	1.00E-05	1.00E-07	9.54E-01	2.83E-05	4.13E-01
1.00E-06	1.00E-05	5.00E-07	9.54E-01	3.67E-05	3.09E-01
1.00E-06	1.00E-05	1.00E-06	9.57E-01	3.70E-05	4.33E-01
1.00E-06	1.00E-05	5.00E-06	NULL	NULL	NULL
1.00E-06	1.00E-05	1.00E-05	9.73E-01	1.16E-04	2.46E-01
1.00E-06	1.00E-05	5.00E-05	NULL	NULL	NULL
1.00E-06	1.00E-05	1.00E-04	1.00E+00	0.00E+00	0.00E+00
1.00E-06	5.00E-05	1.00E-08	9.90E-01	1.67E-05	2.28E-02
1.00E-06	5.00E-05	5.00E-08	9.90E-01	2.33E-05	8.30E-03
1.00E-06	5.00E-05	1.00E-07	9.90E-01	2.18E-05	2.51E-02
1.00E-06	5.00E-05	5.00E-07	9.90E-01	3.30E-05	1.90E-02
1.00E-06	5.00E-05	1.00E-06	9.91E-01	1.62E-05	7.58E-02
1.00E-06	5.00E-05	5.00E-06	9.91E-01	2.73E-05	1.48E-02
1.00E-06	5.00E-05	1.00E-05	9.91E-01	3.32E-05	2.71E-02
1.00E-06	5.00E-05	5.00E-05	NULL	NULL	NULL
1.00E-06	5.00E-05	1.00E-04	NULL	NULL	NULL
1.00E-06	1.00E-04	1.00E-08	NULL	NULL	NULL
1.00E-06	1.00E-04	5.00E-08	9.95E-01	2.05E-05	1.04E-02
1.00E-06	1.00E-04	1.00E-07	9.95E-01	2.31E-05	1.58E-02
1.00E-06	1.00E-04	5.00E-07	9.95E-01	2.16E-05	9.20E-03
1.00E-06	1.00E-04	1.00E-06	9.95E-01	1.13E-05	3.28E-02
1.00E-06	1.00E-04	5.00E-06	NULL	NULL	NULL
1.00E-06	1.00E-04	1.00E-05	9.95E-01	1.74E-05	3.66E-02
1.00E-06	1.00E-04	5.00E-05	NULL	NULL	NULL
1.00E-06	1.00E-04	1.00E-04	NULL	NULL	NULL
1.00E-05	1.00E-08	1.00E-08	8.72E-03	2.33E-04	5.45E-01
1.00E-05	1.00E-08	5.00E-08	1.57E-02	1.37E-04	5.85E-01
1.00E-05	1.00E-08	1.00E-07	3.07E-02	2.63E-04	6.42E-01
1.00E-05	1.00E-08	5.00E-07	1.06E-01	2.67E-04	4.67E-01
1.00E-05	1.00E-08	1.00E-06	2.03E-01	3.67E-04	4.51E-01
1.00E-05	1.00E-08	5.00E-06	5.31E-01	5.98E-04	1.12E-01
1.00E-05	1.00E-08	1.00E-05	NULL	NULL	NULL
1.00E-05	1.00E-08	5.00E-05	NULL	NULL	NULL
1.00E-05	1.00E-08	1.00E-04	7.80E-01	6.87E-03	3.54E-02
1.00E-05	5.00E-08	1.00E-08	2.73E-02	1.72E-04	7.97E-01
1.00E-05	5.00E-08	5.00E-08	2.62E-02	1.37E-04	5.84E-01
1.00E-05	5.00E-08	1.00E-07	4.46E-02	1.94E-04	6.08E-01
1.00E-05	5.00E-08	5.00E-07	1.23E-01	3.06E-04	3.71E-01
1.00E-05	5.00E-08	1.00E-06	2.00E-01	2.91E-04	3.04E-01
1.00E-05	5.00E-08	5.00E-06	NULL	NULL	NULL
1.00E-05	5.00E-08	1.00E-05	4.66E-01	1.27E-02	6.57E-01
1.00E-05	5.00E-08	5.00E-05	NULL	NULL	NULL

migration	*origination*	*extinction*	*equilibrium delta*	*std. error*	*equilibrium time (Myr)*
1.00E-05	5.00E-08	1.00E-04	NULL	NULL	NULL
1.00E-05	1.00E-07	1.00E-08	5.14E-02	1.89E-04	5.36E-01
1.00E-05	1.00E-07	5.00E-08	4.06E-02	2.29E-04	6.87E-01
1.00E-05	1.00E-07	1.00E-07	6.36E-02	1.94E-04	4.75E-01
1.00E-05	1.00E-07	5.00E-07	1.30E-01	3.14E-04	4.17E-01
1.00E-05	1.00E-07	1.00E-06	2.01E-01	2.83E-04	3.98E-01
1.00E-05	1.00E-07	5.00E-06	5.60E-01	5.58E-04	1.57E-01
1.00E-05	1.00E-07	1.00E-05	NULL	NULL	NULL
1.00E-05	1.00E-07	5.00E-05	9.04E-01	6.34E-03	4.73E-02
1.00E-05	1.00E-07	1.00E-04	NULL	NULL	NULL
1.00E-05	5.00E-07	1.00E-08	1.55E-01	2.06E-04	4.84E-01
1.00E-05	5.00E-07	5.00E-08	1.51E-01	2.60E-04	4.85E-01
1.00E-05	5.00E-07	1.00E-07	1.76E-01	2.32E-04	3.49E-01
1.00E-05	5.00E-07	5.00E-07	2.22E-01	2.11E-04	3.75E-01
1.00E-05	5.00E-07	1.00E-06	2.78E-01	2.70E-04	4.46E-01
1.00E-05	5.00E-07	5.00E-06	5.38E-01	5.94E-04	1.36E-01
1.00E-05	5.00E-07	1.00E-05	NULL	NULL	NULL
1.00E-05	5.00E-07	5.00E-05	NULL	NULL	NULL
1.00E-05	5.00E-07	1.00E-04	NULL	NULL	NULL
1.00E-05	1.00E-06	1.00E-08	2.62E-01	2.05E-04	5.01E-01
1.00E-05	1.00E-06	5.00E-08	2.60E-01	1.76E-04	3.04E-01
1.00E-05	1.00E-06	1.00E-07	2.70E-01	1.96E-04	2.64E-01
1.00E-05	1.00E-06	5.00E-07	3.04E-01	1.84E-04	2.97E-01
1.00E-05	1.00E-06	1.00E-06	3.39E-01	2.17E-04	3.06E-01
1.00E-05	1.00E-06	5.00E-06	5.82E-01	3.05E-04	2.56E-01
1.00E-05	1.00E-06	1.00E-05	NULL	NULL	NULL
1.00E-05	1.00E-06	5.00E-05	NULL	NULL	NULL
1.00E-05	1.00E-06	1.00E-04	8.11E-01	7.56E-03	2.97E-02
1.00E-05	5.00E-06	1.00E-08	5.74E-01	6.93E-05	3.14E-01
1.00E-05	5.00E-06	5.00E-08	5.73E-01	8.23E-05	2.05E-01
1.00E-05	5.00E-06	1.00E-07	5.77E-01	7.70E-05	2.05E-01
1.00E-05	5.00E-06	5.00E-07	5.90E-01	8.82E-05	2.22E-01
1.00E-05	5.00E-06	1.00E-06	6.07E-01	1.19E-04	2.26E-01
1.00E-05	5.00E-06	5.00E-06	6.91E-01	1.07E-04	8.35E-02
1.00E-05	5.00E-06	1.00E-05	7.66E-01	5.14E-04	7.65E-02
1.00E-05	5.00E-06	5.00E-05	NULL	NULL	NULL
1.00E-05	5.00E-06	1.00E-04	NULL	NULL	NULL
1.00E-05	1.00E-05	1.00E-08	7.09E-01	1.20E-04	1.76E-01
1.00E-05	1.00E-05	5.00E-08	7.09E-01	9.38E-05	1.33E-01
1.00E-05	1.00E-05	1.00E-07	7.10E-01	1.21E-04	1.83E-01
1.00E-05	1.00E-05	5.00E-07	7.15E-01	1.05E-04	1.56E-01
1.00E-05	1.00E-05	1.00E-06	7.23E-01	9.58E-05	2.31E-01
1.00E-05	1.00E-05	5.00E-06	7.69E-01	8.86E-05	1.12E-01
1.00E-05	1.00E-05	1.00E-05	8.07E-01	1.13E-04	1.61E-01
1.00E-05	1.00E-05	5.00E-05	NULL	NULL	NULL
1.00E-05	1.00E-05	1.00E-04	NULL	NULL	NULL
1.00E-05	5.00E-05	1.00E-08	9.14E-01	1.12E-04	7.66E-02
1.00E-05	5.00E-05	5.00E-08	9.10E-01	7.98E-05	3.04E-02
1.00E-05	5.00E-05	1.00E-07	9.12E-01	5.25E-05	3.62E-02
1.00E-05	5.00E-05	5.00E-07	9.12E-01	7.97E-05	3.30E-02
1.00E-05	5.00E-05	1.00E-06	9.13E-01	7.90E-05	5.05E-02
1.00E-05	5.00E-05	5.00E-06	9.19E-01	6.84E-05	3.08E-02
1.00E-05	5.00E-05	1.00E-05	9.23E-01	9.52E-05	2.04E-02

migration	*origination*	*extinction*	*equilibrium delta*	*std. error*	*equilibrium time (Myr)*
1.00E-05	5.00E-05	5.00E-05	9.53E-01	6.72E-05	3.45E-02
1.00E-05	5.00E-05	1.00E-04	NULL	NULL	NULL
1.00E-05	1.00E-04	1.00E-08	9.53E-01	8.25E-05	3.78E-02
1.00E-05	1.00E-04	5.00E-08	9.54E-01	8.88E-05	2.67E-02
1.00E-05	1.00E-04	1.00E-07	9.54E-01	7.28E-05	5.52E-02
1.00E-05	1.00E-04	5.00E-07	9.53E-01	6.49E-05	3.95E-02
1.00E-05	1.00E-04	1.00E-06	9.53E-01	5.35E-05	3.47E-02
1.00E-05	1.00E-04	5.00E-06	9.54E-01	5.90E-05	1.56E-02
1.00E-05	1.00E-04	1.00E-05	9.56E-01	1.08E-04	3.32E-02
1.00E-05	1.00E-04	5.00E-05	9.36E-01	1.65E-01	2.00E-04
1.00E-05	1.00E-04	1.00E-04	9.74E-01	3.41E-04	5.10E-03
1.00E-04	1.00E-08	1.00E-08	9.49E-04	5.97E-05	1.07E-01
1.00E-04	1.00E-08	5.00E-08	1.22E-03	6.49E-05	6.12E-02
1.00E-04	1.00E-08	1.00E-07	2.74E-03	6.34E-05	9.79E-02
1.00E-04	1.00E-08	5.00E-07	1.07E-02	8.72E-05	6.30E-02
1.00E-04	1.00E-08	1.00E-06	1.95E-02	1.06E-04	7.41E-02
1.00E-04	1.00E-08	5.00E-06	9.41E-02	2.11E-04	5.92E-02
1.00E-04	1.00E-08	1.00E-05	1.68E-01	2.50E-04	4.04E-02
1.00E-04	1.00E-08	5.00E-05	NULL	NULL	NULL
1.00E-04	1.00E-08	1.00E-04	5.04E-01	3.42E-02	1.58E-02
1.00E-04	5.00E-08	1.00E-08	NULL	NULL	NULL
1.00E-04	5.00E-08	5.00E-08	3.45E-03	6.64E-05	6.67E-02
1.00E-04	5.00E-08	1.00E-07	3.40E-03	6.29E-05	6.43E-02
1.00E-04	5.00E-08	5.00E-07	1.32E-02	8.09E-05	5.43E-02
1.00E-04	5.00E-08	1.00E-06	2.12E-02	1.10E-04	6.04E-02
1.00E-04	5.00E-08	5.00E-06	9.16E-02	2.00E-04	4.66E-02
1.00E-04	5.00E-08	1.00E-05	1.74E-01	2.71E-04	4.06E-02
1.00E-04	5.00E-08	5.00E-05	NULL	NULL	NULL
1.00E-04	5.00E-08	1.00E-04	NULL	NULL	NULL
1.00E-04	1.00E-07	1.00E-08	4.37E-03	6.39E-05	9.03E-02
1.00E-04	1.00E-07	5.00E-08	5.84E-03	6.62E-05	6.47E-02
1.00E-04	1.00E-07	1.00E-07	NULL	NULL	NULL
1.00E-04	1.00E-07	5.00E-07	1.51E-02	1.08E-04	5.78E-02
1.00E-04	1.00E-07	1.00E-06	2.51E-02	1.14E-04	4.44E-02
1.00E-04	1.00E-07	5.00E-06	9.39E-02	1.91E-04	6.76E-02
1.00E-04	1.00E-07	1.00E-05	1.84E-01	2.71E-04	5.21E-02
1.00E-04	1.00E-07	5.00E-05	NULL	NULL	NULL
1.00E-04	1.00E-07	1.00E-04	7.65E-01	2.57E-02	5.30E-03
1.00E-04	5.00E-07	1.00E-08	1.96E-02	6.86E-05	5.92E-02
1.00E-04	5.00E-07	5.00E-08	1.90E-02	7.79E-05	4.87E-02
1.00E-04	5.00E-07	1.00E-07	2.17E-02	7.21E-05	5.79E-02
1.00E-04	5.00E-07	5.00E-07	2.87E-02	8.84E-05	8.09E-02
1.00E-04	5.00E-07	1.00E-06	3.94E-02	1.10E-04	6.35E-02
1.00E-04	5.00E-07	5.00E-06	1.10E-01	1.48E-04	5.05E-02
1.00E-04	5.00E-07	1.00E-05	1.88E-01	2.17E-04	3.51E-02
1.00E-04	5.00E-07	5.00E-05	5.35E-01	6.91E-03	1.57E-02
1.00E-04	5.00E-07	1.00E-04	7.12E-01	6.61E-03	1.73E-02
1.00E-04	1.00E-06	1.00E-08	3.69E-02	7.96E-05	5.52E-02
1.00E-04	1.00E-06	5.00E-08	3.78E-02	7.99E-05	5.07E-02
1.00E-04	1.00E-06	1.00E-07	4.11E-02	7.93E-05	5.37E-02
1.00E-04	1.00E-06	5.00E-07	4.74E-02	7.88E-05	7.88E-02
1.00E-04	1.00E-06	1.00E-06	5.62E-02	8.23E-05	4.73E-02
1.00E-04	1.00E-06	5.00E-06	NULL	NULL	NULL

migration	*origination*	*extinction*	*equilibrium delta*	*std. error*	*equilibrium time (Myr)*
1.00E-04	1.00E-06	1.00E-05	1.98E-01	1.43E-04	4.72E-02
1.00E-04	1.00E-06	5.00E-05	5.49E-01	3.11E-03	1.69E-02
1.00E-04	1.00E-06	1.00E-04	NULL	NULL	NULL
1.00E-04	5.00E-06	1.00E-08	1.53E-01	1.65E-04	5.52E-02
1.00E-04	5.00E-06	5.00E-08	1.55E-01	1.28E-04	6.93E-02
1.00E-04	5.00E-06	1.00E-07	1.54E-01	1.28E-04	3.97E-02
1.00E-04	5.00E-06	5.00E-07	1.59E-01	1.19E-04	4.40E-02
1.00E-04	5.00E-06	1.00E-06	1.67E-01	1.22E-04	4.16E-02
1.00E-04	5.00E-06	5.00E-06	2.19E-01	1.16E-04	3.63E-02
1.00E-04	5.00E-06	1.00E-05	2.73E-01	1.51E-04	6.12E-02
1.00E-04	5.00E-06	5.00E-05	5.43E-01	2.20E-03	2.88E-02
1.00E-04	5.00E-06	1.00E-04	NULL	NULL	NULL
1.00E-04	1.00E-05	1.00E-08	2.52E-01	1.63E-04	2.93E-02
1.00E-04	1.00E-05	5.00E-08	2.54E-01	2.09E-04	3.80E-02
1.00E-04	1.00E-05	1.00E-07	2.52E-01	2.64E-04	4.09E-02
1.00E-04	1.00E-05	5.00E-07	2.60E-01	1.77E-04	3.77E-02
1.00E-04	1.00E-05	1.00E-06	2.66E-01	2.39E-04	5.76E-02
1.00E-04	1.00E-05	5.00E-06	3.00E-01	2.26E-04	3.56E-02
1.00E-04	1.00E-05	1.00E-05	3.40E-01	2.31E-04	3.34E-02
1.00E-04	1.00E-05	5.00E-05	NULL	NULL	NULL
1.00E-04	1.00E-05	1.00E-04	6.86E-01	4.84E-03	1.09E-02
1.00E-04	5.00E-05	1.00E-08	5.76E-01	4.73E-04	3.47E-02
1.00E-04	5.00E-05	5.00E-08	5.73E-01	2.90E-04	2.35E-02
1.00E-04	5.00E-05	1.00E-07	5.71E-01	3.77E-04	1.71E-02
1.00E-04	5.00E-05	5.00E-07	5.73E-01	2.63E-04	2.15E-02
1.00E-04	5.00E-05	1.00E-06	5.77E-01	2.82E-04	3.22E-02
1.00E-04	5.00E-05	5.00E-06	5.89E-01	3.07E-04	2.28E-02
1.00E-04	5.00E-05	1.00E-05	6.00E-01	2.29E-04	1.82E-02
1.00E-04	5.00E-05	5.00E-05	6.92E-01	2.41E-04	2.02E-02
1.00E-04	5.00E-05	1.00E-04	7.62E-01	1.52E-04	1.15E-02
1.00E-04	1.00E-04	1.00E-08	7.07E-01	2.80E-04	1.70E-02
1.00E-04	1.00E-04	5.00E-08	7.06E-01	2.89E-04	1.57E-02
1.00E-04	1.00E-04	1.00E-07	7.07E-01	3.44E-04	1.62E-02
1.00E-04	1.00E-04	5.00E-07	7.10E-01	2.69E-04	1.32E-02
1.00E-04	1.00E-04	1.00E-06	7.04E-01	4.26E-04	1.45E-02
1.00E-04	1.00E-04	5.00E-06	7.13E-01	3.93E-04	1.94E-02
1.00E-04	1.00E-04	1.00E-05	7.23E-01	2.58E-04	1.14E-02
1.00E-04	1.00E-04	5.00E-05	7.72E-01	3.59E-04	2.09E-02
1.00E-04	1.00E-04	1.00E-04	8.10E-01	1.80E-04	5.80E-03

Appendix B — The list of Paleobiology Database collections used in the Chapter 2 analyses on Ordovician migration, origination, and extinction rates. The data were downloaded (paleodb.org) on 7 March 2007.

240,241,242,243,247,249,284,336,374,375,1685,1686,1687,1688,1689
1690,1691,1692,1693,1694,1695,1696,1697,1698,1699,1700,1701,1702,1703,1704
1705,1706,1707,1708,1709,1710,1711,1892,1893,1894,1895,1896,1897,1898,1902
1905,1908,1913,1916,1918,1919,1921,1922,1923,1924,1925,1926,1927,1928,1929
1930,1931,1932,1933,1934,1935,1936,1937,1938,1939,1940,1941,1942,1943,1944
1945,1946,1947,1948,1949,1950,1951,1952,1953,1954,1955,1956,1957,1958,1960
1961,1962,1963,1964,1965,1966,1967,1968,1969,1970,1971,1972,1973,1974,1975
1976,1977,1978,1979,2687,2693,2694,2700,2701,2702,2703,2731,2732,2768,2866
2868,2869,2870,2871,2872,2873,2874,2875,2876,2877,2878,2879,2880,2881,2882
2883,2884,2885,2886,2887,2888,2889,2890,2891,2892,2893,2894,2979,2980,2981
2990,2993,3000,3001,3002,3003,3022,3023,3024,3026,3032,3034,3035,3036,3037
3038,3039,3040,3041,3042,3043,3044,3045,3046,3047,3048,3050,3051,3052,3053
3054,3055,3056,3057,3058,3059,3060,3061,3062,3063,3064,3065,3066,3067,3068
3069,3106,3134,3136,3137,3147,3149,3151,3159,3160,3162,3163,3164,3165,3167
3168,3170,3171,3172,3173,3174,3176,3178,3185,3186,3187,3188,3189,3190,3191
3192,3193,3200,3201,3202,3203,3204,3205,3206,3207,3219,3221,3222,3224,3225
3227,3228,3230,3231,3233,3234,3236,3238,3239,3240,3281,3282,3340,3341,3342
3343,3344,3346,3348,3349,3350,3351,3352,3450,3453,3459,3461,3462,3463,3464
3465,3466,3467,3468,3469,3470,3471,3472,3473,3495,3496,3497,3498,3499,3500
3501,3502,3976,4686,4689,4690,4708,4709,4710,4711,4712,4713,4714,4715,4716
4718,4719,4720,4721,4722,4723,4724,4726,4727,4728,4729,4730,4735,4737,4738
4745,4746,4749,4750,4751,4753,4754,4755,4756,4757,4758,4759,4760,4761,4762
4763,4764,4765,4766,4767,4769,4770,4772,4773,4774,4775,4776,4927,4928,4929
4930,4931,4932,4933,4934,4935,4937,4938,4939,4940,4941,4942,4943,4944,4945
4946,4947,4948,4949,4950,4951,4952,4953,4954,4955,4956,4957,4958,4959,4960
4961,4962,4963,4964,4965,4966,4967,4968,4969,4970,4972,4973,4974,4975,4976
4977,4978,4979,4980,4981,4982,4983,4984,4985,4986,4987,4988,4989,4990,4991
4992,4993,4994,4995,4996,4997,4998,4999,5000,5001,5002,5003,5004,5005,5006
5007,5008,5009,5010,5011,5012,5013,5014,5015,5016,5017,5018,5019,5021,5022
5023,5024,5025,5026,5027,5028,5029,5030,5031,5032,5033,5034,5035,5036,5037
5038,5039,5040,5041,5042,5043,5044,5045,5046,5047,5048,5049,5050,5051,5052
5053,5054,5055,5056,5057,5058,5059,5060,5061,5062,5063,5064,5065,5066,5067
5068,5069,5070,5071,5072,5073,5074,5075,5076,5077,5078,5079,5080,5081,5082
5083,5084,5085,5086,5087,5088,5089,5090,5091,5092,5093,5094,5095,5096,5097
5098,5099,5100,5101,5102,5103,5104,5105,5106,5107,5108,5109,5110,5111,5112
5131,5133,5135,5137,5141,5142,5143,5145,5146,5147,5148,5149,5150,5151,5152
5153,5154,5156,5250,5251,5252,5253,5254,5255,5256,5257,5258,5259,5260,5262
5263,5264,5265,5266,5267,5268,5269,5270,5271,5272,5273,5274,5275,5276,5277
5278,5279,5280,5281,5282,5283,5336,5338,5401,5402,5403,5404,5405,5406,5407
5408,5409,5410,5411,5412,5415,5416,5417,5418,5419,5420,5421,5422,5423,5424
5425,5426,5427,5428,5429,5430,5431,5432,5433,5434,5435,5784,5785,6870,6871
7250,7254,7255,7257,7263,7264,7265,7266,7267,7268,7269,7270,7271,7273,7278
7280,7281,7283,7290,7291,7292,7333,7340,7341,7342,7343,7344,7345,7346,7347
7350,7351,7352,7353,7354,7355,7357,7358,7359,7360,7361,7362,7363,7364,7366
7367,7368,7369,7371,7382,7384,7385,7386,7387,7388,7635,7636,7637,7638,7639
7640,7644,7645,7646,7647,7648,7649,7650,7651,7652,7653,7654,7655,7656,7659
7660,7661,7662,7663,7664,7665,7667,7669,7670,7671,7672,7673,7675,7678,7679
7680,7681,7688,7689,7690,7691,7692,7693,7694,7695,7697,7698,7700,7702,7703
7712,7714,7715,7716,7717,7718,7719,7720,7721,7722,7723,7724,7725,7726,7727
7728,7729,7732,7733,7734,7735,7736,7741,7742,7743,7744,7747,7749,7750,7758
7759,7765,7766,7767,7768,7769,7773,7774,7775,7776,7779,7780,7781,7792,7794
7795,7802,7803,7804,7805,7807,7808,7809,7810,7815,7817,7828,7829,7830,7831
7832,7833,7834,7835,7836,7837,7838,7839,7840,7841,7842,7843,7844,7845,7846
7847,7848,7854,7855,7856,7858,7859,7860,7861,7862,7863,7872,7875,7876,7878

7879,7880,7881,7882,7883,7884,7885,7886,7887,7917,7918,7921,7922,7923,7924
7925,7927,7929,7933,7935,7938,7942,7943,7944,7949,7950,7951,7955,7956,7957
7958,7960,7961,7962,7963,7964,7966,7967,7968,7969,7972,7975,7977,7978,7979
7980,7981,7982,7983,7984,7985,8005,8028,8086,8087,8294,8530,8538,8539,8540
8662,8751,8870,8872,8933,8934,8935,8947,8948,8949,8950,8951,8952,8953,8954
8955,8956,8957,8958,8976,8977,9042,9043,9044,9045,9046,9047,9048,9049,9050
9051,9052,9053,9054,9055,9056,9057,9059,9060,9136,9137,9143,9144,9145,9146
9147,9148,9149,9150,9151,9152,9153,9154,9155,9156,9157,9158,9159,9160,9161
9162,9163,9164,9165,9166,9167,9168,9184,9185,9186,9187,9188,9189,9190,9191
9192,9194,9195,9196,9197,9198,9199,9200,9201,9202,9203,9204,9205,9206,9207
9208,9209,9211,9212,9586,9618,9619,9625,9711,9712,9713,9714,9715,9716,9717
9723,9724,9725,9726,9727,9728,9729,9730,9731,9732,9733,9734,9735,9736,9737
9738,9739,9740,9741,9742,9743,9744,9745,9746,9747,9748,9749,9750,9751,9752
9753,9754,9756,9757,9758,9759,9763,9765,9766,9767,9768,9769,9770,9771,9773
9774,9775,9776,9779,9889,9890,10775,10776,10777,10897,10899,10900,10901,10902,10903
10904,10905,10906,10908,10909,10910,10911,10912,10913,10914,10915,10916,10917,10918,10919
10920,10921,10922,10923,10924,10925,10926,10927,10928,10929,10930,10932,10933,10934,10935
10936,10937,10938,10943,10944,10945,10946,10947,10948,10949,10950,10951,10952,10954,10955
10956,10957,10958,10959,10960,10961,10962,10985,10986,10987,10988,10989,10990,10991,10992
10993,10994,10995,10996,10998,10999,11001,11002,11003,11005,11007,11010,11011,11012,11014
11019,11020,11021,11022,11023,11024,11027,11028,11031,11033,11034,11036,11037,11038,11039
11040,11044,11045,11046,11047,11048,11049,11050,11052,11059,11060,11061,11062,11063,11064
11065,11066,11067,11068,11069,11070,11071,11072,11074,11075,11076,11077,11078,11079,11080
11081,11317,11353,11385,11391,11407,11408,11411,11412,11413,11416,11417,11418,11422,11423
11424,11437,11439,11554,11555,11556,11557,11689,11690,11702,11703,11706,11707,11723,11724
11725,11735,11736,11737,11822,11845,11927,11928,11930,11934,11936,11937,11938,12058,12059
12060,12061,12062,12063,12070,12145,12146,12180,12181,12182,12282,12295,12296,12297,12298
12582,12583,13204,13261,13262,13290,13329,13605,13638,13806,13807,13808,13814,14229,14232
14238,14241,20969,20996,22952,22954,23099,23100,23276,23277,23278,23279,23280,23281,23282
24105,24313,24399,25085,25252,25735,25736,25744,25788,25789,25815,25846,25851,25869,26027
26028,26029,26030,26031,26032,26033,26036,26037,26038,26039,26040,26043,26044,26045,26046
26070,26071,26078,26307,26308,26309,26311,26312,26313,26314,26315,26316,26317,26331,26333
26711,26777,27323,27329,27499,27500,27772,27797,27888,34843,37193,37639,37641,38037,38038
39399,39401,40018,42637,42735,44050,44746,45286,45945,45986,45987,48728,48729,48730,48731
48732,48733,48734,48735,48736,48737,48738,48739,48740,48741,48742,48743,48744,48745,48746
48747,48748,48749,48750,48751,48752,48753,48754,48755,48756,48757,48758,48759,48761,48762
48763,48764,48765,48766,48767,48768,48769,48770,48771,48772,48773,48774,48775,48776,48777
48778,48779,48780,48781,48782,48783,48784,48785,48786,48787,48788,48789,48790,48791,48792
48793,48794,48795,48796,48797,48798,48799,48800,48801,48802,48803,48804,48805,48806,48807
48808,48809,48810,48811,48812,48813,48814,48815,48816,48817,48818,48819,48820,48821,49049
49050,49192,49193,49194,49195,49196,49210,49303,49341,49345,49346,49347,49348,49349,49350
49351,49352,49579,49580,49581,49583,49584,49600,49601,49602,49603,49604,49635,49638,49639
49827,49828,49829,49961,49962,50060,50062,50063,50065,50131,50132,50134,50135,50142,50143
50144,50145,50146,50148,50152,50153,50154,50156,50158,50159,50160,50162,50164,50165,50202
50203,50204,50205,50206,50207,50261,50263,50264,50275,50277,50278,50281,50282,50283,50285
50286,50287,50288,50289,50290,50592,50595,50599,50600,50601,50602,50603,50605,50606,50607
50608,50609,50610,50611,50612,50613,50614,50615,50616,50617,50618,50619,50620,50621,50622
50623,50624,50625,50626,50627,50628,50629,50630,50631,50632,50633,50634,50635,50636,50637
50638,50639,50640,50641,50642,50643,50644,50645,50646,50647,50648,50649,50650,50651,50652
50653,50654,50655,50656,50657,51515,51519,51520,51522,51523,51524,51525,51528,51530,51531
51533,51536,51537,51539,51541,51542,51543,52737,52739,54076,54077,54078,54084,54085,54086
54087,54088,54090,54091,54092,54093,54094,54096,54119,54120,54121,54122,54135,54180,54187
54235,54236,55210,55211,55213,55215,55216,55217,55220,55221,55222,55223,55224,55225,55226
55231,55232,55233,55234,55240,55241,55243,55277,55278,55279,55280,55281,55282,55284,55285
55300,55301,55302,55303,55304,55305,55307,55308,55310,55311,55312,55313,55315,55344,55345
55711,55712,55714,55715,55716,56134,56140,56145,56146,56147,56150,56151,56152,56153,56154
56180,56181,56182,56183,56184,56185,56191,56194,56195,56200,56201,56203,56204,56205,56206
56207,56208,56209,56210,56211,56212,56213,56214,56215,56394,56395,56396,56397,56433,56461

56464,56465,56466,56467,56468,56470,56471,56472,56473,56475,56476,56487,56489,56490,56491
56492,56493,56494,56495,56496,56497,56516,56517,56642,56643,56661,57172,57173,57210,57211
57212,60037,60038,61382,61383,61386,61387,61389,61779,61782,61783,61785,61786,61788,61789
61790,61791,61792,61796,61797,61798,61799,61800,61801,61802,61803,62047,62048,62064,62065
62066,62067,62068,62069,62070,62071,62075,62076,62077,62078,62079,62080,62081,62082,62083
62084,62085,62086,62087,62088,62089,62090,62091,62092,62093,62094,62095,62099,62100,62101
62102,62103,62104,62105,62106,62107,62108,62109,62110,62111,62112,62113,62114,62115,62116
62117,62118,62119,62120,62121,62122,62123,62124,62184,62199,62201,62202,62204,62205,62223
62224,62226,62274,62275,62277,62278,62280,62281,62336,62337,62338,62339,62340,62342,62345
62346,63097,63297,63445,63558,63559,63625,63660,63667,63675,63728,63767,63773,63786,63810
63839,63840,63842,63843,63846,63848,63926,63927,63928,63929,63931,63932,63933,63965,64038
64041,64043,64047,64048,64049,64050,64051,64052,64164,64165,64166,64167,64168,64169,64170
64224,64225,64226,64227,64228,64229,64230,64231,64232,64233,64234,64235,64340,64403,64404
64416,64417,64418,64419,64420,64421,64422,64423,64424,64425,64426,64475,64476,64477,64478
64479,64480,64482,64493,64496,64502,64508,64516,64522,64543,64546,64548,64550,64551,64552
64555,64558,64561,64563,64596,64598,64601,64609,64612,64615,64637,64666,64686,64687,64778
64779,64780,64782,64783,64784,64796,64797,64798,64799,64800,64801,64802,64803,64805,64812
66186,66187,66188,66189,66196,66205,66258,66259,66260,66261,66802,66803,66804,66805,66806
66807,66808,66820,66821,66822,66823,66824,66825,66826,66827,66828,66829,66832,66837,66838
66839,66840,66841,66842,66843,66844,66845,66846,66847,66848,66849,66850,66851,66852,66853
66854,66855,66856,66857,66858,66859,66860,66861,66863,66864,66865,66866,66867,66868,66869
66870,66871,66872,66873,66874,66889,66891,66929,67297,69026,69027,69028,69030,69031,69035
69036,69041,69096,69097,69196,69215,69217,69218,69220,69221,69222,69223,69224,69225,69228
69229,69230,69231,69232,69233,69234,69235,69236,69240,69241,69261

Appendix C — C code for the migration model presented in Chapter 2.

```
#include <stdio.h>
#include <stdlib.h>
#include <math.h>
#include "statistics.h"
#include "fileUtilities.h"
#include "randomNumbers.h"
#include "diversityMetrics.h"

#define MAXNUMBERTAXA 1000000

int main (void)
{
    FILE *fpDataIn;
    FILE *fpDataOut;
    FILE *fpDataCreate;
     //FILE *fpFinalTaxonList;

    double extinctionProb;
    double originationProb;
    double migrationProb;
     double migrationValues[5];
     double originationValues[9];
     double extinctionValues[9];
     long nMig = 5;
     long nOrig = 10;
     long nExt = 10;
     long mig;
     long orig;
     long ext;
    long timeSteps;
    long i;
     long n;
    long t;
     long numberOfRegions;
    long numberOfTaxa;
    long initialNumberOfTaxa;
    long *region1;
    long *region2;
    long *region3;
    long globalRichness;
    long richnessRegion1;
    long richnessRegion2;
    long richnessRegion3;
     double averageAlpha;
     double globalBeta;
     long regionalBeta12;
     long regionalBeta13;
     long regionalBeta23;
    double jaccard12;
    double jaccard13;
    double jaccard23;
    double averageJaccard;
    double evolFate[3];
     double nonZero1;
     double nonZero2;
     double nonZero3;
```

```
    double migration;

     migrationValues[0] = (0.000001);
     migrationValues[1] = (0.00001);
     migrationValues[2] = (0.0001);
     migrationValues[3] = (0.001);
     migrationValues[4] = (0.01);

     originationValues[0] = extinctionValues[0] =  0.000001;
     originationValues[1] = extinctionValues[1] =  0.00005;
     originationValues[2] = extinctionValues[2] =  0.00001;
     originationValues[3] = extinctionValues[3] =  0.0005;
     originationValues[4] = extinctionValues[4] =  0.0001;
     originationValues[5] = extinctionValues[5] =  0.005;
     originationValues[6] = extinctionValues[6] =  0.001;
     originationValues[7] = extinctionValues[7] =  0.05;
     originationValues[8] = extinctionValues[8] =  0.01;

     timeSteps = 10000;   //each time step is 10,000 years
    numberOfRegions = 3;

     // Change file name on lines 81 & 163

     // create output file and write column names
     fpDataCreate  = fopen("migrationModelResults6Jan07.txt", "w");  // also change file name on
line 152
     fprintf(fpDataCreate, "Migration\tOrigination\tExtinction\tRichness\tGlobal_Alpha
\tGlobal_Beta\tRegion1\tRegion2\tRegion3\tregionalBeta12\tregionalBeta13\tregionalBeta23
\tjaccard12\tjaccard13\tjaccard23\tAverage_Jaccard\n");
        fclose(fpDataCreate);

     // print labels to the screen
     printf("Migration\tOrigination\tExtinction\tRichness\tGlobal Alpha\tGlobal Beta\tRegion1
\tRegion2\tRegion3\tregionalBeta12\tregionalBeta13\tregionalBeta23\tjaccard12\tjaccard13
\tjaccard23\tAverage Jaccard\n");

     // loop through all combinations of origination, extinction and migration
     for (mig = 0; mig < nMig; ++mig)
        {
     for (orig = 0; orig < nOrig; ++orig)
        {
     for (ext = 0; ext < nExt; ++ext)
        {
     breakPoint:
          if (ext >= nExt)
               break;
    migrationProb  =  migrationValues[mig];
    originationProb = originationValues[orig];
    extinctionProb  = extinctionValues[ext];

     // Check validity of probabilities
     if (extinctionProb+originationProb+migrationProb > 1)
               {
          printf("Error: Sum of Origination, Extinction and Migration probabilities is greater
than 1.\nThis is BAD MATH!!\n\nPROGRAM TERMINATED\n");
          break;
               }

    numberOfTaxa = 100;  //this is TOTAL at time = 0, not per region
```

```
	InitRandNum();

    //generate initial random faunal list
     writeFaunalList(numberOfRegions, numberOfTaxa);

    // setting aside memory for data
    region1 = (long *)malloc(MAXNUMBERTAXA * sizeof(long));
    checkForMemoryError(region1);
    region2 = (long *)malloc(MAXNUMBERTAXA * sizeof(long));
    checkForMemoryError(region2);
    region3 = (long *)malloc(MAXNUMBERTAXA * sizeof(long));
    checkForMemoryError(region3);

    // initalizing regions
    for (i=0; i<MAXNUMBERTAXA; ++i)
        {
        region1[i] = 0;
        region2[i] = 0;
        region3[i] = 0;
        }

    // read in initial data
    fpDataIn = fopen("dataFile.txt", "r");
    checkForFileError(fpDataIn);
    for (i=0; i<numberOfTaxa; ++i)
        fscanf(fpDataIn, "%ld%ld%ld", &region1[i], &region2[i], &region3[i]);
    fclose(fpDataIn);

    //calculate stastics for initial data
    //calculate global richness
    globalRichness = 0;
    for (i=0; i<numberOfTaxa; ++i)
        if (region1[i] == 1 || region2[i] == 1 || region3[i] == 1)
            ++globalRichness;

    // calculate diversity values
    richnessRegion1 = richness(region1, numberOfTaxa);
    richnessRegion2 = richness(region2, numberOfTaxa);
    richnessRegion3 = richness(region3, numberOfTaxa);
     averageAlpha = ((double)richnessRegion1 + (double)richnessRegion2 + (double)
richnessRegion3)/(double)numberOfRegions;
     globalBeta = (double)globalRichness-averageAlpha;
     regionalBeta12 = abs(richnessRegion1 - richnessRegion2);
     regionalBeta13 = abs(richnessRegion1 - richnessRegion3);
     regionalBeta23 = abs(richnessRegion2 - richnessRegion3);

    //calculate jaccard
    jaccard12 = jaccard(region1, region2, numberOfTaxa);
    jaccard13 = jaccard(region1, region3, numberOfTaxa);
    jaccard23 = jaccard(region2, region3, numberOfTaxa);
    averageJaccard = (jaccard12 + jaccard13 + jaccard23)/(double)numberOfRegions;

    // print first run to screen and file
    // write to file
     fpDataOut  = fopen("migrationModelResults6Jan07.txt", "a");
     fprintf(fpDataOut, "%f\t%f\t%f\t%ld\t%f\t%f\t%ld\t%ld\t%ld\t%ld\t%ld\t%ld\t%f\t%f\t%f\t%f
\n", migrationProb, originationProb, extinctionProb, globalRichness, averageAlpha, globalBeta,
richnessRegion1, richnessRegion2, richnessRegion3, regionalBeta12, regionalBeta13,
regionalBeta23, jaccard12, jaccard13, jaccard23, averageJaccard);
```

```
    // write to screen
    printf("%f\t%f\t%f\t%ld\t%f\t%f\t%ld\t%ld\t%ld\t%ld\t%ld\t%ld\t%f\t%f\t%f\t%f\n",
migrationProb, originationProb, extinctionProb, globalRichness, averageAlpha, globalBeta,
richnessRegion1, richnessRegion2, richnessRegion3, regionalBeta12, regionalBeta13,
regionalBeta23, jaccard12, jaccard13, jaccard23, averageJaccard);
    fflush(stdout);

    for (t=0; t<timeSteps; ++t)
        {
        initialNumberOfTaxa = numberOfTaxa;
        fflush(stdout);
        for (i=0; i<initialNumberOfTaxa; ++i)
            {
               // assign random step
            for (n=0; n<3; ++n)
                              {
                evolFate[n] = RandNum();
                    if (evolFate[n] == 0)
                                     {
                              nonZero1 = RandNum();
                              nonZero2 = RandNum();
                              nonZero3 = RandNum();
                              evolFate[n] = (nonZero1+nonZero2+nonZero3)/3;
                                     }
                              }

            // extnction
            if (region1[i] > 0 && evolFate[0] <= extinctionProb)
                region1[i] = 0;
            if (region2[i] > 0 && evolFate[1] <= extinctionProb)
                region2[i] = 0;
            if (region3[i] > 0 && evolFate[2] <= extinctionProb)
                region3[i] = 0;

            // origination
            if (region1[i] > 0 && evolFate[0] <= extinctionProb+originationProb && evolFate[0] >
extinctionProb)
                {
                              ++numberOfTaxa;
                    if (numberOfTaxa > MAXNUMBERTAXA-1)
                    {
                         fclose(fpDataOut);
                                     ++ext;
                         goto breakPoint;
                    //printf("ERROR:  the array for Region 2 has overwritten its bounds\nProgram
Terminated\n");
                    //exit(1);
                    }
                region1[numberOfTaxa] = 1;
                }
            if (region2[i] > 0 && evolFate[1] <= extinctionProb+originationProb && evolFate[1] >
extinctionProb)
                {
                ++numberOfTaxa;
                if (numberOfTaxa > MAXNUMBERTAXA-1)
                    {
                                     fclose(fpDataOut);
                         ++ext;
```

```
                         goto breakPoint;
                    //printf("ERROR:  the array for Region 2 has overwritten its bounds\nProgram
Terminated\n");
                    //exit(1);
                    }
                region2[numberOfTaxa] = 1;
                }
            if (region3[i] > 0 && evolFate[2] <= extinctionProb+originationProb && evolFate[2] >
extinctionProb)
                {
                ++numberOfTaxa;
                if (numberOfTaxa > MAXNUMBERTAXA-1)
                    {
                                      fclose(fpDataOut);
                         ++ext;
                         goto breakPoint;
                    //printf("ERROR:  the array for Region 3 has overwritten its bounds\nProgram
Terminated\n");
                    //exit(1);
                    }
                region3[numberOfTaxa] = 1;
                }


            //  migration
            if (region1[i] > 0 && evolFate[0] <= extinctionProb+originationProb+migrationProb &&
evolFate[0] > extinctionProb+originationProb)
                {
                migration = RandNum();
                    if (migration == 0)
                                      {
                         nonZero1 = RandNum();
                         nonZero2 = RandNum();
                         nonZero3 = RandNum();
                         migration = (nonZero1+nonZero2+nonZero3)/3;
                                      }
                if (migration <= 0.5)
                    region2[i] = 1;
                else
                    region3[i] = 1;
                }
            if (region2[i] > 0 && evolFate[1] <= extinctionProb+originationProb+migrationProb &&
evolFate[1] > extinctionProb+originationProb)
                {
                migration = RandNum();
                if (migration == 0)
                                      {
                                      nonZero1 = RandNum();
                         nonZero2 = RandNum();
                         nonZero3 = RandNum();
                         migration = (nonZero1+nonZero2+nonZero3)/3;
                                      }
                    if (migration <= 0.5)
                    region1[i] = 1;
                else
                    region3[i] = 1;
                }
            if (region3[i] > 0 && evolFate[2] <= extinctionProb+originationProb+migrationProb &&
evolFate[2] > extinctionProb+originationProb)
```

```
                {
                              migration = RandNum();
                if (migration == 0)
                                     {
                                     nonZero1 = RandNum();
                         nonZero2 = RandNum();
                         nonZero3 = RandNum();
                         migration = (nonZero1+nonZero2+nonZero3)/3;
                                     }
                    if (migration <= 0.5)
                    region1[i] = 1;
                else
                    region2[i] = 1;
                }
            }

        //calculate global richness
        globalRichness = 0;
        for (i=0; i<numberOfTaxa; ++i)
            if (region1[i] == 1 || region2[i] == 1 || region3[i] == 1)
                ++globalRichness;

        // calculate diversity values
        richnessRegion1 = richness(region1, numberOfTaxa);
        richnessRegion2 = richness(region2, numberOfTaxa);
        richnessRegion3 = richness(region3, numberOfTaxa);
          averageAlpha = ((double)richnessRegion1 + (double)richnessRegion2 + (double)
richnessRegion3)/(double)numberOfRegions;
          globalBeta = (double)globalRichness - averageAlpha;
          regionalBeta12 = abs(richnessRegion1 - richnessRegion2);
          regionalBeta13 = abs(richnessRegion1 - richnessRegion3);
          regionalBeta23 = abs(richnessRegion2 - richnessRegion3);

        //calculate jaccard
        jaccard12 = jaccard(region1, region2, numberOfTaxa);
        jaccard13 = jaccard(region1, region3, numberOfTaxa);
        jaccard23 = jaccard(region2, region3, numberOfTaxa);
        averageJaccard = (jaccard12 + jaccard13 + jaccard23)/(double)numberOfRegions;

        // write to screen
        printf("%f\t%f\t%f\t%ld\t%f\t%f\t%ld\t%ld\t%ld\t%ld\t%ld\t%ld\t%f\t%f\t%f\t%f\t%ld\n",
migrationProb, originationProb, extinctionProb, globalRichness, averageAlpha, globalBeta,
richnessRegion1, richnessRegion2, richnessRegion3, regionalBeta12, regionalBeta13,
regionalBeta23, jaccard12, jaccard13, jaccard23, averageJaccard, t);
               fflush(stdout);

        // write to file
        fprintf(fpDataOut, "%f\t%f\t%f\t%ld\t%f\t%f\t%ld\t%ld\t%ld\t%ld\t%ld\t%ld\t%f\t%f\t%f\t%f
\n", migrationProb, originationProb, extinctionProb, globalRichness, averageAlpha, globalBeta,
richnessRegion1, richnessRegion2, richnessRegion3, regionalBeta12, regionalBeta13,
regionalBeta23, jaccard12, jaccard13, jaccard23, averageJaccard);
        if (globalRichness == 0 || numberOfTaxa == (MAXNUMBERTAXA-2))
                      {
                      fclose(fpDataOut);
               break;
                      }
          }

     // empty memory to use in next iteration
```

```
        free(region1);
        free(region2);
      free(region3);

    fclose(fpDataOut);
}}}
return 0;
}


########## code for my diversity metrics

#include <stdio.h>
#include <stdlib.h>
#include <math.h>
#include "diversityMetrics.h"

double jaccard(long taxaRegion1[], long taxaRegion2[], long numberOfTaxa)
{
    long richnessRegion1;
    long richnessRegion2;
    long taxaInCommon;
    long i;
    double jaccardCoeff;

    // calculate the number of eaxa in each region
    richnessRegion1 = richness(taxaRegion1, numberOfTaxa);
    richnessRegion2 = richness(taxaRegion2, numberOfTaxa);

    // calculate number of taxa in common
    taxaInCommon = 0;
    for (i=0; i<numberOfTaxa; ++i)
        if (taxaRegion1[i] == 1 && taxaRegion2[i] == 1)
            ++taxaInCommon;

    // calculate Jaccard Coefficient
     if (richnessRegion1 == 0 && richnessRegion2 == 0)
          jaccardCoeff = 0;
     else
          jaccardCoeff = (double)taxaInCommon/((double)(richnessRegion1 + richnessRegion2 -
taxaInCommon));

    return jaccardCoeff;
}

long richness(long taxa[], long numberOfTaxa)
{
    long richness;
    long i;

    richness = 0;
    for (i=0; i<numberOfTaxa; ++i)
        if (taxa[i] == 1)
            ++richness;

    return richness;
}
```

Appendix D — R code used in Chapter 2 analyses

```
##############################
#####  Format the data from the Paleobiology Database
##############################

setwd("/Users/noelheim/Documents/Papers/MigrationModel/PBDB_7March07/")

t0 <- Sys.time()

# read in raw output matrix from PBDB
      # first columns are genus resolution & genus name
      # last cols are class, order and family
      # rest of columns are collection numbers (preceeded by X)
      # rows at end are collection info
x <- read.csv(file="NHeim-matrix.csv", header=TRUE)
y <- x[x$genus_reso=="",-1]

collectionInfo <- t(x[grep("collections.", x[,1]),-(grep("_", colnames(x)))])
colnames(collectionInfo) <- x[grep("collections.", x[,1]),1]
remove(x)

# find column with genus names
yNames <- colnames(y)
for (i in 1:ncol(y)) {
      if (yNames[i] == "genus_name") {
            break
      }
}
genusCol <- i

yColNames <- colnames(y)
yCols <- grep("_", yColNames)
taxonInfo <- y[,c(yCols)]
#rownames(taxonInfo) <- y[, genusCol]

# convert faunal data to binary instead of "X"
z <- y[,-c(yCols)]
faunal <- matrix(1,nrow=nrow(z), ncol=ncol(z))
for(i in 1:nrow(z)) {
      for(j in 1:ncol(z)) {
            if(z[i,j] == "") {
                  faunal[i,j] <- 0
            }
      }
}
remove(z)

# merge rows of the same genus
uniqueGenera <- unique(y[,genusCol])

faunal2 <- matrix(nrow=length(uniqueGenera), ncol=ncol(faunal))
for (i in 1:nrow(faunal2)) {
```

```
      rowsToGroup <- grep(uniqueGenera[i], y[,genusCol])
      if (length(rowsToGroup) > 1) {
            faunal2[i,] <- abundance2occurrence(colSums(faunal[c
(rowsToGroup),]))
      } else {
            faunal2[i,] <- abundance2occurrence(faunal[rowsToGroup,])
      }
}

faunalData <- t(faunal2)
rownames(faunalData)  <- rownames(collectionInfo)
colnames(faunalData) <- uniqueGenera
remove(y, faunal, faunal2)

t1 <- Sys.time()
difftime(t1, t0)

# save the output

save(faunalData, file="fauna")
save(taxonInfo, file="taxa")
save(collectionInfo, file="collections")

remove(faunalData, taxonInfo, collectionInfo)

t1 <- Sys.time()
difftime(t1, t0)
```

```
##############################
#####  Subsample the data so that rates can be calculated
##############################

setwd("/Users/noelheim/Documents/Papers/MigrationModel/PBDB_7March07")

t0 <- Sys.time()

load("fauna")
load("taxa")
load("collections")

saveFiles <- TRUE

nCollections <- nrow(fauna)
nGenera <- ncol(fauna)

# subset by time interval & Paleocontinent
	# Laurentia 		=  101 102 104 106 108 109 123 128 135 (USA, 
Canada, Mexico, Greenland)
	# South China 		=  611

	# columns of faunna = collections
	# paleocontinent is row 2 of collections data frame
	# stage is row 7 of collections data frame
	# remove empty collections from each

# variable collumns
plate <- grep("collections.tectonic_plate_id", colnames(collectionInfo))
timeBin <- grep("collections.10mybin", colnames(collectionInfo))


bins <- c("Ordovician 1",  "Ordovician 2", "Ordovician 3", "Ordovician 4", 
"Ordovician 5")
nBins <- length(bins)
global <- list()
global.occurrences <- vector(length=nBins, mode="numeric")
global.diversity <- vector(length=nBins, mode="numeric")

laurentia <- list()
southChina <- list()
other <- list()

laurentia.occurrences <- vector(length=nBins, mode="numeric")
southChina.occurrences <- vector(length=nBins, mode="numeric")
other.occurrences <- vector(length=nBins, mode="numeric")

laurentia.diversity <- vector(length=nBins, mode="numeric")
southChina.diversity <- vector(length=nBins, mode="numeric")
other.diversity <- vector(length=nBins, mode="numeric")

for (i in 1:nBins) {
	# global data by time bins
	global[[i]] <- fauna[collectionInfo[,timeBin] == bins[i], ]
```

```
	global.occurrences[i] <- sum(colSums(global[[i]]))
	global.diversity[i] <- length(colSums(global[[i]])[colSums(global[[i]])
>=1])

	# contnental data by time bins
	laurentia[[i]] <- fauna[collectionInfo[,timeBin] == bins[i] &
collectionInfo[,plate] >= 101 & collectionInfo[,plate] <= 135, ]
	southChina[[i]] <- fauna[collectionInfo[,timeBin] == bins[i] &
collectionInfo[,plate] == 611, ]
	other[[i]] <- fauna[collectionInfo[,timeBin] == bins[i] &
collectionInfo[,plate] != 611 & (collectionInfo[,plate] < 101 |
collectionInfo[,plate] > 135), ]

	laurentia.occurrences[i] <- sum(colSums(laurentia[[i]]))
	southChina.occurrences[i] <- sum(colSums(southChina[[i]]))
	other.occurrences[i] <- sum(colSums(other[[i]]))

	laurentia.diversity[i] <- length(colSums(laurentia[[i]])[colSums
(laurentia[[i]])>=1])
	southChina.diversity[i] <- length(colSums(southChina[[i]])[colSums
(southChina[[i]])>=1])
	other.diversity[i] <- length(colSums(other[[i]])[colSums(other[[i]])
>=1])
}

########## SUBSAMPLED GLOBAL RICHNESS ##########
# subsample global richness using UW method (Bush et al. 2004)
# subsample collections (up to sampling level) and tabulate unique genera

# find time bin with minimum number of collections
N <- vector(mode="numeric")
for (i in 1:nBins) {
	N[i] <- nrow(global[[i]])
}
n <- trunc(min(N)/10)*10
print(n)

iterations <- 100

global.subsample <- matrix(nrow=4, ncol=nBins,
	dimnames=list(c("meanRichness", "stdevRichness", "meanOccurrences",
"stdevOccurrences"), bins))
globalSubsampleData <- list()

for (i in 1:nBins) {
	richness <- vector(mode="numeric")
	occurrences <- vector(mode="numeric")
	globalSubsample <- list()
	for (j in 1:iterations) {
		randomNumbers <- runif(nrow(global[[i]]))
		rowNumbers <- seq(from=1, to=nrow(global[[i]]), by=1)
		A <- cbind(randomNumbers, rowNumbers)
		subsampledRows <- A[c(order(A[,1])),2]
		subsample <- global[[i]][subsampledRows[1:n],]
```

```
			richness[j] <- sum(abundance2occurrence(colSums(subsample)))
			occurrences[j] <- sum(rowSums(subsample))
			globalSubsample[[j]] <- subsample
		}
		global.subsample[1,i] <- mean(richness)
		global.subsample[2,i] <- sd(richness)
		global.subsample[3,i] <- mean(occurrences)
		global.subsample[4,i] <- sd(occurrences)
		globalSubsampleData[[i]] <- globalSubsample
}

# calculate 95% CI and plot
degrees.freedom <- iterations-1
alpha <- 0.05
t.crit <- qt(p=(alpha/2), df=degrees.freedom)
stdevDiversity <- global.subsample[2,]

CI.plus <- global.subsample[1,] + t.crit * stdevDiversity / sqrt(iterations)
CI.minus <- global.subsample[1,] - t.crit * stdevDiversity / sqrt(iterations)

polyX <- c(1:nBins, nBins:1)
polyY <- c(CI.minus, rev(CI.plus))

quartz(height=11, width=11)
plot(global.subsample[1,], xaxt="n", main="Global Richness", ylim=c(0,500),
xlab="Time Bin", ylab="Number of Genera", type="n", pch=16)
polygon(polyX, polyY, col="lightgray", border=NA)
points(global.subsample[1,], type="b", pch=16)
axis(side=1, at=c(1:(nBins)), labels=c("O1", "O2", "O3", "O4", "O5"))

if (saveFiles == TRUE) {
		save(global.subsample, file="globalSubsampleUW")
		save(globalSubsampleData, file="globalSubsampleDataUW")
		remove(globalSubsampleData)
}



########## SUBSAMPLED CONTINENTAL RICHNESS ##########

# find time bin with minimum number of collections
N.laurentia <- vector(mode="numeric")
N.southChina <- vector(mode="numeric")
N.other <- vector(mode="numeric")
for (i in 1:nBins) {
		N.laurentia[i] <- nrow(laurentia[[i]])
		N.southChina[i] <- nrow(southChina[[i]])
		N.other[i] <- nrow(other[[i]])
}

N <- min(min(N.laurentia), min(N.southChina), min(N.other))
n <- N

iterations <- iterations
```

```
laurentia.subsample <- matrix(nrow=4, ncol=nBins,
      dimnames=list(c("meanRichness", "stdevRichness", "meanOccurrences",
"stdevOccurrences"), bins))
laurentiaSubsampleData <- list()
southChina.subsample <- matrix(nrow=4, ncol=nBins,
      dimnames=list(c("meanRichness", "stdevRichness", "meanOccurrences",
"stdevOccurrences"), bins))
southChinaSubsampleData <- list()
other.subsample <- matrix(nrow=4, ncol=nBins,
      dimnames=list(c("meanRichness", "stdevRichness", "meanOccurrences",
"stdevOccurrences"), bins))
otherSubsampleData <- list()
for (i in 1:nBins) {
      richness.L <- vector(mode="numeric")
      occurrences.L <- vector(mode="numeric")
      laurentiaSubsample <- list()
      richness.SC <- vector(mode="numeric")
      occurrences.SC <- vector(mode="numeric")
      southChinaSubsample <- list()
      richness.O <- vector(mode="numeric")
      occurrences.O <- vector(mode="numeric")
      otherSubsample <- list()
      for (j in 1:iterations) {
            randomNumbers <- runif(nrow(laurentia[[i]]))
            rowNumbers <- seq(from=1, to=nrow(laurentia[[i]]), by=1)
            A <- cbind(randomNumbers, rowNumbers)
            subsampledRows.L <- A[c(order(A[,1])),]
            subsample.L <- laurentia[[i]][subsampledRows.L[1:n,2],]

            randomNumbers <- runif(nrow(southChina[[i]]))
            rowNumbers <- seq(from=1, to=nrow(southChina[[i]]), by=1)
            A <- cbind(randomNumbers, rowNumbers)
            subsampledRows.SC <- A[c(order(A[,1])),]
            subsample.SC <- southChina[[i]][subsampledRows.SC[1:n,2],]

            randomNumbers <- runif(nrow(other[[i]]))
            rowNumbers <- seq(from=1, to=nrow(other[[i]]), by=1)
            A <- cbind(randomNumbers, rowNumbers)
            subsampledRows.O <- A[c(order(A[,1])),]
            subsample.O <- other[[i]][subsampledRows.O[1:n,2],]

            if (is.vector(subsample.L) == FALSE) {
                  richness.L[j] <- sum(abundance2occurrence(colSums
(subsample.L)))
                  occurrences.L[j] <- sum(rowSums(subsample.L))
            } else {
                  richness.L[j] <- sum(subsample.L)
                  occurrences.L[j] <- sum(subsample.L)
            }

            if (is.vector(subsample.SC) == FALSE) {
                  richness.SC[j] <- sum(abundance2occurrence(colSums
(subsample.SC)))
```

```
                  occurrences.SC[j] <- sum(rowSums(subsample.SC))
            } else {
                  richness.SC[j] <- sum(subsample.SC)
                  occurrences.SC[j] <- sum(subsample.SC)
            }

            if (is.vector(subsample.O) == FALSE) {
                  richness.O[j] <- sum(abundance2occurrence(colSums
(subsample.O)))
                  occurrences.O[j] <- sum(rowSums(subsample.O))
            } else {
                  richness.O[j] <- sum(subsample.O)
                  occurrences.O[j] <- sum(subsample.O)
            }

            laurentiaSubsample[[j]] <- subsample.L
            southChinaSubsample[[j]] <- subsample.SC
            otherSubsample[[j]] <- subsample.O
      }
      laurentia.subsample[1,i] <- mean(richness.L)
      laurentia.subsample[2,i] <- sd(richness.L)
      laurentia.subsample[3,i] <- mean(occurrences.L)
      laurentia.subsample[4,i] <- sd(occurrences.L)

      southChina.subsample[1,i] <- mean(richness.SC)
      southChina.subsample[2,i] <- sd(richness.SC)
      southChina.subsample[3,i] <- mean(occurrences.SC)
      southChina.subsample[4,i] <- sd(occurrences.SC)

      other.subsample[1,i] <- mean(richness.O)
      other.subsample[2,i] <- sd(richness.O)
      other.subsample[3,i] <- mean(occurrences.O)
      other.subsample[4,i] <- sd(occurrences.O)

      laurentiaSubsampleData[[i]] <- laurentiaSubsample
      southChinaSubsampleData[[i]] <- southChinaSubsample
      otherSubsampleData[[i]] <- otherSubsample
}

# calculate 95% CI and plot
degrees.freedom <- iterations-1
alpha <- 0.05
t.crit <- qt(p=(alpha/2), df=degrees.freedom)

stdevDiversity.L <- laurentia.subsample[2,]
stdevDiversity.SC <- southChina.subsample[2,]
stdevDiversity.O <- other.subsample[2,]

CI.plus.L <- laurentia.subsample[1,] + t.crit * stdevDiversity.L / sqrt
(iterations)
CI.minus.L <- laurentia.subsample[1,] - t.crit * stdevDiversity.L / sqrt
(iterations)
CI.plus.SC <- southChina.subsample[1,] + t.crit * stdevDiversity.SC / sqrt
(iterations)
```

```
CI.minus.SC <- southChina.subsample[1,] - t.crit * stdevDiversity.SC / sqrt
(iterations)
CI.plus.O <- other.subsample[1,] + t.crit * stdevDiversity.O / sqrt
(iterations)
CI.minus.O <- other.subsample[1,] - t.crit * stdevDiversity.O / sqrt
(iterations)

polyX.L <- c(1:nBins, nBins:1)
polyY.L <- c(CI.minus.L, rev(CI.plus.L))
polyX.SC <- c(1:nBins, nBins:1)
polyY.SC <- c(CI.minus.SC, rev(CI.plus.SC))
polyX.O <- c(1:nBins, nBins:1)
polyY.O <- c(CI.minus.O, rev(CI.plus.O))

quartz(height=11, width=11)
plot(laurentia.subsample[1,], xaxt="n", main="Subsampled Genus Richness",
ylim=c(0,75), xlab="Time Bin", ylab="Number of Genera", type="n")
# Laurentia
polygon(polyX.L, polyY.L, col="lightgray", border=NA)
points(laurentia.subsample[1,], type="b", cex=2, pch=15)
# South China
polygon(polyX.SC, polyY.SC, col="lightgray", border=NA)
points(southChina.subsample[1,], type="b", cex=2, pch=16)
# other paleocontinents
polygon(polyX.O, polyY.O, col="lightgray", border=NA)
points(other.subsample[1,], type="b", cex=2, pch=17)
axis(side=1, at=c(1:nBins), labels=c("O1", "O2", "O3", "O4", "O5"))
legend(x="topleft", legend=c("Laurentia", "South China", "Other
Paleocontinents"), pch=c(15:17), pt.cex=2.5, bty="n", cex=1.5)


if (saveFiles == TRUE) {
      save(laurentia.subsample, file="laurentiaSubsampleUW")
      save(southChina.subsample, file="southChinaSubsampleUW")
      save(other.subsample, file="otherSubsampleUW")
      save(laurentiaSubsampleData, file="laurentiaSubsampleDataUW")
      save(southChinaSubsampleData, file="southChinaSubsampleDataUW")
      save(otherSubsampleData, file="otherSubsampleDataUW")
      remove(laurentiaSubsampleData, southChinaSubsampleData,
otherSubsampleData)
}

t1 <- Sys.time()
difftime(t1, t0)
```

```
##############################
#####  Calculating origination, extinction, and migration rates
##############################

setwd("/Users/noelheim/Documents/Papers/MigrationModel/PBDB_7March07")

t0 <- Sys.time()

load("fauna")
load("collections")

#bins <- c("Ordovician 1",  "Ordovician 2", "Ordovician 3", "Ordovician 4",
"Ordovician 5")
bins <- c("Cambrian 4", "Ordovician 1",  "Ordovician 2", "Ordovician 3",
"Ordovician 4", "Ordovician 5", "Silurian 1")
nBins <- length(bins)
taxa <- colnames(fauna)
nTaxa <- length(taxa)

plate <- grep("collections.tectonic_plate_id", colnames(collectionInfo))
timeBin <- grep("10mybin", colnames(collectionInfo))

a <- c(as.numeric(sub("X", "", rownames(collectionInfo[collectionInfo[,10]!
="",]))), rep(NA,4))
b <- matrix(a, nrow=136, ncol=15, byrow=TRUE)
write.csv(b, file = "collectionAppendix.csv", row.names=FALSE)

global <- list()
laurentia <- list()
southChina <- list()
otherCont <- list()

for (i in 1:nBins) {
      # data by time bins
      global[[i]] <- fauna[collectionInfo[,timeBin] == bins[i], ]
      laurentia[[i]] <- fauna[collectionInfo[,timeBin] == bins[i] &
collectionInfo[,plate] >= 101 & collectionInfo[,plate] <= 135, ]
      southChina[[i]] <- fauna[collectionInfo[,timeBin] == bins[i] &
collectionInfo[,plate] == 611, ]
      otherCont[[i]] <- fauna[collectionInfo[,timeBin] == bins[i] &
collectionInfo[,plate] != 611 & collectionInfo[,plate] > 135, ]
}

globalAppearances <- matrix(nrow=nBins, ncol=nTaxa, dimnames=list(bins,
taxa))
laurentiaAppearances <- matrix(nrow=nBins, ncol=nTaxa, dimnames=list(bins,
taxa))
southChinaAppearances <- matrix(nrow=nBins, ncol=nTaxa, dimnames=list(bins,
taxa))
otherContAppearances <- matrix(nrow=nBins, ncol=nTaxa, dimnames=list(bins,
taxa))
for(i in 1:nBins) {
      globalAppearances[i,] <- abundance2occurrence(colSums(global[[i]]))
```

```
      laurentiaAppearances[i,] <- abundance2occurrence(colSums(laurentia
[[i]]))
      southChinaAppearances[i,] <- abundance2occurrence(colSums(southChina
[[i]]))
      otherContAppearances[i,] <- abundance2occurrence(colSums(otherCont
[[i]]))
}


for (i in 2:(nBins-1)) {
      for (j in 1:nTaxa) {
            if (globalAppearances[i,j] == 0 & globalAppearances[(i-1),j] == 1
& sum(globalAppearances[(i+1):nBins,j]) >= 1) {
                  globalAppearances[i,j] <- 1
            }

            if (laurentiaAppearances[i,j] == 0 & laurentiaAppearances
[(i-1),j] == 1 & sum(laurentiaAppearances[(i+1):nBins,j]) >= 1) {
                  laurentiaAppearances[i,j] <- 1
            }

            if (southChinaAppearances[i,j] == 0 & southChinaAppearances
[(i-1),j] == 1 & sum(southChinaAppearances[(i+1):nBins,j]) >= 1) {
                  southChinaAppearances[i,j] <- 1
            }

            if (otherContAppearances[i,j] == 0 & otherContAppearances
[(i-1),j] == 1 & sum(otherContAppearances[(i+1):nBins,j]) >= 1) {
                  otherContAppearances[i,j] <- 1
            }
      }
}


# origination, extinction and migration rates
globalOrig <- vector(mode="numeric")
globalExt <- vector(mode="numeric")

for (i in 2:nBins) {
      origCounter <- 0
      extCounter <- 0
      for (j in 1:nTaxa) {
            # global origination and extinction
            if (globalAppearances[i,j]==1 & globalAppearances[(i-1),j]==0) {
                  origCounter <- origCounter + 1
            } else if (globalAppearances[i,j]==0 & globalAppearances[(i-1),j]
==1) {
                  extCounter <- extCounter + 1
            }
      }
      globalOrig[i-1] <- origCounter/(sum(globalAppearances[i,])-origCounter)
      globalExt[i-1] <- extCounter/sum(globalAppearances[(i-1),])
}
```

```
# rates
rateData <- laurentiaAppearances + southChinaAppearances +
otherContAppearances
laurSoChinaData <- laurentiaAppearances + southChinaAppearances

contOrig <- vector(mode="numeric")
contExt <- vector(mode="numeric")
contMig <- vector(mode="numeric")
LaurSoChinaMig <- vector(mode="numeric")

contExtPerGenus <- vector(mode="numeric")

for (i in 1:(nBins-1)) {
      origCounter <- 0
      extCounter <- 0
      migCounter <- 0
      exchangeCounter <- 0
      for (j in 1:nTaxa) {
            delta <- rateData[(i+1),j] - rateData[i,j]
            if (rateData[i,j]==0 & delta > 0) {
                  origCounter <- origCounter + 1
                  migCounter <- migCounter + delta-1
            } else if (rateData[i,j] != 0 & delta > 0) {
                  migCounter <- migCounter + delta
            } else if (delta < 0) {
                  extCounter <- extCounter + abs(delta)
            }

            deltaExchange <- laurSoChinaData[(i+1),j] - laurSoChinaData[i,j]
            if (laurSoChinaData[i,j]==0 & deltaExchange > 0) {
                  exchangeCounter <- exchangeCounter + deltaExchange-1
            } else if (laurSoChinaData[i,j] != 0 & deltaExchange > 0) {
                  exchangeCounter <- exchangeCounter + deltaExchange
            }


      }
      contOrig[i] <- origCounter/(sum(laurentiaAppearances[i+1,],
southChinaAppearances[i+1,], otherContAppearances[i+1,])-origCounter)
      contExt[i] <- extCounter/sum(laurentiaAppearances[i,],
southChinaAppearances[i,], otherContAppearances[i,])
      contMig[i] <- migCounter/(sum(laurentiaAppearances[i+1,],
southChinaAppearances[i+1,], otherContAppearances[i+1,])-migCounter)
      LaurSoChinaMig[i] <- exchangeCounter/sum(laurentiaAppearances[i+1,],
southChinaAppearances[i+1,])

      contExtPerGenus[i] <- extCounter/sum(globalAppearances[i,])
}

# calcualte Jaccard
J.LS <- vector(mode="numeric", length=nBins)
J.LO <- vector(mode="numeric", length=nBins)
J.OS <- vector(mode="numeric", length=nBins)
J <- vector(mode="numeric", length=nBins)
```

```
for (i in 1:nBins) {
      J.LS[i] <- jaccard(laurentiaAppearances[i,], southChinaAppearances[i,])
      J.LO[i] <- jaccard(laurentiaAppearances[i,], otherContAppearances[i,])
      J.OS[i] <- jaccard(otherContAppearances[i,], southChinaAppearances[i,])
      J[i] <- mean(c(J.LS[i], J.LO[i], J.OS[i]))
}

# continental rates
originationRate <- contOrig[1:5]
extinctionRate <- contExt[2:6]
migrationRate <- contMig[1:5]
exchangeRate <- LaurSoChinaMig[1:5]
deltaDiversity <- 1-J[2:6]

# global Rates
globalOriginationRate <- globalOrig[1:5]
globalExtinctionRate <- globalExt[2:6]


ageBoundaries <- c(490, 479, 466, 460.5, 449.5, 443.7)
ageMid <- c(484.8, 472.5, 463.25, 455, 446.6)

quartz(width=3, height=6)
layout(matrix(c(1:3), nrow=3, ncol=1), widths = 1, heights = c(0.1, 0.82,
0.08))
# frame 1: leged
par(cex.lab=0.75, cex.axis=0.75, lwd=1.25, las=1, mar=c(0, 2, 0, 2) + 0.1,
mgp=c(3, 1, 0))
plot(1:10,1:10, type="n", axes=FALSE, xlab="", ylab="", frame.plot=FALSE)
legend(x="topleft", pch=c(15,22,16,1,17,5), bty="n", pt.cex=1, cex=0.75,
      legend=c("global origination", "continental origination", "global
extinction", "continental extinction",
      "migration", "delta diversity"))

# frame 2: data
par(mar=c(0, 3, 0, 2) + 0.1)
plot(ageMid, globalExtinctionRate, type="b", xlim=c(ageBoundaries[1],
ageBoundaries[6]), ylim=c(0.01,10), xlab="", ylab="",
      xaxt="n", yaxt="n",pch=16, lty=2, frame.plot=FALSE, log="y")
points(ageMid, migrationRate, type="o", ylim=c(0,1), pch=17)
points(ageMid, originationRate, pch=22, lty=3, type="b")
points(ageMid, extinctionRate, pch=1, type="b", lty=2)
points(ageMid, globalOriginationRate, pch=15, lty=3, type="b")
points(ageMid, deltaDiversity, type="b", pch=5, lty=4)
axis(side=2, at=c(0.01,0.1,1,10), labels=c("0.01", "0.1", "1", "10"))

# frame 3: axis
par(cex.lab=0.75, cex.axis=0.75, lwd=0.75, las=1, mar=c(1.2, 3, 0, 1) + 0.1,
mgp=c(0, 0, 0))
plot(ageMid, c(1:5), xlim=c(ageBoundaries[1],ageBoundaries[6]), ylim=c(1,5),
type="n", xlab="time bin", ylab="", xaxt="n", yaxt="n", frame.plot=FALSE)
polygon(x=c(ageBoundaries[1],ageBoundaries[6], ageBoundaries[6],
ageBoundaries[1]), y=c(1,1,5,5))
lines(x=rep.int(ageBoundaries[2],2),  y=c(1, 5))
```

```
lines(x=rep.int(ageBoundaries[3],2),  y=c(1, 5))
lines(x=rep.int(ageBoundaries[4],2),  y=c(1, 5))
lines(x=rep.int(ageBoundaries[5],2),  y=c(1, 5))
text(x=ageMid[1], y=3, labels="T")
text(x=ageMid[2], y=3, labels="Ar")
text(x=ageMid[3], y=3, labels="L")
text(x=ageMid[4], y=3, labels="C")
text(x=ageMid[5], y=3, labels="As")



## multiple regression
multRegression <- lm(deltaDiversity~migrationRate + originationRate +
extinctionRate)
summary(multRegression)


#################
#  Caluclate the percentage of widespread taxa

wideTable <- rateData[2:6,]
widespread <- matrix(nrow=nrow(wideTable), ncol=4, dimnames=list(bins[2:6], c
(0:3)))
widespreadPct <- matrix(nrow=nrow(wideTable), ncol=3, dimnames=list(bins
[2:6], c(1:3)))

for (i in 1:nrow(wideTable)) {
      widespread[i,] <- table(wideTable[i,])
      widespreadPct[i,] <- widespread[i,-1]/(nTaxa-widespread[i,1])
      widespreadLogit <- log10(widespreadPct) - log10(1-widespreadPct)
}

quartz(width=3, height=6)
layout(matrix(c(1,2), nrow=2, ncol=1), widths = 1, heights = c(0.9, 0.1))

# frame 1: data
par(cex.lab=0.75, cex.axis=0.75, lwd=0.75, las=1, mar=c(0, 4, 0, 1) + 0.1,
mgp=c(3, 1, 0))
plot(ageMid, widespreadLogit[,1], xlim=c(ageBoundaries[1], ageBoundaries[6]),
ylim=c(-3,2), frame.plot=FALSE, pch=15,
      xaxt="n", xlab="Time bin",  ylab="logit(percent genera)", type="o")
points(ageMid, widespreadLogit[,2], pch=16, type="o")
points(ageMid, widespreadLogit[,3], pch=17, type="o")
points(ageMid, log10(deltaDiversity) - log10(1-deltaDiversity), pch=5, lty=4,
type="b")
text(x=ageMid[1],y=0.40, labels="one paleocontinent", adj=c(0,0), cex=0.75)
text(x=ageMid[1],y=-0.58, labels="two paleocontinents", adj=c(0,0), cex=0.75)
text(x=ageMid[1],y=-1.2, labels="three paleocontinents", adj=c(0,0),
cex=0.75)
text(x=ageMid[1],y=1.1, labels="delta diversity", adj=c(0,0), cex=0.75)

#frame 2: axis
par(cex.lab=0.75, cex.axis=0.75, lwd=0.75, las=1, mar=c(1, 4, 0, 1) + 0.1,
mgp=c(0, 0, 0))
```

```
plot(ageMid, c(1:5), xlim=c(ageBoundaries[1],ageBoundaries[6]), ylim=c(1,5),
type="n", xlab="time bin", ylab="", xaxt="n", yaxt="n", frame.plot=FALSE)
polygon(x=c(ageBoundaries[1],ageBoundaries[6], ageBoundaries[6],
ageBoundaries[1]), y=c(1,1,5,5))
lines(x=rep.int(ageBoundaries[2],2),  y=c(1, 5))
lines(x=rep.int(ageBoundaries[3],2),  y=c(1, 5))
lines(x=rep.int(ageBoundaries[4],2),  y=c(1, 5))
lines(x=rep.int(ageBoundaries[5],2),  y=c(1, 5))
text(x=ageMid[1], y=3, labels="T")
text(x=ageMid[2], y=3, labels="Ar")
text(x=ageMid[3], y=3, labels="L")
text(x=ageMid[4], y=3, labels="C")
text(x=ageMid[5], y=3, labels="As")

#################
#  Caluclate the old taxa for O3-O5 of widespread taxa
ageTable <- globalAppearances[1:6,]
age <- matrix(nrow=5, ncol=nTaxa, dimnames=list(bins[2:6], taxa))
taxonAge <- matrix(data=0, nrow=5, ncol=7, dimnames=list(bins[2:6], c(0:6)))
taxonAgePct <- matrix(nrow=5, ncol=6, dimnames=list(bins[2:6], c(1:6)))

for (i in 1:nrow(age)) {
      age[i,] <- colSums(ageTable[1:(i+1),])
      ageCount <- table(age[i,])
      taxonAge[i,1:length(ageCount)] <- ageCount
      taxonAgePct[i,] <- taxonAge[i,-1]/(nTaxa-taxonAge[i,1])
      taxonAgeLogit <- log10(taxonAgePct) - log10(1-taxonAgePct)
}

quartz(width=3, height=6)
par(cex.lab=0.75, cex.axis=0.75, lwd=1.25, las=1, mar=c(4, 4, 0, 2) + 0.1,
mgp=c(3, 1, 0))
plot(taxonAgeLogit[3:5,1], ylim=c(-2,1), frame.plot=FALSE, pch=15, xaxt="n",
xlab="Time bin",
       ylab="logit(percent genus age)", type="o")
points(taxonAgeLogit[3:5,2], pch=16, type="o")
points(taxonAgeLogit[3:5,3], pch=17, type="o")
#points(taxonAgeLogit[3:5,4], pch=18, type="o", cex=1.5)
text(x=3,y=0.5, labels="one stage", adj=c(1,0), cex=0.75)
text(x=3,y=-0.6, labels="two stages", adj=c(1,0), cex=0.75)
text(x=3,y=-1.1, labels="three stages", adj=c(1,0), cex=0.75)
#text(x=5,y=-2, labels="four stages", adj=c(1,0), cex=0.75)
axis(side=1, at=c(1:3), labels=c("O3", "O4", "O5"))

quartz()
plot(widespreadLogit,taxonAgeLogit[,1:3])

t1 <- Sys.time()
difftime(t1, t0)
```

Appendix E — The list of Paleobiology Database collections used in the analyses of the Chapter 3 analyses of the Carboniferous latitudinal diversity gradient. The data were downloaded (paleodb.org) on 27 March 2008.

1,2,3,4,5,6,7,8,9,20,21,24,25,26,27
59,60,61,62,63,64,65,66,67,68,69,70,71,72,73
74,75,76,77,78,79,80,81,82,83,84,85,86,87,88
89,90,91,92,93,94,95,96,97,98,99,100,101,102,103
105,106,107,108,109,110,111,112,113,114,115,116,117,118,119
120,121,122,123,124,125,126,127,128,129,130,131,132,133,134
135,136,137,138,139,140,141,142,143,144,145,146,147,148,149
150,151,152,153,154,155,156,157,158,159,160,161,162,163,164
165,166,167,168,169,170,171,172,174,175,176,178,179,180,544
545,546,547,548,550,551,554,558,562,568,569,570,571,572,573
574,576,586,587,699,718,719,720,721,722,723,724,725,726,727
728,785,786,787,789,791,792,794,797,800,805,806,807,808,810
811,818,819,820,823,824,827,828,830,831,832,833,834,835,838
840,841,842,843,844,845,846,847,849,850,852,854,855,856,858
860,861,862,864,865,866,868,870,871,872,874,875,876,877,879
880,881,884,886,902,903,905,906,920,921,922,923,924,925,926
927,928,929,930,931,932,933,934,935,936,938,939,940,941,942
943,944,945,946,947,948,949,950,951,953,954,955,956,957,958
959,960,961,962,964,965,966,967,968,969,970,971,972,973,974
976,977,978,979,980,981,982,983,984,985,986,987,988,989,990
991,992,993,995,996,997,998,999,1000,1002,1003,1004,1005,1006,1007
1008,1009,1010,1011,1012,1014,1015,1016,1017,1018,1019,1020,1021,1022,1023
1024,1025,1026,1027,1029,1030,1031,1032,1033,1034,1035,1036,1037,1038,1039
1040,1041,1042,1044,1045,1046,1047,1048,1049,1051,1052,1053,1054,1055,1057
1058,1059,1060,1061,1062,1063,1064,1065,1066,1067,1068,1069,1070,1071,1072
1073,1074,1075,1076,1079,1080,1081,1082,1083,1084,1086,1087,1088,1089,1091
1096,1101,1103,1104,1112,1113,1114,1115,1125,1126,1127,1128,1129,1130,1131
1132,1133,2059,2184,2185,2187,2191,2202,2204,2207,2208,2249,2250,2251,2252
2257,2439,2442,2445,2448,2455,2640,2641,2642,2643,2644,2672,2673,2675,2676
2677,2678,2680,2681,2682,2683,2688,2689,2690,2710,2711,2713,2774,2778,2779
2780,2781,2820,2822,2826,2827,2828,2829,2830,2831,2833,2835,2853,2854,3294
3296,3310,3313,3314,3339,5517,5518,5519,5520,5521,5522,5523,5525,5526,5528
5530,5596,5611,5613,5614,5616,5618,5621,5622,5623,5624,5625,5626,5627,5628
5629,5630,5631,5632,5633,5634,5635,5636,5637,5638,5639,5640,5641,5642,5643
5644,5645,5646,5648,5649,5650,5651,5652,5653,5654,5672,5673,5674,5675,5677
5678,5679,5680,5681,5682,5683,5685,5686,5687,5688,5691,5692,5693,5694,5695
5696,5697,5698,5699,5700,5701,5711,5712,5713,5716,5717,5718,5720,5721,5722
5723,5724,5725,5726,5727,5728,5731,5732,5733,5735,5736,5737,5738,5739,5740
5741,5749,5750,5751,5752,5753,5754,5755,5756,5795,5801,5808,5810,5811,5812
5813,5814,5868,5869,5870,5871,5929,5930,5931,5932,5933,6200,6201,6202,6203
6204,6205,6206,6207,6272,6273,6274,6279,6281,6282,6283,6284,6285,6286,6287
6288,6289,6290,6291,6292,6293,6294,6295,6296,6297,6298,6299,6300,6301,6302
6303,6304,6305,6306,6307,6308,6309,6310,6311,6312,6313,6314,6315,6316,6317
6318,6319,6320,6321,6322,6323,6324,6669,6670,6672,6673,6676,6678,6679,6681
6698,6699,6714,6715,6716,6730,6731,6732,6733,6734,6737,6738,6739,6740,6742

6744,6747,6749,6750,6751,6754,6755,6757,6758,6759,6760,6761,6762,6763,6764
6765,6766,6769,6772,6773,6776,6777,6778,6780,6782,6783,6784,6787,6789,6790
6791,6792,6793,6794,6795,6796,6797,6798,6799,6800,6801,6803,6804,6805,6806
6807,6808,6809,6810,6811,6812,6821,6823,6824,6826,6829,6830,6831,6832,6833
6834,6835,6836,6837,6839,6840,6841,6842,6843,6844,6845,6846,6847,6848,6849
6878,6879,6880,6881,6882,6883,6884,6885,6886,6887,6888,6889,6890,6891,6892
6893,6894,6914,6915,6916,6917,6918,6919,6920,6921,6922,6923,6924,6925,6926
6927,6928,6929,6930,6931,6932,6933,6934,6935,6936,6937,6938,6939,6940,6941
6942,6943,6944,6945,6946,6961,6962,6963,6964,6965,6966,6967,6968,6969,6970
6976,6981,6995,6996,6997,6998,6999,7000,7001,7002,7003,7004,7005,7006,7007
7008,7009,7010,7011,7012,7013,7014,7015,7016,7017,7018,7019,7020,7021,7022
7023,7024,7025,7026,7027,7028,7029,7030,7031,7032,7033,7035,7037,7041,7042
7044,7046,7047,7048,7049,7050,7051,7052,7053,7060,7061,7062,7063,7064,7065
7066,7067,7068,7069,7070,7071,7072,7073,7074,7084,7085,7086,7087,7088,7089
7090,7091,7092,7115,7116,7118,7119,7120,7121,7122,7123,7124,7125,7126,7127
7128,7129,7130,7131,7133,7134,7135,7136,7137,7138,7139,7140,7143,7144,7145
7146,7147,7148,7149,7150,7151,7152,7153,7154,7155,7156,7157,7158,7159,7160
7161,7162,7163,7164,7165,7166,7167,7168,7311,7312,7313,7314,7315,7372,7389
7390,7391,8067,8068,8069,8070,8071,8072,8073,8074,8075,8079,8080,8107,8108
8109,8110,8111,8112,8113,8114,8115,8116,8117,8118,8119,8120,8121,8126,8127
8128,8129,8130,8131,8132,8133,8134,8135,8136,8137,8138,8139,8140,8141,8142
8606,8607,8610,8611,8632,8633,8634,8635,8636,8637,8638,8639,8640,8641,8642
8643,8644,8645,8646,8647,8648,8649,8650,8651,9762,9857,9858,9859,9860,9867
9868,9869,9870,9951,9953,9954,9955,9980,9981,9983,9985,9986,9987,9988,9989
10005,10050,10051,10052,10053,10054,10055,10056,10058,10066,10070,10071,10072,10074,10075
10076,10077,10078,10079,10158,10159,10160,10161,10182,10240,10269,10270,10271,10272,10273
10275,10277,10278,10284,10375,10376,10377,10405,10707,10708,10709,10724,10725,11086,11098
11127,11196,11303,11323,11494,11501,11507,11514,11515,11516,11517,11518,11519,11523,11525
11526,11528,11529,11530,11531,11532,11533,11534,11535,11541,11547,11548,11550,11558,11559
11560,11561,11563,11565,11566,11567,11570,11572,11573,11574,11575,11577,11578,11579,11580
11581,11583,11584,11585,11590,11591,11593,11594,11595,11597,11600,11603,11607,11608,11612
11613,11614,11615,11616,11617,11618,11619,11620,11621,11624,11627,11629,11632,11633,11634
11635,11636,11637,11638,11639,11640,11642,11643,11644,11645,11646,11647,11648,11649,11650
11651,11652,11653,11654,11655,11656,11657,11658,11659,11660,11661,11662,11663,11664,11665
11666,11667,11668,11669,11670,11671,11672,11673,11674,11675,11676,11677,11678,11679,11681
11682,11683,11684,11685,11686,11687,11688,11691,11692,11693,11694,11695,11696,11697,11698
11699,11700,11701,11704,11705,11708,11709,11710,11711,11712,11713,11714,11715,11716,11717
11726,11727,11728,11729,11730,11731,11732,11733,11734,11738,11739,11741,11742,11745,11746
11747,11748,11749,11750,11751,11752,11753,11754,11755,11756,11757,11758,11759,11760,11761
11764,11765,11766,11767,11768,11769,11773,11774,11775,11776,11777,11778,11779,11780,11781
11783,11784,11786,11787,11788,11789,11790,11791,11792,11794,11810,11823,11827,11830,11831
11832,11834,11835,11836,11837,11838,11839,11840,11841,11842,11843,11844,11846,11847,11848
11849,11858,11859,11860,11861,11862,11863,11864,11865,11866,11867,11868,11869,11875,11876
11877,11878,11879,11880,11884,11885,11886,11889,11891,11921,11922,11926,11929,11933,11939
11940,11941,11948,11949,11950,11952,11953,11954,11955,11956,11957,11958,11959,11960,11987
11988,11989,11990,11991,11992,11993,11995,11996,11998,12000,12002,12003,12004,12021,12022
12023,12024,12025,12026,12027,12028,12029,12035,12036,12037,12038,12042,12044,12045,12046
12047,12050,12051,12054,12055,12056,12057,12064,12069,12105,12344,12346,12771,12780,12782
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12799,12800,12801,12802,12803,12804,12805,12806,12807,12809,12810,12811,12812,12813,12814
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12876,12878,12879,12880,12881,12882,12883,12884,12885,12886,12887,12890,12891,12892,12894
12895,12896,12897,12898,12899,12900,12901,12902,12903,12904,12905,12906,12907,12908,12909
12910,12911,12912,12913,12914,12915,12916,12917,13084,13085,13086,13087,13088,13361,13362
13363,13364,28544,34753,37215,37838,37839,37840,37841,37879,39158,39813,39983,39984,39985
39986,39987,39988,39989,39990,39991,39992,39993,39994,39995,39996,39997,40465,40773,41204
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42697,42699,42700,42702,42704,42707,42708,42709,42710,42711,42712,42713,42714,42715,42786
42796,42800,42802,42806,42822,43450,43451,43452,43453,43454,43455,43456,43457,43458,43476
43477,43483,43484,43485,43486,43487,43488,43489,43490,43502,43503,43506,43507,43508,43521
43522,43523,43524,43527,43536,43537,43538,43539,43547,43587,43623,43626,43627,43862,43863
43864,43866,43868,43871,43873,43876,43877,43878,43879,43880,43881,43882,43883,43884,43885
43886,43887,43888,43889,43959,43960,43961,43968,43970,43971,43972,43973,43974,43975,43976
43977,43978,43979,43980,43981,43982,43983,43984,43985,43986,43987,43988,43989,43990,43991
43992,43993,43994,43995,43996,43997,43998,43999,44118,44120,44123,44126,44129,44133,44136
44138,44162,44163,44165,44166,44167,44168,44169,44170,44171,44290,44297,44305,44324,44331
44332,44333,44411,46512,46536,49666,49667,49709,49754,49756,49788,49809,49810,49823,49824
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59857,59858,59859,59860,59861,59862,59863,59864,59889,59891,59932,59936,59937,59938,59939
59941,59942,59943,59944,59945,59946,59947,59948,59949,59950,59951,59952,59953,60041,60042
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62379,62380,62381,62382,62383,62384,62385,62387,62388,62389,62391,62392,62393,62394,62395
62396,62397,62398,62399,62400,62401,62402,62403,62404,62405,62406,62407,62409,62417,62418
62430,62431,62432,62433,62434,62435,62438,62439,62440,62482,62491,62492,62493,62494,62495
62496,62497,62498,62499,62500,62563,62564,62565,62566,62567,62569,62570,62571,62572,62574
62575,62578,62579,62580,62581,62582,62583,62585,62586,62587,62588,62589,62590,62591,62592
62593,62597,62602,62605,62606,62610,62615,62616,62617,62618,62619,62620,62622,62623,62624
62625,62627,62628,62646,62647,62652,62674,62694,62695,62696,62697,62698,62729,62735,62839
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67294,67295,67298,67299,67300,67301,67302,67303,67304,67305,67306,67307,67308,67309,67310
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67326,67327,67328,67329,67330,67331,67332,67333,67334,67335,67336,67337,67338,67339,67678
67679,67680,67681,67682,67801,67802,67803,68188,68852,69282,69283,69284,69285,69286,69305

69457,69458,69459,69720,69721,69722,69770,69771,69772,69773,69919,70134,70135,70137,70187
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70286,70287,70288,70289,70290,70291,70292,70294,70296,70297,70298,70300,70307,70308,70309
70379,70381,70382,70383,70467,70468,70474,70480,70482,70483,70484,70485,70486,70487,71481
71482,71483,71489,71490,71491,71492,71493,71494,71495,71496,71497,71498,71499,71500,71501
71502,71503,71504,71505,71506,71507,71508,71510,71511,71512,71513,71514,71515,71516,71517
71518,71519,71520,71521,71522,71523,71525,71526,71527,71528,71529,71530,71531,71532,71677
71684,71686,71687,71917,71918,71919,71920,71921,71922,71923,71944,71945,71946,71947,71948
71949,71950,71951,71952,71953,71954,71955,71956,71957,71958,71959,71960,71961,71962,71963
71964,71965,71966,71967,71968,71969,71970,71971,71972,71973,71974,71986,71987,71988,71989
71990,71991,71992,71993,71994,71995,71996,71997,71998,71999,72000,72001,72002,72003,72004
72005,72006,72007,72008,72009,72010,72034,72036,72185,72365,72366,72367,72368,72369,72371
72372,72373,72374,72375,72376,72377,72378,72379,72380,72382,72383,72384,72385,73163,73201
73202,73273,73274,75144,75145,75146,75147,75182,75869,75870,75871,76117,76118,76130,76131
76132,76133,76138,76139,76140,76142,76143,76144,76146,76148,76149,76151,76152,76153,76154
76155,76158,76650,76651,77065,79324,79325,79349,79350,79351,79377,79379,79386,79388,79390
79391,79816,79817,79818,79819,79820,79821,79822,79823,79824,79825,79826,79827,79828,79829
79830,79831,79832,79833,79838,79839,79840,79841,79849,79850,79851,79852,79853,79854,79856
79857,79860,79861,79862,79863,79864,79865,79866,79867,79868,79869,79870,79872,79873,79883
79884,79885,79886,79887,79888,79891,79895,79896,79898,79899,79900,79905,79906,79907,79913
79914,79915

Appendix F — R code used in Chapter 3 analyses.

```
##############################
#####  Format the data from the Paleobiology Database, including
#####  assigning orphan taxa to a PBDB time bin.
##############################

setwd("/Users/noelheim/Documents/Papers/LatDiversity/PBDB_27March2008")

t0 <- Sys.time()

# read in raw output matrix from PBDB
      # col 1 = genus resolution
      # col 2 = genus name
      # last two cols are class and order
      # rest of columns are collection numbers (preceeded by X)
      # rows at end are collection info
y <- read.csv(file="NHeim-matrix.csv", header=TRUE)

x <- rbind(y[y[,1]=="",], y[grep("collections.", y[,1]),])

collectionInfo <- t(x[grep("collections.", x[,1]) ,-(grep("_", colnames
(x)))])
colnames(collectionInfo) <- x[grep("collections.", x[,1]) ,1]

taxonInfo <- x[-(grep("collections.", x[,1])) ,grep("_", colnames(x))]

dataMtx <- t(x[-(grep("collections.", x[,1])) ,-(grep("_", colnames(x)))])
colnames(dataMtx) <- rownames(taxonInfo)

nCollections <- nrow(dataMtx)
nGenera <- ncol(dataMtx)

fauna <- matrix(data=0, nrow=nCollections, ncol=nGenera, dimnames=list
(rownames(dataMtx), colnames(dataMtx)))
abundance <- matrix(data=0, nrow=nCollections, ncol=nGenera, dimnames=list
(rownames(dataMtx), colnames(dataMtx)))
for (i in 1:nCollections) {
      for (j in 1:nGenera) {
            if (dataMtx[i,j] != "") {
                  fauna[i,j] <- as.numeric(1)
            }
            if (dataMtx[i,j] != "X" & dataMtx[i,j] != "") {
                  abundance[i,j] <- round(as.numeric(dataMtx[i,j]))
            }
      }
}

taxonColumns <- colnames(taxonInfo)
for (i in 1:ncol(taxonInfo)) {
      if (taxonColumns[i] == "genus_name") {
            genName <- i
      } else if (taxonColumns[i] == "taxon_no") {
```

```
            genNum <- i
      }
}

genera <- unique(taxonInfo$genus_name)
faunaData <- matrix(nrow=nCollections, ncol=length(genera), dimnames=list
(rownames(fauna), genera))
abundanceData <- matrix(nrow=nCollections, ncol=length(genera), dimnames=list
(rownames(abundance), genera))
taxonData <- matrix(nrow=length(genera), ncol=ncol(taxonInfo)); colnames
(taxonData) <- colnames(taxonInfo)
for (i in 1:length(genera)) {
      z <- fauna[,taxonInfo[,genName]==genera[i]]
      zz <- abundance[,taxonInfo[,genName]==genera[i]]
      q <- as.matrix(taxonInfo[taxonInfo[,genName]==genera[i],])
      if (is.matrix(z) == TRUE) {
            faunaData[,i] <- abundance2occurrence(rowSums(z))
            abundanceData[,i] <- abundance2occurrence(rowSums(zz))
            taxonData[i,] <- q[1,]
      } else {
            faunaData[,i] <- z
            abundanceData[,i] <- zz
            taxonData[i,] <- q
      }
}


remove(x, y, dataMtx, taxonInfo, fauna)

####### assign [most] orphan taxa to a time bin
for (i in 1:ncol(collectionInfo)) {
      if (colnames(collectionInfo)[i] == "collections.reference_no") {
            ref <- i
      } else if (colnames(collectionInfo)[i] == "collections.10mybin") {
            age <- i
      }
}

orphans <- collectionInfo[collectionInfo[,age]=="",]

orphanRefs <- sort(unique(as.numeric(orphans[,ref])))
orphanColls <- rownames(orphans)

bins <- c("Carboniferous 1","Carboniferous 2","Carboniferous
3","Carboniferous 4","Carboniferous 5")
nBins <- length(bins)

collNum <- as.numeric(sub("X", "", rownames(collectionInfo)))
collections.10mybin <- collectionInfo[,age]

#Carboniferous 1
C1 <- c(4:9, 550:551, 5616, 5618, 5750, 5751, 5752, 5753, 5754, 5755, 5756,
6272, 6273, 6277, 6914, 6915, 6916, 6917, 6918, 6919, 6920, 6921, 6922, 6923,
8140,
```

```
10182, 10284, 12771, 13361, 41437, 41442, 41444, 28544)

#Carboniferous 2
C2 <- c(557,  6669, 6670, 6672, 6673, 6676, 6678, 6735, 6737, 6738, 6739,
6740, 6746, 6753, 6758, 6760, 6772, 6778, 6779, 6783, 6784, 6787, 6820, 6821,
6824,
6827, 6829, 6830, 6832, 6834, 6836, 6842, 6843, 12870, 12871, 12872, 12873,
12874, 12875, 12876, 12878, 12879, 12880, 12881, 12882, 12883, 12884, 12885,
12886, 12887, 12890, 12891, 12892, 12894, 12895, 12896, 12897, 12898, 12899,
12900, 12901, 12902, 12903, 12904, 12905, 12906, 12907, 12908, 12909, 12910,
12911, 12912, 12913, 12914, 12915, 12916, 12917, 12876, 12878, 12879, 12880,
12881, 12882, 12883, 12884, 12885, 12886, 12887, 12890, 12891, 12892, 12894,
12895, 12896, 12897, 12898, 12899, 12900, 12901, 12902, 12903, 12904, 12905,
12906, 12907, 12908, 12909, 12910, 12911, 12912, 12913, 12914, 12915, 12916,
12917, 41216, 41261, 41263, 41292, 62409, 62417, 64667, 64755, 64756, 64757,
64758, 64759, 64760, 64761, 73201, 75144,  20, 21, 25, 26, 27, 59, 60, 61,
62,
63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 718, 719, 720, 721, 722, 723, 724,
725, 726, 727, 728, 6200, 6201, 6202, 6203, 6204, 6205, 6206, 6207, 6996,
37838,
37839, 37840, 57988, 67167, 72034, 79816, 79817, 79818, 79819, 79820, 79821,
79822, 79823, 79824, 79825, 79826, 79827, 79828, 79829, 79830, 79831, 79832,
79833)

#Carboniferous 3
C3 <- c(2774, 2853, 5685, 5686, 5687, 5688, 5691, 5692, 5693, 5694, 5696,
5697, 5698, 5699, 5700, 5701, 5711, 5712, 5716, 5717, 5718, 5720, 5721, 5722,
5723, 5733,
5735, 5736, 5737, 5738, 5739, 5740, 5741, 6714, 6715, 6849, 6878, 6879, 6880,
6881, 6882, 6883, 6884, 6885, 6886, 6887, 6888, 6889, 6890, 6891, 6892, 6893,
6894, 6924, 6925, 6926, 6927, 6928, 6929, 6930, 6931, 6932, 6933, 6934, 6936,
6937, 6938, 6939, 6940, 6941, 6943, 6944, 6945, 6946, 6962, 6963, 6964, 6966,
6967, 6968, 6969, 6970, 7000, 7002, 7003, 7004, 7005, 7006, 7007, 7008, 7009,
7010, 7011, 7012, 7013, 7014, 7015, 7017, 7018, 7019, 7020, 7021, 7022, 7023,
7024, 7025, 7026, 7027, 7028, 7029, 7030, 7031, 7032, 7033, 7035, 7048, 7061,
7062, 7063, 7064, 7065, 7066, 7067, 7068, 7069, 7070, 7071, 7072, 7073, 7074,
7084, 7085, 7086, 7087, 7088, 7089, 7090, 7091, 7092, 12786, 12787, 12788,
12789, 13084, 13084, 13085, 13086, 13087, 13088, 13362, 13363, 41204, 41214,
41215,
59863, 59864, 62329, 62372, 62373, 62374, 62375, 62376, 62377, 62378, 62379,
62380, 62381, 62382, 62383, 62384, 62418, 62432, 62433, 62439, 62440, 62627,
62628, 67678, 67679, 67680, 67681, 68188, 77065, 6961, 6965, 7060, 10240,
10405, 12346,
79836, 79837, 79838, 79839, 79840, 79841, 79849, 79850, 79851, 79852, 79853,
79854, 79860, 79861, 79862, 79863, 79864, 79865, 79866, 79867, 79868, 79869)

#Carboniferous 4
C4 <- c(109, 9762, 9857, 9858, 9859, 9860, 9867, 9868, 9869, 9870, 9951,
9953, 9954, 9955, 12344, 12780, 12782, 12783, 12784, 12785, 13364, 75145,
75146, 75182,
11196, 43623, 43625, 43626, 43627, 58108)

#Carboniferous 5
C5 <- c(113:117, 157:159, 163, 172, 174, 61571, 61573, 61634, 61636)
```

```
orph <- list(C1,C2,C3,C4,C5)

############ remaining orphans
#22, 23, 543, 549, 553, 555, 559, 560, 561, 563, 564, 567, 577, 578, 579,
581, 582, 583, 584, 585, 588, 589, 1077, 1078, 1098, 1119, 1120, 1121
#5714, 7034, 7036, 7043, 7320, 7323, 7326, 7373, 10137, 10241, 10282, 10283,
12345, 12697, 12700, 13091, 13152, 13153, 13154, 13155, 13239, 13240
#13241, 13243, 13244, 13245, 13246, 13247, 13248, 13249, 13252, 13253, 13254,
13255, 13272, 25266, 39938, 39939, 39940, 41339,
#58996, 58997, 58998, 59823, 59824, 59825, 59826, 59827, 74055, 74056, 74057,
74058, 74059, 75138

for (i in 1:nBins) {
      replacement <- match(orph[[i]], collNum)
      collections.10mybin[replacement] <- bins[i]
}

collectionInfo[,age] <- collections.10mybin


##### remove precordillarian collections from Alaska that were not part of
Laurentia during the Carboniferous
ref9811 <- match(9811, collectionInfo[,ref])
ref19343 <- match(19343, collectionInfo[,ref])
collectionInfo <- collectionInfo[-c(ref9811,ref19343),]
faunaData <- faunaData[-c(ref9811,ref19343),]

save(faunaData, file="fauna")
save(abundanceData, file="abundance")
save(taxonData, file="taxa")
save(collectionInfo, file="collectionInfo")

remove(faunaData, abundanceData, taxonData, collectionInfo)

t1 <- Sys.time()
difftime(t1, t0)
```

```
##############################
#####  Subsample the data by collection
##############################

setwd("/Users/noelheim/Documents/Papers/LatDiversity/PBDB_27March2008")

t0 <- Sys.time()

saveData <- TRUE
nSubsamples <- 1000
minNumCollections <- 10
minNumGlboalCollections <- 250


#Permian 1              299.0       Asselian
#Carboniferous 5  306.5       Gzhelian, Missourian
#Carboniferous 4  318.1       Bashkirian, Morrowan
#Mississippian/Pennsylvanian Boundary
#Carboniferous 3  336.0       Chesterian, Serpukhovian
#Carboniferous 2  349.5       Aleksian
#Carboniferous 1  360.7       Kinderhookian, Tournaisian
#Devonian 5             376.1       Famennian

load(file="latTimeData") # includes: latTime, newData, occ, coll, collInfo,
collections, taxa, bins, latitude, latBins, latPlot

for (i in 1:ncol(collInfo)) {
      columnNames <- colnames(collInfo)
      if (columnNames[i] == "collections.paleolatdec") {
            lat <- i
      } else if (columnNames[i] == "collections.paleolngdec") {
            long <- i
      } else if (columnNames[i] == "collections.stage") {
            stage <- i
      } else if (columnNames[i] == "collections.10mybin") {
            bin <- i
      } else if (columnNames[i] == "collections.environment") {
            env <- i
      }
}

nTaxa <- length(taxa)
nBins <- length(bins)
nLat <- length(latBins)

########### subsample the data OW method of bush et al. 2004 (sample
collections until a set number of occurrences is reached
# find the number of occurrences to sample
# first get rid of all data with fewer than a specified number of collections
coll2 <- coll
for (i in 1:length(coll)) {
      if (is.na(coll[i])==FALSE & coll[i]<minNumCollections) {
            coll2[i] <- NA
      }
```

```
}
minColl <- min(coll2, na.rm=TRUE)

# begin subsampling
subsampleData <- list()
globalData <- list()
subsampleS <- list()
subsampleJwithin <- list()
subsampleJbetween <- list()
for (i in 1:nBins) {
      subsampleBin <- list()
      subRich <- matrix(nrow=nLat, ncol=nSubsamples, dimnames=list(latBins, c
(1:nSubsamples)))
      subSim <- matrix(nrow=nLat, ncol=nSubsamples, dimnames=list(latBins, c
(1:nSubsamples)))
      subSimBet <- matrix(nrow=nLat-1, ncol=nSubsamples, dimnames=list(c
("<-20/-10", "-10/0", "0/10", "10/>10"), c(1:nSubsamples)))
      globalSubsamp <- list()
      for (j in 1:nLat) {
            if (is.na(coll2[i,j])==FALSE) {
                  x <- latTime[[i]][[j]]
                  subsampleLat <- list()
                  for (k in 1:nSubsamples) {
                        if (sum(x)==0) {
                              subsamp <- rep(NA,nTaxa); names(subsamp) <-
taxa
                              subRich[j,k] <- NA
                              subSim[j,k] <- NA
                        } else if (is.vector(x)==TRUE) {
                              subsamp <- x
                              subRich[j,k] <- sum(abundance2occurrence
(subsamp))
                              subSim[j,k] <- NA
                        } else {
                              sampledRows <- sample(c(1:nrow(x)),minColl)
                              subsamp <- x[sampledRows,]
                              subRich[j,k] <- sum(abundance2occurrence
(colSums(subsamp, na.rm=TRUE)))
                              subSim[j,k] <- mean(1-vegdist(subsamp,
method="jaccard", binary=TRUE))
                        }
                        subsampleLat[[k]] <- subsamp
                        if (j>1 & is.na(subsampleLat[[k]])==FALSE) {
                              if (is.na(subsampleBin[[j-1]])==FALSE) {
                                    if(is.matrix(subsampleLat[[k]])==TRUE) {
                                          a <- abundance2occurrence(colSums
(subsampleLat[[k]]))
                                    } else {
                                          a <- subsampleLat[[k]]
                                    }
                                    if(is.matrix(subsampleBin[[j-1]][[k]])
==TRUE) {
                                          b <- abundance2occurrence(colSums
(subsampleBin[[j-1]][[k]]))
```

```
                        } else {
                            b <- subsampleBin[[j-1]][[k]]
                        }
                        subSimBet[j-1,k] <- jaccard(a,b)
                    }
                }
            }
            subsampleBin[[j]] <- subsampleLat
        } else {
            subsampleBin[[j]] <- NA
        }
    }
    subsampleData[[i]] <- subsampleBin
    subsampleS[[i]] <- subRich
    subsampleJwithin[[i]] <- subSim
    subsampleJbetween[[i]] <- subSimBet
}


#### combine subsamples into global
globalSubData <- list()
globalSubRich <- matrix(nrow=nBins, ncol=nSubsamples, dimnames=list(bins, c
(1:nSubsamples)))
subsampleGlobalS <- matrix(nrow=nBins, ncol=nSubsamples, dimnames=list(bins,
c(1:nSubsamples)))
subsampleGlobalJ <- matrix(nrow=nBins, ncol=nSubsamples, dimnames=list(bins,
c(1:nSubsamples)))
for (i in 1:nBins) {
    global <- collections[collInfo[,bin]==bins[i],]
    tempGlobalData <- list()
    for (k in 1:nSubsamples) {
        globalSubRows <- sample(c(1:nrow
(global)),minNumGlboalCollections)
        globalSub <- global[globalSubRows,]
        subsampleGlobalS[i,k] <- sum(abundance2occurrence(colSums
(globalSub)))
        subsampleGlobalJ[i,k] <- mean(1-vegdist(globalSub,
method="jaccard", binary=TRUE))
        latDataHolder <- matrix(0, nrow=minNumCollections, ncol=nTaxa,
dimnames=list(c(1:minNumCollections), taxa))
        for (j in 1:nLat) {
            if (is.list(subsampleData[[i]][[j]])==TRUE) {
                latDataHolder <- latDataHolder + subsampleData[[i]]
[[j]][[k]]
            }
        }
        tempGlobalData[[k]] <- latDataHolder
        globalSubRich[i,k] <- sum(abundance2occurrence(colSums
(latDataHolder)))
    }
    globalSubData[[i]] <- tempGlobalData
}

########### save data
```

```
if (saveData == TRUE) {
      save(subsampleS, subsampleJwithin, subsampleJbetween, nSubsamples,
globalSubRich, subsampleGlobalS, subsampleGlobalJ,
            minColl, minNumCollections, minNumGlboalCollections, latitude,
taxa, bins, latBins, latPlot, coll, coll2, occ,
            file="subsampledDataLatUW")
      save(subsampleData, globalSubData, nSubsamples, latitude, taxa, bins,
latBins, latPlot, coll, coll2, occ, file="subsampleData")
}

t1 <- Sys.time()
difftime(t1, t0)
```

```
##############################
#####  Bootstrap the raw data for 95% CI
##############################

setwd("/Users/noelheim/Documents/Papers/LatDiversity/PBDB_27March2008")

t0 <- Sys.time()

#Permian 1              299.0       Asselian
#Carboniferous 5  306.5       Gzhelian, Missourian
#Carboniferous 4  318.1       Bashkirian, Morrowan
#Mississippian/Pennsylvanian Boundary
#Carboniferous 3  336.0       Chesterian, Serpukhovian
#Carboniferous 2  349.5       Aleksian
#Carboniferous 1  360.7       Kinderhookian, Tournaisian
#Devonian 5             376.1       Famennian

load(file="latTimeData") # includes: latTime, newData, occ, coll, collInfo,
collections, taxa, bins, binNames, latBins, latitude, latPlot

nBoots <- 1000
saveData <- TRUE

nTaxa <- length(taxa)
nBins <- length(bins)
nLat <- length(latBins)

## bootstrapData
latTimeBootRich <- matrix(0, nrow=nBins, ncol=nLat, dimnames=list(binNames,
latBins))
latTimeBootSD <- matrix(0, nrow=nBins, ncol=nLat, dimnames=list(binNames,
latBins))
latTimeBoot <- list()
for (i in 1:nBins) {
      latBootHolder <- list()
      for (j in 1:nLat) {
            if (sum(latTime[[i]][[j]]) > 0 & is.matrix(latTime[[i]][[j]])
==TRUE) {
                  ltBoot <- matrix(0, nrow=nBoots, ncol=nTaxa, dimnames=list
(c(1:nBoots), taxa))
                  for (k in 1:nBoots) {
                        resample <- as.count(sample(census(colSums(latTime
[[i]][[j]])), replace=TRUE))
                        ltBoot[k,match(names(resample), colnames(ltBoot))] <-
abundance2occurrence(as.vector(resample))
                  }
                  latTimeBootRich[i,j] <- mean(apply(ltBoot,1,sum))
                  latTimeBootSD[i,j] <- sd(apply(ltBoot,1,sum))
            } else if (sum(latTime[[i]][[j]]) > 0 & is.vector(latTime[[i]]
[[j]])==TRUE) {
                  ltBoot <- matrix(0, nrow=nBoots, ncol=nTaxa, dimnames=list
(c(1:nBoots), taxa))
                  for (k in 1:nBoots) {
```

```
                        resample <- as.count(sample(census(latTime[[i]]
[[j]]), replace=TRUE))
                        ltBoot[k,match(names(resample), colnames(ltBoot))] <-
abundance2occurrence(as.vector(resample))
                  }
                  latTimeBootRich[i,j] <- mean(apply(ltBoot,1,sum))
                  latTimeBootSD[i,j] <- sd(apply(ltBoot,1,sum))
            } else {
                  ltBoot <- NA
                  latTimeBootRich[i,j] <- NA
                  latTimeBootSD[i,j] <- NA
            }
            latBootHolder[[j]] <- ltBoot
      }
      latTimeBoot[[i]] <- latBootHolder
}

## calc mean richness and SD for alpha and gamma
latTimeBootGamma <- vector(mode="numeric", length=nBins); names
(latTimeBootGamma) <- binNames
latTimeBootGammaSD <- vector(mode="numeric", length=nBins); names
(latTimeBootGammaSD) <- binNames

latTimeBootBeta <- vector(mode="numeric", length=nBins); names
(latTimeBootBeta) <- binNames
latTimeBootBetaSD <- vector(mode="numeric", length=nBins); names
(latTimeBootBetaSD) <- binNames

latTimeAlphaBar <- vector(mode="numeric", length=nBins); names
(latTimeAlphaBar) <- binNames
latTimeAlphaBarSD <- vector(mode="numeric", length=nBins); names
(latTimeAlphaBarSD) <- binNames

for (i in 1:nBins) {
      gammaBootHolder <- latTimeBoot[[1]][[1]] * 0
      alphaBarHolder <- matrix(nrow=nBoots, ncol=nLat, dimnames=list(c
(1:nBoots),latBins))
      for (j in 1:nLat) {
            if (is.matrix(latTimeBoot[[i]][[j]])==TRUE) {
                  gammaBootHolder <- gammaBootHolder + latTimeBoot[[i]][[j]]
                  alphaBarHolder[,j] <- apply(latTimeBoot[[i]][[j]],1,sum)

            }
      }
      latTimeBootGamma[i] <- mean(apply(abundance2occurrence
(gammaBootHolder),1,sum))
      latTimeBootGammaSD[i] <- sd(apply(abundance2occurrence
(gammaBootHolder),1,sum))

      latTimeBootBeta[i] <- mean(apply(abundance2occurrence(gammaBootHolder),
1,sum) - apply(alphaBarHolder,1,mean, na.rm=TRUE))
      latTimeBootBetaSD[i] <- sd(apply(abundance2occurrence(gammaBootHolder),
1,sum) - apply(alphaBarHolder,1,mean, na.rm=TRUE))
```

```
      latTimeAlphaBar[i] <- mean(apply(alphaBarHolder,1,mean, na.rm=TRUE))
      latTimeAlphaBarSD[i] <- sd(apply(alphaBarHolder,1,mean, na.rm=TRUE))
}

if (saveData==TRUE) {
      save(latTimeBoot, latTimeBootRich, latTimeBootSD, nBoots,
latTimeBootGamma, latTimeBootGammaSD, latTimeBootBeta, latTimeBootBetaSD,
            latTimeAlphaBar, latTimeAlphaBarSD, collInfo, taxa, bins,
binNames, latBins, latitude, latPlot,
            file="latTimeDataBoot")
}

t1 <- Sys.time()
difftime(t1, t0)
```

```
##############################
#####  Additive diversity partitioning for subsampled data
##############################

setwd("/Users/noelheim/Documents/Papers/LatDiversity/PBDB_27March2008")

t0 <- Sys.time()

#Permian 1              299.0       Asselian
#Carboniferous 5  306.5       Gzhelian, Missourian
#Carboniferous 4  318.1       Bashkirian, Morrowan
#Mississippian/Pennsylvanian Boundary
#Carboniferous 3  336.0       Chesterian, Serpukhovian
#Carboniferous 2  349.5       Aleksian
#Carboniferous 1  360.7       Kinderhookian, Tournaisian
#Devonian 5             376.1       Famennian

load(file="subsampledDataLatUW")  # contains:  subsampleS, subsampleJwithin,
subsampleJbetween, nSubsamples, globalSubRich, subsampleGlobalS,
#
subsampleGlobalJ, minColl, minNumGlboalCollections, latitude, taxa, bins,
latBins, latPlot, coll, coll2, occ
#  globalSubRich is the matrix of global richness of compled from each of the
subasmpled latitudinal bins

nTaxa <- length(taxa)
nBins <- length(bins)
nLat <- length(latBins)

# hierarchy: latitude, time bin
alphaMean <- matrix(nrow=nBins, ncol=nSubsamples, dimnames=list(bins, c
(1:nSubsamples)))
gammaDiversity <- apply(globalSubRich, 1, mean)
gammaSD <- apply(globalSubRich,1, sd)

# alpha1 and alpha1 bar (of collections)
for (i in 1:nBins) {
      alphaMean[i,] <- apply(subsampleS[[i]][2:4,],2,mean, na.rm=TRUE)
}

# for all lat bins
alphaBar <- apply(alphaMean,1,mean, na.rm=TRUE)
alphaSD <- apply(alphaMean,1,sd, na.rm=TRUE)
betaDiversity <- apply(globalSubRich-alphaMean,1,mean)
betaSD <- apply(globalSubRich-alphaMean,1,sd)

adp <- rbind(alphaBar, betaDiversity)

n <- nSubsamples
alpha <- 0.05
degrees.freedom <- n-1
t.crit <- abs(qt(p=(alpha/2), df=degrees.freedom))

ciGamma <- t.crit * gammaSD
```

```
ciAlpha <- t.crit * alphaSD
ciBeta <- t.crit * betaSD

binAbrev <- c("M1","M2","M3","P1","P2")
barColors <- c("gray20", "gray70")
quartz(height=3.5, width=7)
par (mfrow=c(1,2), las=1, mar=c(2.75, 4, 0.5, 0.5) + 0.1, mgp=c(3, 1, 0))
x <- barplot(adp, ylim=c(0,250), ylab="taxonomic richness",
names.arg=binAbrev, col=barColors, yaxt="n")
axis(side=2, at=seq(0,250,50))
text(x=x, y=colSums(adp)+65, labels=expression(gamma), cex=1.5)
text(x=x, y=rep(9, nBins), labels=expression(alpha), cex=1.5, col="white")
barLength <- (x[2]-x[1])/7
betaPos <- c(100,100,115,85,73)
for (i in 1:nBins) {
	lines(rep(x[i],2), c(gammaDiversity[i]+ciGamma[i], gammaDiversity[i]-
ciGamma[i]), lwd=1.5)
	lines(rep(x[i],2), c(alphaBar[i], alphaBar[i]+ciAlpha[i]), lwd=1.5)
	lines(rep(x[i],2), c(alphaBar[i], alphaBar[i]-ciAlpha[i]), col="white",
lwd=1.5)
	lines(x=c(x[i]-barLength, x[i]+barLength), y=rep(17,2), lwd=2,
col="white")
	text(x=x[i], y=betaPos[i], labels=expression(beta), cex=1.5)
}
text(x=x[5], y=250, labels="A", cex=1.5, font=2, adj=c(0,1))

x <- barplot(adp[2,], ylim=c(0,150), ylab="", names.arg=binAbrev,
col=barColors[2], yaxt="n")
axis(side=2, at=seq(0,150,50))
text(x=x, y=rep(30,nBins), labels=expression(beta), cex=1.5)
for (i in 1:nBins) {
	lines(rep(x[i],2), c(adp[2,i]+ciBeta[i], adp[2,i]-ciBeta[i]), lwd=1.5)
}
text(x=x[5], y=150, labels="B", cex=1.5, font=2, adj=c(0,1))

t1 <- Sys.time()
difftime(t1, t0)
```

Appendix G — Locality register for field collectons.

Locality	**Lat**	**Long**	**Age**	**Formation**
West Fork (WFW)	35.921611	-94.200528	Chesterian	Pitkin
Alpena (ALN)	36.295778	-93.234417	Chesterian	Hindsville
Braggs Mtn. (BM)	35.755630	-95.195840	Chesterian & Morrowan	Pitkin & Sausbee
Tenkiller Bridge (TKB)	35.754267	-94.892410	Morrowan	McCully
Webber Falls Dam (WFD)	35.551450	-95.170020	Morrowan	Sausbee
Fort Gibson (FGE)	35.865389	-95.225210	Chesterian	Pitkin
Evansville Mtn. (EVM)	35.766390	-94.468380	Morrowan	Hale
Mt. Judea (MJH)	35.909740	-93.046710	Chesterian	Hindsville
Boxley 1 (BX1)	35.943180	-93.391980	Chesterian	Hindsville
Indian Road 3 (IR3)	35.631567	-95.062800	Morrowan	McCully
Greenland (GLN)	36.010620	-94.194110	Morrowan	Hale
Adair County (AC)	35.761230	-94.806990	Chesterian	Pitkin

Locality	**Locality Description**
West Fork (WFW)	Road cut on entrance ramp to I 540 South in West Fork, AR
Alpena (ALN)	Large road cut on US 412 ~3.5 mi east of the junction with US 62 in Alpena, AR
Braggs Mtn. (BM)	Road cut on eastern side of OK 10 ~ 4.5 mi south of junction with US 62
Tenkiller Bridge (TKB)	Outcrop on OK 82 just S of bridge over Lake Tenkiller and ~1/3 mi S of junction w/OK 100
Webber Falls Dam (WFD)	W side of Arkansas river at Webber Falls Lock and Dam 16
Fort Gibson (FGE)	Road cut oalong OK 80 on E side of Fort Gibson Dam. Starts at junction of OK 80 & OK 251A
Evansville Mtn. (EVM)	Long outcrop on W side of AR 59, S of Evansivlle & just N of Crawford Co Line
Mt. Judea (MJH)	W. side of AR123 just S of Mt. Jedea and just N. of creek crossing
Boxley 1 (BX1)	South of Boxley on AR21
Indian Road 3 (IR3)	Outcrop on side of Indian Road in Sequoyah County
Greenland (GLN)	Large roadcut just north of Greenland Exit on I540N. Collected exposure at drainage pipe
Adair County (AC)	Road cut on both sides of OK 100 at the Adair - Cherokee County line

Appendix H — Counts of field data. Counts are bast on the minimum number of individuals method.

	Lingula	Orbiculoidea	Antiquatonia	Buxtonia	Desmoinesia	Diaphragmus	Dictyoclostus	Echinaria	Echinoconchus	Eomarginifera	Inflatia
WFW_B3_C1_Mound				17		1			3		
WFW_B3_C2_Mound	1					1					12
WFW_B1_C1	1	1									46
WFW_B1_C2											31
WFW_B1_C3		1									34
WFW_B1_C4		1									28
ALN_B5_C1											6
ALN_B5_C2											2
ALN_B5_C3											1
BM_B1_C1_2005											
BM_B1_C2_2005											3
BM_B1_C3_2005											12
BM_B2_C1_2005				3							1
BM_B2_C2_2005				1							3
BM_B2_C3_2005				5							5
ALN_B1_C1_S									42		
ALN_B1_C2_S									78		
ALN_B1_C3_S									88		
ALN_B1_C1									19		
ALN_B1_C2									19		
ALN_B1_C3									18		
TKB_B1_C1			12					2			
TKB_B1_C2	1		4					1			
TKB_B1_C3			11					1			
WFD_B1_C1		1									
WFD_B1_C2											
WFD_B1_C3		1									
WFD_B2_C1					9			3			
WFD_B2_C2			6		5						
WFD_B2_C3			3		1			6			
FGE_B1_C1											7
FGE_B1_C2											3
FGE_B1_C3						1					7
BM1_B1_C1			16		4						
BM1_B1_C2			35								
EVM7_B1_C1			1					1			
EVM7_B1_C2											
EVM7_B1_C3			1								

	Lingula	Orbiculoidea	Antiquatonia	Buxtonia	Desmoinesia	Diaphragmus	Dictyoclostus	Echinaria	Echinoconchus	Eomarginifera	Inflatia
EVM7_B2_C1											
EVM7_B2_C2											
EVM7_B2_C3											
MJH_B2_C1											4
MJH_B2_C2											5
MJH_B2_C3											5
BX1_B1_C1											3
BX1_B1_C2											3
IR3_B1_C1											
IR3_B1_C2											
IR3_B1_C3											
GLN_B1_C1			11					4			
GLN_B1_C2			7		1						
GLN_B1_C3			7					2			
AC_B2_C1						6			1		
AC_B2_C2						5					
AC_B2_C3						3			2		
AC_B1_C1						4					1
AC_B1_C2						4					
AC_B1_C3						14					1
AC_B1_C4						1					3
AC_B4_C1											
ALN_B4_C2											
ALN_B4_C3	1	18									
ALN_B3_C1									2		7
ALN_B3_C2									3		1

	Krotovia	Linoproductus	Ovatia	Productus	Protoniella	Pulchratia	Sandia	Scoloconcha	Zia	Adectorhynchus	Chonetes
WFW_B3_C1_Mound											
WFW_B3_C2_Mound			17	2							
WFW_B1_C1										2	
WFW_B1_C2											
WFW_B1_C3											
WFW_B1_C4											
ALN_B5_C1											
ALN_B5_C2											
ALN_B5_C3											
BM_B1_C1_2005			40								
BM_B1_C2_2005			43								
BM_B1_C3_2005			26								
BM_B2_C1_2005			30								
BM_B2_C2_2005			13								
BM_B2_C3_2005			28								
ALN_B1_C1_S											
ALN_B1_C2_S				2							
ALN_B1_C3_S				1							
ALN_B1_C1											
ALN_B1_C2											
ALN_B1_C3				3							
TKB_B1_C1		4									
TKB_B1_C2		2					4				
TKB_B1_C3		3					2				
WFD_B1_C1											
WFD_B1_C2											
WFD_B1_C3											
WFD_B2_C1		2					1				
WFD_B2_C2	1	2					3				
WFD_B2_C3		3					1				
FGE_B1_C1			2								
FGE_B1_C2			3								
FGE_B1_C3			9								
BM1_B1_C1	6					1	1				
BM1_B1_C2	8						2				
EVM7_B1_C1	1						1		1		
EVM7_B1_C2							2				
EVM7_B1_C3									2		

	Krotovia	Linoproductus	Ovatia	Productus	Protoniella	Pulchratia	Sandia	Scoloconcha	Zia	Adectorhynchus	Chonetes
EVM7_B2_C1											
EVM7_B2_C2											
EVM7_B2_C3							1				
MJH_B2_C1											
MJH_B2_C2											
MJH_B2_C3											
BX1_B1_C1		1									2
BX1_B1_C2											3
IR3_B1_C1						1					
IR3_B1_C2											
IR3_B1_C3											
GLN_B1_C1		2					14				
GLN_B1_C2							13				
GLN_B1_C3		1					16				
AC_B2_C1											
AC_B2_C2											
AC_B2_C3											
AC_B1_C1											
AC_B1_C2											
AC_B1_C3											
AC_B1_C4											
AC_B4_C1		27									
ALN_B4_C2											
ALN_B4_C3											
ALN_B3_C1											
ALN_B3_C2											

	Derbyia	Eolissochonetes	Leptaena	Neochonetes	Orthotetes	Plicochonetes	Schellwienella	Schuchertella	Streptorhynchus	Camarophoria	Camarotoechia
WFW_B3_C1_Mound											
WFW_B3_C2_Mound										1	
WFW_B1_C1					1						
WFW_B1_C2											
WFW_B1_C3											
WFW_B1_C4											
ALN_B5_C1					2						
ALN_B5_C2											
ALN_B5_C3											
BM_B1_C1_2005											
BM_B1_C2_2005											
BM_B1_C3_2005					1						
BM_B2_C1_2005											
BM_B2_C2_2005					1				2		
BM_B2_C3_2005					1				3		
ALN_B1_C1_S					3		6	4	2		
ALN_B1_C2_S					4			2		1	
ALN_B1_C3_S					4			3		1	
ALN_B1_C1					4			3	1		
ALN_B1_C2					4						
ALN_B1_C3					2						
TKB_B1_C1											
TKB_B1_C2	1					1					
TKB_B1_C3						1					
WFD_B1_C1						4					
WFD_B1_C2						5					
WFD_B1_C3						8					
WFD_B2_C1	3					2					
WFD_B2_C2	7					2					
WFD_B2_C3	6										
FGE_B1_C1											
FGE_B1_C2											
FGE_B1_C3					2						
BM1_B1_C1											
BM1_B1_C2						3					
EVM7_B1_C1						1					
EVM7_B1_C2											
EVM7_B1_C3						1					

	Derbyia	Eolissochonetes	Leptaena	Neochonetes	Orthotetes	Plicochonetes	Schellwienella	Schuchertella	Streptorhynchus	Camarophoria	Camarotoechia
EVM7_B2_C1						2					
EVM7_B2_C2											
EVM7_B2_C3				2		3					
MJH_B2_C1											
MJH_B2_C2											
MJH_B2_C3											
BX1_B1_C1					3						
BX1_B1_C2											
IR3_B1_C1											
IR3_B1_C2											
IR3_B1_C3						1					
GLN_B1_C1			4								
GLN_B1_C2			1								
GLN_B1_C3			2								
AC_B2_C1					1						
AC_B2_C2					1						
AC_B2_C3											
AC_B1_C1											
AC_B1_C2											
AC_B1_C3					1						
AC_B1_C4											
AC_B4_C1											
ALN_B4_C2											
ALN_B4_C3										2	
ALN_B3_C1					1						
ALN_B3_C2											

	Leiorhynchus	Rhynchopora	Stenoscisma	Rhipidomella	Schizophoria	Anthracospirifer	Athyris	Brachythyris	Cleiothyridina	Composita	Eumetria
WFW_B3_C1_Mound											
WFW_B3_C2_Mound					5	8			4	5	
WFW_B1_C1						6	7		4		
WFW_B1_C2							1		2		
WFW_B1_C3						2	3		1		
WFW_B1_C4						5			2		
ALN_B5_C1						16	1		1		2
ALN_B5_C2						1			3		
ALN_B5_C3										1	1
BM_B1_C1_2005											
BM_B1_C2_2005											
BM_B1_C3_2005											
BM_B2_C1_2005						1	1				1
BM_B2_C2_2005						3	1		4		
BM_B2_C3_2005						2	2		1		4
ALN_B1_C1_S						12			69	8	1
ALN_B1_C2_S				3		15			88	16	1
ALN_B1_C3_S				4		22			66	19	1
ALN_B1_C1						11			3	10	
ALN_B1_C2						2			17	18	
ALN_B1_C3						2			9	8	
TKB_B1_C1						7			1	9	
TKB_B1_C2						5			2		
TKB_B1_C3					2	1			2	3	
WFD_B1_C1		2			7	2				31	
WFD_B1_C2		2			1					23	
WFD_B1_C3		2				1				8	
WFD_B2_C1						1				1	
WFD_B2_C2						2					
WFD_B2_C3						3				4	
FGE_B1_C1					6		1			3	2
FGE_B1_C2									2	4	
FGE_B1_C3					3					1	1
BM1_B1_C1						2			1	3	
BM1_B1_C2						5				7	
EVM7_B1_C1									1	8	
EVM7_B1_C2					1					3	
EVM7_B1_C3		1			3	1				3	

	Leiorhynchus	Rhynchopora	Stenoscisma	Rhipidomella	Schizophoria	Anthracospirifer	Athyris	Brachythyris	Cleiothyridina	Composita	Eumetria
EVM7_B2_C1				2		1				5	
EVM7_B2_C2				1		1				7	
EVM7_B2_C3									2	9	
MJH_B2_C1						1				7	
MJH_B2_C2										12	
MJH_B2_C3						1				16	
BX1_B1_C1				2		2		2			
BX1_B1_C2		3				7				2	
IR3_B1_C1						5			1	8	
IR3_B1_C2						3				3	
IR3_B1_C3						8				1	
GLN_B1_C1					1						
GLN_B1_C2						1					
GLN_B1_C3											
AC_B2_C1						2			8	15	3
AC_B2_C2						2			5	5	4
AC_B2_C3						2			12	11	3
AC_B1_C1										4	1
AC_B1_C2									1	1	
AC_B1_C3									2	3	3
AC_B1_C4										2	1
AC_B4_C1											
ALN_B4_C2						5				1	
ALN_B4_C3									1	4	
ALN_B3_C1										2	
ALN_B3_C2						1				1	

	Hustedia	Phricodothyris	Punctospirifer	Reticulariina	Spirifer	Spiriferellina	Tetracamera	Torynifer	Beecheria	Dielasma	Girtyella
WFW_B3_C1_Mound			1								
WFW_B3_C2_Mound										3	
WFW_B1_C1				2							
WFW_B1_C2											
WFW_B1_C3			1	1							
WFW_B1_C4				1							
ALN_B5_C1								1			
ALN_B5_C2					23			2		6	
ALN_B5_C3					18			1		2	
BM_B1_C1_2005											
BM_B1_C2_2005											
BM_B1_C3_2005											
BM_B2_C1_2005			1								
BM_B2_C2_2005				4							
BM_B2_C3_2005				1						2	
ALN_B1_C1_S							1				
ALN_B1_C2_S							3				
ALN_B1_C3_S							2				
ALN_B1_C1											
ALN_B1_C2											
ALN_B1_C3											
TKB_B1_C1											
TKB_B1_C2			1								
TKB_B1_C3										1	
WFD_B1_C1	1		1						2		
WFD_B1_C2									1		
WFD_B1_C3											
WFD_B2_C1						1			1		
WFD_B2_C2											
WFD_B2_C3						2					
FGE_B1_C1											4
FGE_B1_C2											
FGE_B1_C3											
BM1_B1_C1		5				1			1		
BM1_B1_C2	1	2				1					
EVM7_B1_C1	1	1							1		
EVM7_B1_C2						1					
EVM7_B1_C3		1				1			1		

	Hustedia	Phricodothyris	Punctospirifer	Reticulariina	Spirifer	Spiriferellina	Tetracamera	Torynifer	Beecheria	Dielasma	Girtyella
EVM7_B2_C1	1	6									
EVM7_B2_C2	2	12									
EVM7_B2_C3	1	1									
MJH_B2_C1	3									3	
MJH_B2_C2										5	
MJH_B2_C3											
BX1_B1_C1				5							
BX1_B1_C2				2							
IR3_B1_C1		25							1		
IR3_B1_C2		20							1		
IR3_B1_C3		15							4		
GLN_B1_C1			1						1		
GLN_B1_C2											
GLN_B1_C3									2		
AC_B2_C1			1			1					
AC_B2_C2											
AC_B2_C3			1								
AC_B1_C1								4			
AC_B1_C2				2				1		1	
AC_B1_C3				1				3		3	
AC_B1_C4								2			
AC_B4_C1											
ALN_B4_C2			3								
ALN_B4_C3							6				
ALN_B3_C1			3								
ALN_B3_C2			1					3			

	Terebratuloid_indet	**total individuals**
WFW_B3_C1_Mound	1	**23**
WFW_B3_C2_Mound		**59**
WFW_B1_C1		**70**
WFW_B1_C2		**34**
WFW_B1_C3		**43**
WFW_B1_C4		**37**
ALN_B5_C1		**29**
ALN_B5_C2		**37**
ALN_B5_C3		**24**
BM_B1_C1_2005		**40**
BM_B1_C2_2005		**46**
BM_B1_C3_2005		**39**
BM_B2_C1_2005		**38**
BM_B2_C2_2005		**32**
BM_B2_C3_2005		**54**
ALN_B1_C1_S		**148**
ALN_B1_C2_S		**213**
ALN_B1_C3_S		**211**
ALN_B1_C1		**51**
ALN_B1_C2		**60**
ALN_B1_C3		**42**
TKB_B1_C1		**35**
TKB_B1_C2		**22**
TKB_B1_C3		**27**
WFD_B1_C1		**51**
WFD_B1_C2		**32**
WFD_B1_C3		**20**
WFD_B2_C1		**24**
WFD_B2_C2		**28**
WFD_B2_C3		**29**
FGE_B1_C1		**25**
FGE_B1_C2		**12**
FGE_B1_C3		**24**
BM1_B1_C1		**41**
BM1_B1_C2		**64**
EVM7_B1_C1		**18**
EVM7_B1_C2		**7**
EVM7_B1_C3		**15**

	Terebratuloid_indet	**total individuals**
EVM7_B2_C1		**17**
EVM7_B2_C2		**23**
EVM7_B2_C3		**19**
MJH_B2_C1		**18**
MJH_B2_C2		**22**
MJH_B2_C3		**22**
BX1_B1_C1		**20**
BX1_B1_C2		**20**
IR3_B1_C1		**41**
IR3_B1_C2		**27**
IR3_B1_C3		**29**
GLN_B1_C1		**38**
GLN_B1_C2		**23**
GLN_B1_C3		**30**
AC_B2_C1		**38**
AC_B2_C2		**22**
AC_B2_C3		**34**
AC_B1_C1		**14**
AC_B1_C2		**10**
AC_B1_C3		**31**
AC_B1_C4		**9**
AC_B4_C1		**27**
ALN_B4_C2		**9**
ALN_B4_C3		**32**
ALN_B3_C1		**15**
ALN_B3_C2		**10**

Appendix I — The list of Paleobiology Database collections used in the Chapter 4 analyses on Carboniferous brachiopod latitudinal ranges. The data were downloaded (paleodb.org) on 09 April 2007.

383,392,450,452,458,459,462,463,472,474,475,480,481,482,490
491,492,517,518,527,531,534,541,542,543,544,545,546,547,548
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578,579,580,581,582,588,589,590,593,595,596,601,602,603,604
605,608,610,611,613,615,620,621,626,627,630,632,633,634,636
642,643,644,647,650,651,652,653,654,659,669,670,798,840,920
922,925,926,931,938,940,965,979,980,983,986,997,998,1000,1002
1006,1010,1012,1023,1024,2184,2185,2187,2191,2202,2204,2207,2208,2455,2640
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2689,2690,2710,2711,2713,2774,2778,2779,2780,2781,2820,2822,2826,2827,2828
2829,2830,2831,2833,2835,2853,2854,3294,3296,3309,3310,3313,3314,3339,3374
3379,3380,3382,3398,3399,3400,3402,3403,3404,3407,3408,3433,3437,3442,3443
3449,3451,3454,3456,3457,3615,3619,3623,3625,3633,3660,3664,3665,3798,3802
3804,3806,3809,3810,3830,3845,3846,3847,3853,3921,3922,3925,3944,3945,3946
3984,4013,4029,4694,4801,4840,4862,4864,5509,5510,5511,5513,5534,5603,5605
5611,5613,5614,5615,5616,5619,5620,5621,5622,5623,5624,5625,5626,5627,5628
5630,5632,5633,5635,5638,5639,5640,5641,5642,5644,5645,5646,5650,5651,5653
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5853,5855,5856,5858,5859,5861,5862,5863,5864,5925,5928,5929,5930,5931,5933
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5994,5995,6016,6018,6019,6020,6022,6026,6027,6029,6032,6033,6040,6041,6048
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6249,6435,6437,6439,6441,6442,6443,6447,6448,6450,6451,6452,6453,6454,6455
6456,6457,6459,6460,6462,6669,6670,6673,6676,6678,6679,6698,6699,6714,6715
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6769,6772,6773,6777,6778,6780,6782,6783,6787,6789,6790,6791,6792,6793,6794
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9550,9551,9552,9553,9554,9556,9557,9558,9559,9560,9562,9563,9564,9571,9572
9573,9574,9581,9582,9583,9584,9600,9601,9603,9604,9605,9606,9608,9609,9610
9611,9612,9613,9614,9615,9617,9657,9659,9661,9662,9664,9667,9674,9675,9704
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79895,79896,79898,79899,79900,79905,79906,79907,79913,79914,79915,80104

Appendix J — R code used in Chapter 4 analyses.

```
##############################
#####  Additive diversity partitioning.
##############################

setwd("/Users/noelheim/Documents/Papers/OzarkPaper")
t0 <- Sys.time()

runSubsample <- FALSE
if (runSubsample == TRUE) {
      # read in data
      collections <- remove.rare(na2zero(as.matrix(read.csv
(file="countData.csv", header=TRUE, row.names=1))),1)[-60,] # 60 is a single
monospecific bed/collection
      collInfo <- read.csv(file="collectionInfo.csv", header=TRUE,
row.names=1)[-60,]
      bedInfo <- read.csv(file="bedInfo.csv", header=TRUE, row.names=1)[-21,]

      nColl <- nrow(collections)
      nTaxa <- ncol(collections)
      taxa <- colnames(collections)
      nBed <- nrow(bedInfo)
      nInt <- 2
      intervalSubSize <- sum(bedInfo$Age)

      missData <- collections[collInfo$Age==0,]
      missInfo <- collInfo[collInfo$Age==0,]
      pennData <- collections[collInfo$Age==1,]
      pennInfo <- collInfo[collInfo$Age==1,]

      # subsample all beds so there are 2 collections per bed
      nSubsamples <- 1000
      nCollPerBeds <- 2
      nBeds <- 8 # this is the total number of subsampled beds per time
interval
      metrics <- c(2,3,5,6) # diversity metrics of interest (range between 2
& 6

      missIntSub <- list()
      missBedSub <- list()
      missCollSub <- list()

      pennIntSub <- list()
      pennBedSub <- list()
      pennCollSub <- list()

      missAlpha1 <- list()
      missAlpha1Bar <- list()
      missAlpha1DoubleBar <- list()

      missAlpha2 <- list()
      missAlpha2Bar <- list()
```

```
      missBeta1 <- list()
      missBeta1Bar <- list()

      missTotalDiversity <- matrix(nrow=nSubsamples, ncol=length(metrics))
      missBeta2 <- list()

      pennAlpha1 <- list()
      pennAlpha1Bar <- list()
      pennAlpha1DoubleBar <- list()

      pennAlpha2 <- list()
      pennAlpha2Bar <- list()
      pennBeta1 <- list()
      pennBeta1Bar <- list()

      pennTotalDiversity <- matrix(nrow=nSubsamples, ncol=length(metrics))
      pennBeta2 <- list()

      for (i in 1:nSubsamples) {
            missIntSub[[i]] <- matrix(nrow=(nInt), ncol=nTaxa, dimnames=list
(c(1:nInt), taxa))
            missBedSub[[i]] <- matrix(nrow=(intervalSubSize), ncol=nTaxa,
dimnames=list(c(1:intervalSubSize), taxa))
            missCollSub[[i]] <- matrix(nrow=(intervalSubSize*2), ncol=nTaxa,
dimnames=list(c(1:(intervalSubSize*2)), taxa))

            pennIntSub[[i]] <- matrix(nrow=(nInt), ncol=nTaxa, dimnames=list
(c(1:nInt), taxa))
            pennBedSub[[i]] <- matrix(nrow=(intervalSubSize), ncol=nTaxa,
dimnames=list(c(1:intervalSubSize), taxa))
            pennCollSub[[i]] <- matrix(nrow=(intervalSubSize*2), ncol=nTaxa,
dimnames=list(c(1:(intervalSubSize*2)), taxa))

            missBeds <- sort(sample(unique(missInfo$Bed_num),
intervalSubSize))
            pennBeds <- sort(sample(unique(pennInfo$Bed_num),
intervalSubSize))
            for (j in 1:intervalSubSize) {
                  k <- c(j*nCollPerBeds-1, j*nCollPerBeds)
                  x <- missData[missInfo[,2] == missBeds[j],]
                  bedColl <- sample(c(1:nrow(x)), 2)
                  missCollSub[[i]][k,] <- x[bedColl,]
                  missBedSub[[i]][j,] <- colSums(missCollSub[[i]][k,])

                  x <- pennData[pennInfo[,2] == pennBeds[j],]
                  bedColl <- sample(c(1:nrow(x)), 2)
                  pennCollSub[[i]][k,] <- x[bedColl,]
                  pennBedSub[[i]][j,] <- colSums(pennCollSub[[i]][k,])
            }
            missIntSub[[i]] <- colSums(missBedSub[[i]])
            pennIntSub[[i]] <- colSums(pennBedSub[[i]])
```

```
            missAlpha1[[i]] <- diversityMetrics(missCollSub[[i]])[,metrics]
            missAlpha1Bar[[i]] <- matrix(nrow=nBeds, ncol=length(metrics))
            for (j in 1:nBeds) {
                  k <- c((j*nCollPerBeds-1),(j*nCollPerBeds))
                  missAlpha1Bar[[i]][j,] <- apply(missAlpha1[[i]][k,], 2,
mean)
            }
            missAlpha1DoubleBar[[i]] <- apply(missAlpha1Bar[[i]], 2, mean)

            missAlpha2[[i]] <- diversityMetrics(missBedSub[[i]])[,metrics]
            missAlpha2Bar[[i]] <- apply(missAlpha2[[i]],2,mean)
            missBeta1[[i]] <- missAlpha2[[i]] - missAlpha1Bar[[i]]
            missBeta1Bar[[i]] <- apply(missBeta1[[i]],2,mean)

            missTotalDiversity[i,] <- diversityMetrics(colSums(missCollSub
[[i]]))[,metrics]
            missBeta2[[i]] <- missTotalDiversity[i,] - missAlpha2Bar[[i]]


            pennAlpha1[[i]] <- diversityMetrics(pennCollSub[[i]])[,metrics]
            pennAlpha1Bar[[i]] <- matrix(nrow=nBeds, ncol=length(metrics))
            for (j in 1:nBeds) {
                  k <- c((j*nCollPerBeds-1),(j*nCollPerBeds))
                  pennAlpha1Bar[[i]][j,] <- apply(pennAlpha1[[i]][k,], 2,
mean)
            }
            pennAlpha1DoubleBar[[i]] <- apply(pennAlpha1Bar[[i]], 2, mean)

            pennAlpha2[[i]] <- diversityMetrics(pennBedSub[[i]])[,metrics]
            pennAlpha2Bar[[i]] <- apply(pennAlpha2[[i]],2,mean)
            pennBeta1[[i]] <- pennAlpha2[[i]] - pennAlpha1Bar[[i]]
            pennBeta1Bar[[i]] <- apply(pennBeta1[[i]],2,mean)

            pennTotalDiversity[i,] <- diversityMetrics(colSums(pennCollSub
[[i]]))[,metrics]
            pennBeta2[[i]] <- pennTotalDiversity[i,] - pennAlpha2Bar[[i]]
      }

      missS <- matrix(nrow=nSubsamples, ncol=3)
      missGini <- missS

      pennS <- matrix(nrow=nSubsamples, ncol=3)
      pennGini <- pennS

      for (i in 1:nSubsamples) {
            missS[i,] <- c(missAlpha1DoubleBar[[i]][1], missBeta1Bar[[i]][1],
missBeta2[[i]][1])
            missGini[i,] <- c(missAlpha1DoubleBar[[i]][3], missBeta1Bar[[i]]
[3], missBeta2[[i]][3])

            pennS[i,] <- c(pennAlpha1DoubleBar[[i]][1], pennBeta1Bar[[i]][1],
pennBeta2[[i]][1])
            pennGini[i,] <- c(pennAlpha1DoubleBar[[i]][3], pennBeta1Bar[[i]]
[3], pennBeta2[[i]][3])
```

```
      }

      save(nColl, nTaxa, taxa, nBed, nInt, intervalSubSize, nSubsamples,
missS, missGini, pennS, pennGini, missAlpha1,
            missAlpha1Bar, missAlpha1DoubleBar, missAlpha2, missAlpha2Bar,
missBeta1, missBeta1Bar, missTotalDiversity,
            missBeta2, pennAlpha1, pennAlpha1Bar, pennAlpha1DoubleBar,
pennAlpha2, pennAlpha2Bar, pennBeta1, pennBeta1Bar,
            pennTotalDiversity, pennBeta2, file="ADP_Subsample")
} else {
      load("ADP_Subsample")
      collections <- remove.rare(na2zero(as.matrix(read.csv
(file="countData.csv", header=TRUE, row.names=1))),1)
}

stageNames <- c("Chesterian", "Morrowan")
Sbar <- cbind(apply(missS, 2, mean), apply(pennS, 2, mean)); colnames(Sbar)
<- stageNames
Ginibar <- cbind(apply(missGini, 2, mean), apply(pennGini, 2, mean));
colnames(Ginibar) <- stageNames

gammaS <- c(mean(apply(missS,1,sum)), mean(apply(pennS,1,sum)))
gammaSsd <- c(sd(apply(missS,1,sum)), sd(apply(pennS,1,sum)))

gammaGini <- c(mean(apply(missGini,1,sum)), mean(apply(pennGini,1,sum)))
gammaGinisd <- c(sd(apply(missGini,1,sum)), sd(apply(pennGini,1,sum)))

# calculate 95% CI
alphaValue <- 0.05
degrees.freedom <- nSubsamples-1
t.crit <- abs(qt(p=(alphaValue/2), df=degrees.freedom))
z.crit <- abs(qnorm(p=(alphaValue/2)))

Ssd <- cbind(apply(missS, 2, sd), apply(pennS, 2, sd)); colnames(Ssd) <-
stageNames
S.CI <- t.crit * Ssd
Splus <- Sbar+S.CI
Sminus <- Sbar-S.CI
Ginisd <- cbind(apply(missGini, 2, sd), apply(pennGini, 2, sd)); colnames
(Ginisd) <- stageNames
Gini.CI <- t.crit * Ginisd
Giniplus <- Ginibar+Gini.CI
Giniminus <- Ginibar-Gini.CI

gammaS.CI <- t.crit * gammaSsd
gammaGini.CI <- t.crit * gammaGinisd

gammaS.plus <- gammaS + gammaS.CI
gammaS.minus <- gammaS - gammaS.CI
gammaGini.plus <- gammaGini + gammaGini.CI
gammaGini.minus <- gammaGini - gammaGini.CI

barColor <- c(gray(0.3), gray(0.6), gray(0.9))
```

```
# S
quartz(height=4, width=7)
plotPct <- rep(0.333,3)
layout(matrix(c(1,1,1,5,5,5,4:2), nrow=3, ncol=3), widths = c(0.4,0.2,0.4),
heights = plotPct)
par(las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3, 3.5, 0.25, 0) + 0.1, mgp=c
(2.25, 0.75, 0))

maxS <- 35
bp <- barplot(Sbar, ylim=c(0,maxS), ylab="taxonomic richness (S)",
col=barColor, cex.lab=1)
for (i in 1:length(bp)) {
      lines(x=c(bp[i],bp[i]), y=c(gammaS.plus[i], gammaS.minus[i]))
}

par(mar=c(3, 2, 0.25, 0) + 0.1)
bp <- barplot(Sbar[1,], col=barColor[1], ylim=c(0,8), ylab="")
for (i in 1:length(bp)) {
      lines(x=c(bp[i],bp[i]), y=c(Splus[1,i], Sminus[1,i]))
}
text(x=bp[1], y=2.75, labels=expression(paste(alpha["c"])), col="white",
cex=1.5)
lines(x=c(bp[1]-.075, bp[1]+.01), y=rep.int(3.5,2), col="white", lwd=0.75)
lines(x=c(bp[1]-.075, bp[1]+.01), y=rep.int(3.75,2), col="white", lwd=0.75)
text(x=bp[2], y=2.75, labels=expression(paste(alpha["c"])), col="white",
cex=1.5)
lines(x=c(bp[2]-.075, bp[2]+.01), y=rep.int(3.5,2), col="white", lwd=0.75)
lines(x=c(bp[2]-.075, bp[2]+.01), y=rep.int(3.75,2), col="white", lwd=0.75)

bp <- barplot(Sbar[2,], col=barColor[2], ylim=c(0,3), axisnames=FALSE,
yaxt="n", ylab="")
for (i in 1:length(bp)) {
      lines(x=c(bp[i],bp[i]), y=c(Splus[2,i], Sminus[2,i]))
}
axis(side=2, at=seq(0,3,1))
text(x=bp[1], y=0.85, labels=expression(paste(beta["w"])), cex=1.5)
lines(x=c(bp[1]-.075, bp[1]+.01), y=rep.int(1.3,2), lwd=0.75)
text(x=bp[2], y=0.85, labels=expression(paste(beta["w"])), cex=1.5)
lines(x=c(bp[2]-.075, bp[2]+.01), y=rep.int(1.3,2), lwd=0.75)

bp <- barplot(Sbar[3,], col=barColor[3], ylim=c(0,25), axisnames=FALSE,
ylab="")
for (i in 1:length(bp)) {
      lines(x=c(bp[i],bp[i]), y=c(Splus[3,i], Sminus[3,i]))
}
text(x=bp[1], y=8, labels=expression(paste(beta["a"])), cex=1.5)
text(x=bp[2], y=8, labels=expression(paste(beta["a"])), cex=1.5)

# arrows
par(mar=c(3, 0, 1.5, 0) + 0.1)
plot(c(1:10), type="n", axes=FALSE, bty="n",ann=FALSE)
arrows(x0=1, y0=1.5, x1=10, y1=1.5, length = 0.15, angle = 20, lwd=2)
arrows(x0=1, y0=3.25, x1=10, y1=5.5, length = 0.15, angle = 20, lwd=2)
arrows(x0=1, y0=6.5, x1=10, y1=9, length = 0.15, angle = 20, lwd=2)
```

```
# Gini
quartz(height=4, width=7)
plotPct <- rep(0.333,3) #c(0.25, 0.2, 0.55)
layout(matrix(c(1,1,1,5,5,5,4:2), nrow=3, ncol=3), widths = c(0.4,0.2,0.4),
heights = plotPct)
par(las=1, cex.axis=0.75, mar=c(3, 3.5, 0.25, 0) + 0.1, mgp=c(2.6, 0.75, 0))

maxGini <- 1
bp <- barplot(Ginibar, ylim=c(0,maxGini), ylab="Simpson's D", col=barColor,
cex.lab=1)
for (i in 1:length(bp)) {
      lines(x=c(bp[i],bp[i]), y=c(gammaGini.plus[i], gammaGini.minus[i]))
}

par(mar=c(3, 2.5, 0.25, 0) + 0.1)
bp <- barplot(Ginibar[1,], col=barColor[1], ylim=c(0,0.8), yaxt="n", ylab="")
for (i in 1:length(bp)) {
      lines(x=c(bp[i],bp[i]), y=c(Giniplus[1,i], Giniminus[1,i]))
}
axis(side=2, at=c(0,0.4,0.8))
text(x=bp[1], y=0.27, labels=expression(paste(alpha["c"])), col="white",
cex=1.5)
lines(x=c(bp[1]-.075, bp[1]+.01), y=rep.int(.35,2), col="white", lwd=0.75)
lines(x=c(bp[1]-.075, bp[1]+.01), y=rep.int(.375,2), col="white", lwd=0.75)
text(x=bp[2], y=0.27, labels=expression(paste(alpha["c"])), col="white",
cex=1.5)
lines(x=c(bp[2]-.075, bp[2]+.01), y=rep.int(.35,2), col="white", lwd=0.75)
lines(x=c(bp[2]-.075, bp[2]+.01), y=rep.int(.375,2), col="white", lwd=0.75)

bp <- barplot(Ginibar[2,], col=barColor[2], ylim=c(0,0.1), axisnames=FALSE,
yaxt="n", ylab="")
for (i in 1:length(bp)) {
      lines(x=c(bp[i],bp[i]), y=c(Giniplus[2,i], Giniminus[2,i]))
}
axis(side=2, at=c(0,0.05, 0.1))
text(x=bp[1], y=0.01, labels=expression(paste(beta["w"])), cex=1.5)
lines(x=c(bp[1]-.075, bp[1]+.01), y=rep.int(.02,2), lwd=0.75)
text(x=bp[2], y=0.01, labels=expression(paste(beta["w"])), cex=1.5)
lines(x=c(bp[2]-.075, bp[2]+.01), y=rep.int(.02,2), lwd=0.75)

bp <- barplot(Ginibar[3,], col=barColor[3], ylim=c(0,0.3), axisnames=FALSE,
yaxt="n", ylab="")
for (i in 1:length(bp)) {
      lines(x=c(bp[i],bp[i]), y=c(Giniplus[3,i], Giniminus[3,i]))
}
axis(side=2, at=c(0,0.1,0.2, 0.3))
text(x=bp[1], y=0.05, labels=expression(paste(beta["a"])), cex=1.5)
text(x=bp[2], y=0.05, labels=expression(paste(beta["a"])), cex=1.5)

# arrows
par(mar=c(3, 0, 1.5, 0) + 0.1)
plot(c(1:10), type="n", axes=FALSE, bty="n",ann=FALSE)
arrows(x0=1, y0=2, x1=10, y1=2, length = 0.15, angle = 20, lwd=2)
```

```
arrows(x0=1, y0=7.8, x1=10, y1=5.7, length = 0.15, angle = 20, lwd=2)
arrows(x0=1, y0=9, x1=10, y1=9, length = 0.15, angle = 20, lwd=2)

###############  ABR Plots
# PCH
#     1 = open circle
#     2 = open triangle up
#     5 = open diamond
#     16 = closed circle
#     17 = closed triangle up
#     18 = closed diamond cex=1.5

ABRalpha1bar <- rbind(missAlpha1Bar[[1]], pennAlpha1Bar[[1]])
ABRalpha2 <- rbind(missAlpha2[[1]], pennAlpha2[[1]])
ABRalpha2bar <- rbind(missAlpha2Bar[[1]], pennAlpha2Bar[[1]])
ABRalpha3 <- rbind(apply(missTotalDiversity,2,mean), apply
(pennTotalDiversity,2,mean))
ABRalpha3bar <- apply(ABRalpha3,2,mean)
ABRgamma <- diversityMetrics(colSums(collections))[-c(1,4)]
for (i in 2:nSubsamples) {
      ABRalpha1bar <- ABRalpha1bar + rbind(missAlpha1Bar[[i]], pennAlpha1Bar
[[i]])
      ABRalpha2 <- ABRalpha2 + rbind(missAlpha2[[i]], pennAlpha2[[i]])
      ABRalpha2bar <- ABRalpha2bar + rbind(missAlpha2Bar[[i]], pennAlpha2Bar
[[i]])
}
ABRalpha1bar <- ABRalpha1bar/nSubsamples
ABRalpha2 <- ABRalpha2/nSubsamples
ABRalpha2bar <- ABRalpha2bar/nSubsamples

nAlpha2 <- nrow(ABRalpha2)

quartz(height=3.4, width=7)
par(mfrow=c(1,2), las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3.2, 3, 0, 0.1) +
0.1, mgp=c(2, 0.75, 0))
# richness
maxX <- trunc(nTaxa/10)*10+10
maxY <- maxX-20
plot(c(0:maxY), type="n", xlim=c(0,maxX), xlab="regional richness (S)",
ylim=c(0,maxY), ylab="local richness (S)", bty="n")
lines(x=c(0,maxX), y=c(0,maxX/2), lty="dotted", cex=0.75)
polygon(c(0,maxY,0,0), c(0,maxY,maxY,0), col="lightgray")
text(x=maxX, y=maxY*0.95, labels=expression(paste(alpha > beta)), adj=1)
text(x=maxX, y=maxY*0.35, labels=expression(paste(alpha < beta)), adj=1)

points(ABRalpha2[,1],ABRalpha1bar[,1], pch=c(rep.int(1,nAlpha2/2), rep.int
(16,nAlpha2/2)))
points(ABRalpha3[,1],ABRalpha2bar[,1], pch=c(2,17))
points(ABRgamma[1],ABRalpha3bar[1], pch=18, cex=1.5)

legendLabels <- c("Chesterian (M) beds", "Morrowan (|P) beds", "Chesterian
(M) stage", "Morrowan (|P) stage", "both stages")
legendPch <- c(1,16,2,17,18)
legendFill <- c("white", "black", "white", "black","black")
```

```
legend(x=0,y=maxY, legend=legendLabels, pch=legendPch, pt.cex=c(rep.int(1,4),
1.5), cex=0.75, bty="n")#, fill=legendFill)

# Gini
maxX <- 1
maxY <- maxX
plot(c(0:maxY), type="n", xlim=c(0,maxX), xlab="regional Simpson's D", ylim=c
(0,maxY), ylab="local Simpson's D", bty="n")
lines(x=c(0,maxX), y=c(0,maxX/2), lty="dotted", cex=0.75)
polygon(c(0,maxY,0,0), c(0,maxY,maxY,0), col="lightgray")
text(x=maxX, y=maxY*0.55, labels=expression(paste(alpha > beta)), adj=1)
text(x=maxX, y=maxY*0.05, labels=expression(paste(alpha < beta)), adj=1)

points(ABRalpha2[,3],ABRalpha1bar[,3], pch=c(rep.int(1,nAlpha2/2), rep.int
(16,nAlpha2/2)))
points(ABRalpha3[,3],ABRalpha2bar[,3], pch=c(2,17))
points(ABRgamma[3],ABRalpha3bar[3], pch=18, cex=1.5)

t1 <- Sys.time()
difftime(t1,t0)
```

```
##############################
#####  Gradient analysis
##############################

setwd("/Users/noelheim/Documents/Papers/OzarkPaper")

t0 <- Sys.time()
 runMDS <- FALSE

# read in data
collData <- read.csv(file="collectionInfo.csv", header=TRUE, row.names=1)
[-60,] # 60 is a single monospecific bed/collection
columnNames <- colnames(collData)
taxonData <- read.csv(file="taxonInfo.csv", header=TRUE, row.names=1)

for (i in 1:length(columnNames)) {
      if (columnNames[i]=="Lat") {
            lat <- i
      } else if (columnNames[i]=="Long") {
            long <- i
      } else if (columnNames[i]=="Age") {
            age <- i
      } else if (columnNames[i]=="Formation") {
            formation <- i
      }
}

input <- na2zero(read.csv(file="countData.csv", header=TRUE, row.names=1))
[-60,] # 60 is a single monospecific bed/collection
myData <- cull.rareAndDepaup(data=input, minRichness=2, minNoOccurrences=2)

nTaxa <- ncol(myData)

miss <- colSums(myData[collData$Age==0,])
penn <- colSums(myData[collData$Age==1,])
mississippian <- abundance2occurrence(miss)
pennsylvanian <- abundance2occurrence(penn)

overlap <- vector()
for (i in 1:nTaxa) {
      if (mississippian[i]==1 & pennsylvanian[i]==0) {
            overlap[i] <- 0
      } else if (mississippian[i]==0 & pennsylvanian[i]==1) {
            overlap[i] <- 1
      } else {
            overlap[i] <- 2
      }
}


################  DCA
myData.t1 <- decostand(myData, "total")
myData.t2 <- decostand(myData.t1, "max")
myData.dca <- decorana(myData.t2, iweigh=1)
```

```
myData.dca.taxonscores <- scores(myData.dca, display=c("species"), choices=c
(1,2,3))
myData.dca.samplescores <- scores(myData.dca, display=c("sites"), choices=c
(1,2,3))

# plot site scores coded by formation
myScoresAndTime <- data.frame(dca1=myData.dca.samplescores[,1],
dca2=myData.dca.samplescores[,2], period=collData[,age], formation=collData
[,formation])
formations <- c("Hindsville", "Pitkin", "Hlae", "Bloyd", "Sausbee",
"McCully")
nFormations <- length(formations)

plotSymbols <- c(21,24,16,18,15, 17)
ptSize <- c(1,1,1,1.25,1,1)
quartz(height=4, width=3.4)
par(las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3,2.75,0.5,0), mgp=c(1.75,
0.75, 0))
plot(myScoresAndTime$dca1, myScoresAndTime$dca2, type="n", xlab="DCA Axis 1
(Site Scores)", ylab="DCA Axis 2 (Site Scores)", bty="n", xlim=c(-3,4),
ylim=c(-3,4))
for (i in 1:nFormations) {
      points(myScoresAndTime$dca1[myScoresAndTime$formation==(i-1)],
myScoresAndTime$dca2[myScoresAndTime$formation==(i-1)],
            pch=plotSymbols[i], cex=ptSize[i])
}
legend(x="topleft", legend=formations[sort(unique(myScoresAndTime$formation)
+1)], pt.cex=ptSize[sort(unique(myScoresAndTime$formation)+1)],
      pch=plotSymbols[sort(unique(myScoresAndTime$formation)+1)], bty="n")

######## MS Figure
# coded by stage
quartz(height=3.75, width=7)
par(mfrow=c(1,2), las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3,2.75,1,0),
mgp=c(1.75, 0.75, 0))
plot(myScoresAndTime$dca1, myScoresAndTime$dca2, type="n", xlab="DCA Axis 1
(Collection Scores)", ylab="DCA Axis 2 (Collection Scores)",
      main="Collections Scores", bty="n", xlim=c(-4,4), ylim=c(-3,4))
points(myScoresAndTime$dca1[myScoresAndTime$period==0], myScoresAndTime$dca2
[myScoresAndTime$period==0], pch=21, bg="white")
points(myScoresAndTime$dca1[myScoresAndTime$period==1], myScoresAndTime$dca2
[myScoresAndTime$period==1], pch=16)
legend(x="bottomright", legend=c("Chesterian", "Morrowan"), pch=c(21,16),
bty="n")
text(x=-4, y=4, labels="A", cex=2, adj=c(0,1))

# plot of species scores (axis 1 & 2)
taxonInfo <- taxonData[match(names(myData.dca.taxonscores[,2]), rownames
(taxonData)),]
plot(myData.dca.taxonscores[,1], myData.dca.taxonscores[,2], bty="n", xlim=c
(-4,4), ylim=c(-4,4), type="n",
      main="Genus Scores", xlab="DCA Axis 1 (Genus Scores)", ylab="DCA Axis 2
(Genus Scores)")
```

```
points(myData.dca.taxonscores[overlap==0,1], myData.dca.taxonscores
[overlap==0,2], pch=21)
points(myData.dca.taxonscores[overlap==1,1], myData.dca.taxonscores
[overlap==1,2], pch=16)
points(myData.dca.taxonscores[overlap==2,1], myData.dca.taxonscores
[overlap==2,2], pch=16, col="darkgray")
legend(x="bottomright", legend=c("Chesterian", "Morrowan", "both"), pch=c
(21,16,16), col=c("black", "black", "darkgray"), bty="n")
text(x=-4, y=4, labels="B", cex=2, adj=c(0,1))
########


# plot of species scores (axis 1 & 3) coded by order
taxonInfo <- taxonData[match(names(myData.dca.taxonscores[,1]), rownames
(taxonData)),]
orders <- unique(taxonInfo[,2])
nOrders <- length(orders)
orderColors <- rainbow(nOrders)
quartz(height=3.4, width=3.4)
par(las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3,2.75,0.5,0), mgp=c(1.75,
0.75, 0))
plot(myData.dca.taxonscores[,1], myData.dca.taxonscores[,3], bty="n", xlim=c
(-4,4), ylim=c(-4,4), type="n",
      xlab="DCA Axis 1 (Genus Scores)", ylab="DCA Axis 2 (Genus Scores)")
for (i in 1:nOrders) {
      points(myData.dca.taxonscores[taxonInfo[,2]==orders[i],1],
myData.dca.taxonscores[taxonInfo[,2]==orders[i],3], pch=16, col=orderColors
[i])
}
legend(x="bottomright", legend=orders, pch=16, col=orderColors, bty="n",
cex=0.75, pt.cex=1)


# boxplot of species scores (axis 1 & 3) coded by order
taxonAxis <- cbind(myData.dca.taxonscores, taxonInfo)
whichAxis <- 3
x <- boxplot(taxonAxis[,whichAxis] ~ taxonAxis[,5], taxonAxis, plot=FALSE)
y <- x$stats[3,]; names(y) <- x$names
orderSort <- names(sort(y))
quartz(height=3.4, width=3.4)
par(las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3,2.75,0.5,0), mgp=c(1.75,
0.75, 0))
plot(c(1:nOrders), seq(-5,5,length.out=nOrders), type="n", bty="n",
axes=FALSE, xlab="Order", ylab="DAC Axis 3 Genus Scores")
axis(side=1, at=1:nOrders)
axis(side=2, at=seq(-5,5,1))
for (i in 1:nOrders) {
      boxplot(taxonAxis[taxonAxis[,5]==orderSort[i],whichAxis], add=TRUE,
axes=FALSE, at=i)
}

# plot of species scores (axis 2 & genus abundance)
quartz(height=3.4, width=3.4)
```

```
par(las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3,2.75,0.5,0), mgp=c(1.75,
0.75, 0))
abundReg <- lm(myData.dca.taxonscores[,2] ~ colSums(myData)); summary
(abundReg)
abundEquation <- paste("y = ",round(abundReg$coefficients[1],2), " + ",round
(abundReg$coefficients[2],2),"x")
plot(colSums(myData), myData.dca.taxonscores[,2], bty="n", pch=16, xlim=c
(1,400), ylim=c(-4,4), xaxt="n", log="x",
      xlab="Genus Abundance", ylab="DCA Axis 2 (Genus Scores)")
axis(side=1, at=c(1,10,100,400), labels=TRUE)

# plot DCA axis 3 v. longitude
longReg <- lm(myData.dca.samplescores[,3] ~ collData[,long]); summary
(longReg)
equation <- paste("y = ",round(longReg$coefficients[1],2), " + ",round
(longReg$coefficients[2],2),"x")
quartz(height=3.5, width=3.4)
par(las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3,2.75,0.5,0.5), mgp=c(1.75,
0.75, 0))
plot(collData[,long], myData.dca.samplescores[,3], pch=16, xlab="Longitude",
ylab="DCA Axis 3 (Site Scores)", bty="n",
      xlim=c(-95.5,-93), ylim=c(-3,4))
abline(a=longReg$coefficients[1], longReg$coefficients[2])
text(x=-95.5, y=4, labels=equation, adj=0, font=3)

# site scores by period
myMiss.t1 <- decostand(myData[collData[,age]==0,], "total")
myMiss.t2 <- decostand(myMiss.t1, "max")
myMiss.dca <- decorana(myMiss.t2, iweigh=1)

myPenn.t1 <- decostand(myData[collData[,age]==1,], "total")
myPenn.t2 <- decostand(myPenn.t1, "max")
myPenn.dca <- decorana(myPenn.t2, iweigh=1)

myMiss.dca.samplescores <- scores(myMiss.dca, display=c("sites"), choices=c
(1,2,3))
myPenn.dca.samplescores <- scores(myPenn.dca, display=c("sites"), choices=c
(1,2,3))

myScoresAndTimeMiss <- data.frame(dca1=myMiss.dca.samplescores[,1],
dca2=myMiss.dca.samplescores[,2], dca3=myMiss.dca.samplescores[,3],
      period=collData[collData[,age]==0,age], formation=collData[collData
[,age]==0,formation],
      long=collData[collData[,age]==0,long])
myScoresAndTimePenn <- data.frame(dca1=myPenn.dca.samplescores[,1],
dca2=myPenn.dca.samplescores[,2], dca3=myPenn.dca.samplescores[,3],
      period=collData[collData[,age]==1,age], formation=collData[collData
[,age]==1,formation],
      long=collData[collData[,age]==1,long])

missS <- diversityMetrics(myData[collData[,age]==0,])[,2]
missGini <- diversityMetrics(myData[collData[,age]==0,])[,5]
missE <- diversityMetrics(myData[collData[,age]==0,])[,4]
missPIE <- diversityMetrics(myData[collData[,age]==0,])[,6]
```

```
missN <- diversityMetrics(myData[collData[,age]==0,])[,1]
pennS <- diversityMetrics(myData[collData[,age]==1,])[,2]
pennGini <- diversityMetrics(myData[collData[,age]==1,])[,5]
pennE <- diversityMetrics(myData[collData[,age]==1,])[,4]
pennPIE <- diversityMetrics(myData[collData[,age]==1,])[,6]
pennN <- diversityMetrics(myData[collData[,age]==1,])[,1]

# DCA 1 v. DCA 2 Miss
quartz(height=7, width=7)
par(mfrow=c(2,2), las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3,2.75,0.5,0),
mgp=c(1.75, 0.75, 0))
plot(myMiss.dca.samplescores[,1], myMiss.dca.samplescores[,2], bty="n",
xlim=c(-2,3), ylim=c(-3,3), type="n",
      xlab="DCA Axis 1 (Site Scores)", ylab="DCA Axis 2 (Site Scores)")
for (i in 1:2) {
      points(myMiss.dca.samplescores[,1][myScoresAndTimeMiss$formation==
(i-1)], myMiss.dca.samplescores[,2][myScoresAndTimeMiss$formation==(i-1)],
            pch=plotSymbols[i])
}
legend(x="bottomleft", legend=formations[1:2], pch=plotSymbols[1:2], bty="n")
text(x=-2,y=3, labels="A.   Chesterian (M)", cex=1.25, adj=0)

# DCA 1 v. DCA 2 Penn
plot(myPenn.dca.samplescores[,1], myPenn.dca.samplescores[,2], bty="n",
xlim=c(-2,3), ylim=c(-2,2), type="n",
      xlab="DCA Axis 1 (Site Scores)", ylab="DCA Axis 2 (Site Scores)")
for (i in 3:6) {
      points(myPenn.dca.samplescores[,1][myScoresAndTimePenn$formation==
(i-1)],
               myPenn.dca.samplescores[,2][myScoresAndTimePenn$formation==
(i-1)], pch=plotSymbols[i], cex=ptSize[i])
}
legend(x="bottomleft", legend=formations[sort(unique(myScoresAndTimePenn
$formation)+1)],
      pch=plotSymbols[sort(unique(myScoresAndTimePenn$formation)+1)],
bty="n", pt.cex=ptSize[sort(unique(myScoresAndTimePenn$formation)+1)])
text(x=-2,y=2, labels="B.   Morrowan (|P)", cex=1.25, adj=0)

# DCA 1 v. Gini
GiniRegMiss <- lm(myScoresAndTimeMiss$dca1 ~ missGini); summary(GiniRegMiss)
if (GiniRegMiss$coefficients[2] >= 0) {
      equationMissGini <- paste("y = ",round(GiniRegMiss$coefficients[1],2),
" + ",round(GiniRegMiss$coefficients[2],2),"x")
} else {
      equationMissGini <- paste("y = ",round(GiniRegMiss$coefficients[1],2),
" – ",abs(round(GiniRegMiss$coefficients[2],2)),"x")
}
plot(missGini, myMiss.dca.samplescores[,1], bty="n", pch=21, xlim=c(0,1),
ylim=c(-2,3),
      xlab="Simpson's D", ylab="DCA Axis 1 (Site Scores)")
abline(a=GiniRegMiss$coefficients[1], GiniRegMiss$coefficients[2])
text(x=0,y=3, labels="C.   Chesterian (M)", cex=1.25, adj=0)
text(x=0, y=2.5, labels=equationMissGini, adj=0, font=3)
text(x=0, y=2.15, labels=expression(paste("r"^"2", " =")), adj=0)
```

```
text(x=0.17, y=2.15, labels=round(cor(missGini, myMiss.dca.samplescores[,1])
^2,3))

# DCA 3 v. Longitude
longRegMiss <- lm(myScoresAndTimeMiss$dca3 ~ myScoresAndTimeMiss$long);
summary(longRegMiss)
longRegPenn <- lm(myScoresAndTimePenn$dca3 ~ myScoresAndTimePenn$long);
summary(longRegPenn)
equationMiss <- paste("y = ",round(longRegMiss$coefficients[1],2), " +
",round(longRegMiss$coefficients[2],2),"x")
plot(myScoresAndTimeMiss$long, myScoresAndTimeMiss$dca3, bty="n", xlim=c
(-96,-93), ylim=c(-3,3), pch=21,
      xlab="Longitude", ylab="DCA Axis 3 (Site Scores)")
abline(a=longRegMiss$coefficients[1], longRegMiss$coefficients[2])
text(x=-96,y=3, labels="D.   Chesterian (M)", cex=1.25, adj=0)
text(x=-96.0, y=2.5, labels=equationMiss, adj=0, font=3)
text(x=-96, y=2.15, labels=expression(paste("r"^"2", " =")), adj=0)
text(x=-95.5, y=2.15, labels=round(cor(myScoresAndTimeMiss$long,
myScoresAndTimeMiss$dca3)^2,3))


# DCA 3 v. Longitude Penn
quartz(height=3.4, width=3.4)
par(las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3,2.75,0.5,0), mgp=c(1.75,
0.75, 0))
plot(myScoresAndTimePenn$long, myScoresAndTimePenn$dca3, bty="n", xlim=c
(-96,-93), ylim=c(-2,2), pch=16,
      xlab="Longitude", ylab="DCA Axis 3 (Site Scores)")
text(x=-96,y=2, labels="Morrowan (|P)", cex=1.25, adj=0)


# DCA 2 v. diversity metrics
quartz(height=3.5, width=7)
par(mfrow=c(1,2), las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3,2.75,0.5,0),
mgp=c(1.75, 0.75, 0))
PIERegMiss <- lm(myScoresAndTimeMiss$dca1 ~ missPIE); summary(PIERegMiss)
equationMissPIE <- paste("y = ",round(PIERegMiss$coefficients[1],2), " +
",round(PIERegMiss$coefficients[2],2),"x")
plot(missPIE, myMiss.dca.samplescores[,1], bty="n", pch=21, xlim=c(0,1),
ylim=c(-2,3),
      xlab="PIE", ylab="DCA Axis 1 (Site Scores)")
text(x=0,y=3, labels="Chesterian (M)", cex=1.25, adj=0)
abline(a=PIERegMiss$coefficients[1], PIERegMiss$coefficients[2])
text(x=0, y=2.5, labels=equationMissPIE, adj=0, font=3)

plot(pennPIE, myPenn.dca.samplescores[,1], bty="n", pch=16, #xlim=c(-2,3),
ylim=c(-2,2),
      xlab="PIE", ylab="DCA Axis 1 (Site Scores)")
text(x=-2,y=2, labels="Chesterian (M)", cex=1.25, adj=0)


# boxplot of species scores (axis 1 & 3) coded by order
myMiss.dca.taxonscores <- scores(myMiss.dca, display=c("species"), choices=c
(1,2,3))
```

```
myPenn.dca.taxonscores <- scores(myPenn.dca, display=c("species"), choices=c
(1,2,3))

x <- taxonData[match(rownames(myMiss.dca.taxonscores), rownames(taxonData)),]

myTaxaAndTimeMiss <- cbind(myMiss.dca.taxonscores, x)
myTaxaAndTimePenn <- cbind(myPenn.dca.taxonscores, x)

whichAxis <- 1

sortMedian <- FALSE
if (sortMedian==TRUE) {
      a <- boxplot(myTaxaAndTimeMiss[,whichAxis] ~ myTaxaAndTimeMiss[,5],
myTaxaAndTimeMiss, plot=FALSE)
      b <- a$stats[3,]; names(b) <- a$names

      x <- boxplot(myTaxaAndTimePenn[,whichAxis] ~ myTaxaAndTimePenn[,5],
myTaxaAndTimePenn, plot=FALSE)
      y <- x$stats[3,]; names(y) <- x$names
} else {
      b <- vector(mode="numeric", length=nOrders)
      y <- b
      for (i in 1:nOrders) {
            b[i] <- mean(myTaxaAndTimeMiss[myTaxaAndTimeMiss[,5]==orders
[i],whichAxis])
            y[i] <- mean(myTaxaAndTimePenn[myTaxaAndTimePenn[,5]==orders
[i],whichAxis])
      }
      names(b) <- orders
      names(y) <- orders
}

orderSortMiss <- names(sort(b))
orderSortPenn <- names(sort(y))
orderRankMiss <- vector(mode="numeric", length=nTaxa)
orderRankPenn <- vector(mode="numeric", length=nTaxa)
for (i in 1:nOrders) {
      for (j in 1:nTaxa) {
            if (myTaxaAndTimeMiss[j,5]==orderSortMiss[i]) {
                  orderRankMiss[j] <- i
            }
            if (myTaxaAndTimePenn[j,5]==orderSortPenn[i]) {
                  orderRankPenn[j] <- i
            }
      }
}

linRegMiss <- lm(myTaxaAndTimeMiss[,whichAxis] ~ orderRankMiss); summary
(linRegMiss)
linRegPenn <- lm(myTaxaAndTimePenn[,whichAxis] ~ orderRankPenn); summary
(linRegPenn)

quartz(height=3.5, width=7)
```

```
par(mfrow=c(1,2), las=1, cex.lab=0.75, cex.axis=0.75, mar=c(6,2.75,1.5,0),
mgp=c(1.75, 0.75, 0))
plot(c(1:nOrders), seq(-4,4,length.out=nOrders), type="n", bty="n",
axes=FALSE, xlab="", ylab="DAC Axis 1 (Genus Scores)", main="Chesterian")
axis(side=2, at=seq(-4,4,1))
par(las=2)
axis(side=1, at=1:nOrders, labels <- orderSortMiss)
abline(a=linRegMiss$coefficients[1], b=linRegMiss$coefficients[2])
for (i in 1:nOrders) {
      x <- myTaxaAndTimeMiss[myTaxaAndTimeMiss[,5]==orderSortMiss
[i],whichAxis]
      points(rep(i, length(x)), x, pch=16)
}
text(x=1, y=-4, labels=paste("y = ", round(linRegMiss$coefficients[2],3), "x
- ", abs(round(linRegMiss$coefficients[1],3))), adj=c(0,0))
text(x=1, y=4, labels="A", cex=2, adj=c(0,1))

plot(c(1:nOrders), seq(-4,4,length.out=nOrders), type="n", bty="n",
axes=FALSE, xlab="", ylab="DAC Axis 1 (Genus Scores)", main="Morrowan")
axis(side=2, at=seq(-4,4,1))
par(las=2)
axis(side=1, at=1:nOrders, labels <- orderSortPenn)
abline(a=linRegPenn$coefficients[1], b=linRegPenn$coefficients[2])
for (i in 1:nOrders) {
      x <- myTaxaAndTimePenn[myTaxaAndTimePenn[,5]==orderSortPenn
[i],whichAxis]
      points(rep(i, length(x)), x, pch=16)
}
text(x=1, y=-4, labels=paste("y = ", round(linRegPenn$coefficients[2],3), "x
- ", abs(round(linRegPenn$coefficients[1],3))), adj=c(0,0))
text(x=1, y=4, labels="B", cex=2, adj=c(0,1))

if (runMDS == TRUE) {
#################  NMDS
      myMDS <- metaMDS(myData.t2, distance="bray", trymax=1000, k=3,
noshare=.01, autotransform=FALSE)

      # plot site scores
      myScoresAndTime <- data.frame(nmds1=myMDS$points[,1], nmds2=myMDS
$points[,2], period=collData[,age], formation=collData[,formation])

      plotSymbols <- c(21,24,16,17,15)
      quartz(height=4, width=3.4)
      par(las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3,2.75,0.5,0), mgp=c
(1.75, 0.75, 0))
      plot(myScoresAndTime$nmds1, myScoresAndTime$nmds2, type="n", xlab="NMDS
Axis 1 (Site Scores)", ylab="NMDS Axis 2 (Site Scores)", bty="n", xlim=c
(-2,2), ylim=c(-2,2))
      for (i in 1:5) {
            points(myScoresAndTime$nmds1[myScoresAndTime$formation==(i-1)],
myScoresAndTime$nmds2[myScoresAndTime$formation==(i-1)],
                  pch=plotSymbols[i])
      }
      legend(x="bottomleft", legend=formations, pch=plotSymbols, bty="n")
```

```
      # plot of species scores
      quartz(height=4, width=7)
      par(mfrow=c(1,2), las=1, cex.lab=0.75, cex.axis=0.75, mar=c
(3,2.75,0.5,0), mgp=c(1.75, 0.75, 0))
      plot(myMDS$species[,1], myMDS$species[,2], bty="n", xlim=c(-2,2),
ylim=c(-2,2), type="n",
            xlab="NMDS Axis 1 (Genus Scores)", ylab="NDMS Axis 2 (Genus
Scores)")
      points(myMDS$species[overlap==0,1], myMDS$species[overlap==0,2],
pch=21)
      points(myMDS$species[overlap==1,1], myMDS$species[overlap==1,2],
pch=16)
      points(myMDS$species[overlap==2,1], myMDS$species[overlap==2,2],
pch=16, col="darkgray")
      legend(x="topleft", legend=c("Chesterian", "Morrowan", "both"), pch=c
(21,16,16), col=c("black", "black", "darkgray"), bty="n",)

      plot(colSums(myData), myMDS$species[,2], bty="n", pch=16, xlim=c
(0,350), ylim=c(-2,2), xaxt="n",
            xlab="Genus Abundance", ylab="NMDS Axis 2 (Genus Scores)")
      axis(side=1, at=seq(0,350,50), labels=c("0", NA, "100", NA, "200", NA,
"300", NA))

      # plot NMDS axis 2 v. longitude
      longReg <- lm(myMDS$points[,2] ~ collData[,long]); summary(longReg)
      equation <- paste("y = ",round(longReg$coefficients[1],2), " + ",round
(longReg$coefficients[2],2),"x")
      quartz(height=3.5, width=3.4)
      par(las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3,2.75,0.5,0.5), mgp=c
(1.75, 0.75, 0))
      plot(collData[,long], myMDS$points[,2], pch=16, xlab="Longitude",
ylab="NMDS Axis 2 (Site Scores)", bty="n",
            xlim=c(-95.5,-93), ylim=c(-2,2))
      abline(a=longReg$coefficients[1], longReg$coefficients[2])
      text(x=-95.5, y=2, labels=equation, adj=0, font=3)
      text(x=-95.5, y=1.65, labels="slope not significant", adj=0, font=3,
cex=0.8)


      #################  PROCRUSTES
      quartz()
      myProcrustes <- procrustes(X=myMDS$points[,1:2],
Y=myData.dca.samplescores[,1:2]); myProcrustes; plot(myProcrustes)
}

t1 <- Sys.time()
difftime(t1,t0)
```

```
##############################
#####  Rank-abundance analysis
##############################

setwd("/Users/noelheim/Documents/Papers/OzarkPaper")

t0 <- Sys.time()

runBoot <- FALSE

# read in data
collections <- na2zero(as.matrix(read.csv(file="countData.csv", header=TRUE,
row.names=1)))[-60,] # 60 is a single monospecific bed/collection
collInfo <- read.csv(file="collectionInfo.csv", header=TRUE, row.names=1)
[-60,]
taxa <- colnames(collections)
nTaxa <- ncol(collections)
nCollections <- nrow(collections)
taxonInfo <- read.csv(file="taxonInfo.csv", header=TRUE, row.names=1)

for (i in 1:ncol(collInfo)) {
      if (colnames(collInfo)[i] == "Lat") {
            lat <- i
      } else if (colnames(collInfo)[i] == "Long") {
            long <- i
      } else if (colnames(collInfo)[i] == "Age") {
            age <- i
      }
}

################  RANK - ABUNDANCE
miss <- colSums(collections[collInfo$Age==0,])
penn <- colSums(collections[collInfo$Age==1,])
nMiss <- length(miss[miss>0])
nPenn <- length(penn[penn>0])
mississippian <- miss/sum(miss)*100
pennsylvanian <- penn/sum(penn)*100
both <- apply(rbind(abundance2occurrence(miss), abundance2occurrence(penn)),
2,sum)

pctData <- rbind(mississippian, pennsylvanian, both)

ranks <- c(1:nTaxa)
missPct <- rbind(pctData[,c(order(pctData[1,], decreasing = TRUE))], ranks)
pennPct <- rbind(pctData[,c(order(pctData[2,], decreasing = TRUE))], ranks)

missAbundTaxa <- colnames(missPct)[1:7]
pennAbundTaxa <- colnames(pennPct)[1:7]
pennAbundTaxa[2] <- "Antiquatonia"

maxRank <- trunc(max(length(pctData[1,pctData[1,]>0]), length(pctData
[2,pctData[2,]>0]))/10)*10+10
minPct <- 0.01
```

```
# spearman rank correlation
rankData <- rbind(miss=rank(1-pctData[1,pctData[3,]==2]), penn=rank(1-pctData
[2,pctData[3,]==2]))
spearCor <- cor.test(rankData[1,], rankData[2,], method="pearson") # pearson
== spearman when using ranks
rho <- spearCor$estimate
rho.ci <- spearCor$conf.int

########  Boostrap the data
if (runBoot == TRUE) {
      nBootstraps <- 10000
      missBoot <- matrix(0,nrow=nBootstraps, ncol=nTaxa, dimnames=list(c
(1:nBootstraps), taxa))
      pennBoot <- matrix(0,nrow=nBootstraps, ncol=nTaxa, dimnames=list(c
(1:nBootstraps), taxa))

      for (i in 1:nBootstraps) {
            x <- as.count(sample(census(miss), sum(miss), replace=TRUE))
            y <- match(names(x), names(miss))

            a <- as.count(sample(census(penn), sum(penn), replace=TRUE))
            b <- match(names(a), names(penn))

            for (j in 1:nTaxa) {
                  missBoot[i,y] <- x
                  pennBoot[i,b] <- a
            }
      }

      missPctBoot <- apply(missBoot, 2, mean)/sum(apply(missBoot, 2, mean))
*100
      missSdBoot <- apply(missBoot, 2, sd)/sum(apply(missBoot, 2, mean))*100
      pennPctBoot <- apply(pennBoot, 2, mean)/sum(apply(pennBoot, 2, mean))
*100
      pennSdBoot <- apply(pennBoot, 2, sd)/sum(apply(pennBoot, 2, mean))*100
      alpha <- 0.05
      degrees.freedom <- nBootstraps-1
      t.crit <- abs(qt(p=(alpha/2), df=degrees.freedom))

      missCI <- t.crit * missSdBoot
      pennCI <- t.crit * pennSdBoot

      bothBoot <- apply(rbind(abundance2occurrence(missPctBoot),
abundance2occurrence(pennPctBoot)),2,sum)

      pctBoot <- rbind(missPctBoot, pennPctBoot, both, missCI, pennCI)

      ranks <- c(1:nTaxa)
      missBootData <- rbind(pctBoot[,c(order(pctBoot[1,], decreasing =
TRUE))], ranks)
      pennBootData <- rbind(pctBoot[,c(order(pctBoot[2,], decreasing =
TRUE))], ranks)

      save(missBootData, pennBootData, file="rank_abund_boot")
```

```
} else {
	load("rank_abund_boot")
}

q <- match(colnames(missBootData), colnames(missPct))
cor(missBootData[6,], missPct[4,q], method="spearman")
cor(missBootData[6,1:18], missPct[4,q[1:18]], method="spearman")

q <- match(colnames(pennBootData), colnames(pennPct))
cor(pennBootData[6,], pennPct[4,q], method="spearman")
cor(pennBootData[6,1:7], pennPct[4,q[1:7]], method="spearman")

missPlus <- missBootData[1,1:nMiss]+missBootData[4,1:nMiss]
missMinus <- missBootData[1,1:nMiss]-missBootData[4,1:nMiss]; for (i in
1:nMiss) {if (missMinus[i]<minPct) {missMinus[i] <- minPct}}
pennPlus <- pennBootData[2,1:nPenn]+pennBootData[5,1:nPenn]
pennMinus <- pennBootData[2,1:nPenn]-pennBootData[5,1:nPenn]; for (i in
1:nPenn) {if (pennMinus[i]<minPct) {pennMinus[i] <- minPct}}

# spearman rank correlation
rankDataBoot <- rbind(miss=rank(1-missBootData[1,pctData[3,]==2]), penn=rank
(1-missBootData[2,pctData[3,]==2]))

spearCorBoot <- cor.test(rankDataBoot[1,], rankDataBoot[2,],
method="pearson") # pearson == spearman when using ranks
rhoBoot <- spearCorBoot$estimate
rhoBoot.ci <- spearCorBoot$conf.int

# Kolmogorov-Smirnov 2-sample test
ksData <- ks.test(missBootData[1, missBootData[1,]>0], missBootData[2,
missBootData[2,]>0])

quartz(height=9, width=7)
par(mfrow=c(3,1), cex.lab=0.75, cex.axis=0.75, las=1, mar=c(3.5, 3, 0.5,
0.00) + 0.1, mgp=c(2.25, 1, 0))
plot(missPct[1,missPct[1,]>0], type="n", xlim=c(0,maxRank), ylim=c(minPct,
100), log="y", xaxt="n", yaxt="n",
	xlab="", ylab="percent abundance", bty="n")
points(missPct[4,missPct[1,]>0 & missPct[3,]==1], missPct[1,missPct[1,]>0 &
missPct[3,]==1], pch=21)
points(missPct[4,missPct[1,]>0 & missPct[3,]==2], missPct[1,missPct[1,]>0 &
missPct[3,]==2], pch=15)
axis(side=1, at=c(0,10,20,30,40), labels=FALSE)
axis(side=2, at=c(0.01,0.1,1,10,100), labels=c(0.01,0.1,1,10,100))
text(x=c(1:7)+3, y=missPct[1,1:7]+c(35, 17, 10, 2, 0,-1,1.75),
labels=missAbundTaxa, cex=0.75, font=3, adj=0)
arrows(x0=c(1:7)+2.75, y0=missPct[1,1:7]+c(35, 17, 10, 2, 0,-1,1.75), x1=c
(1:7)+0.5, y1=missPct[1,1:7]+c(5,2,1,0.5,0,-0.5,0.7),
	length = 0.1, angle = 10, lwd=0.5)
legend(x="bottomleft", legend=c("Chesterian only", "Chesterian and
Morrowan"), bty="n", pch=c(21,15), inset=0.03)
text(x=40, y=100, labels="Chesterian (M)", adj=1, cex=1.5)
```

```
plot(pennPct[2,pennPct[2,]>0], type="n", xlim=c(0,maxRank), ylim=c(minPct,
100), log="y", xaxt="n", yaxt="n",
      xlab="", ylab="percent abundance", bty="n")
points(pennPct[4,pennPct[2,]>0 & pennPct[3,]==1], pennPct[2,pennPct[2,]>0 &
pennPct[3,]==1], pch=25)
points(pennPct[4,pennPct[2,]>0 & pennPct[3,]==2], pennPct[2,pennPct[2,]>0 &
pennPct[3,]==2], pch=15)
      axis(side=1, at=c(0,10,20,30,40), labels=FALSE)
axis(side=2, at=c(0.01,0.1,1,10,100), labels=c(0.01,0.1,1,10,100))
text(x=c(1:7)+c(rep(3,6),2), y=pennPct[2,1:7]+c(18, 8, 4, 2, 0,-0.5,-1.5),
labels=pennAbundTaxa, cex=0.75, font=3, adj=0)
arrows(x0=c(1:7)+c(rep(2.75,6),1.75), y0=pennPct[2,1:7]+c(18, 8, 4, 2,
0,-0.5,-1.5), x1=c(1:7)+c(rep(0.8,6),0.5), y1=pennPct[2,1:7]+c
(5,2,1,0.5,0,0,-0.5),
      length = 0.1, angle = 10, lwd=0.5)
legend(x="bottomleft", legend=c("Morrowan only", "Chesterian and Morrowan"),
bty="n", pch=c(25,15), inset=0.03)
text(x=40, y=100, labels="Morrowan (|P)", adj=1, cex=1.5)

missX <- c(1:nMiss)
pennX <- c(1:nPenn)

# mississippian curve
plot(c(1:nMiss)/nMiss, missBootData[1,missBootData[1,]>0], type="n", xlim=c
(0,maxRank), ylim=c(minPct,100), log="y", xaxt="n", yaxt="n",
      xlab="genus rank in abundance", ylab="percent abundance", bty="n")
polygon(c(missX,rev(missX)), c(missPlus,rev(missMinus)), col=rgb(0.2, 0.2,
0.2, 0.2), border=NA)
polygon(c(pennX,rev(pennX)), c(pennPlus,rev(pennMinus)), col=rgb(0.2, 0.2,
0.2, 0.2), border=NA)

points(missX, missBootData[1,missBootData[1,]>0], type="l")
points(missBootData[6,missBootData[1,]>0 & missBootData[3,]==1], missBootData
[1,missBootData[1,]>0 & missBootData[3,]==1], pch=21, bg="white")
points(missBootData[6,missBootData[1,]>0 & missBootData[3,]==2], missBootData
[1,missBootData[1,]>0 & missBootData[3,]==2], pch=15)

# pennsylvanian curve
points(pennX, pennBootData[2,pennBootData[2,]>0], type="l")
points(pennBootData[6,pennBootData[2,]>0 & pennBootData[3,]==1], pennBootData
[2,pennBootData[2,]>0 & pennBootData[3,]==1], pch=25, bg="white")
points(pennBootData[6,pennBootData[2,]>0 & pennBootData[3,]==2], pennBootData
[2,pennBootData[2,]>0 & pennBootData[3,]==2], pch=15)

axis(side=1, at=c(0,10,20,30,40), labels=TRUE)
axis(side=2, at=c(0.01,0.1,1,10,100), labels=c(0.01,0.1,1,10,100))
legend(x="bottomleft", legend=c("Chesterian only", "Chesterian and Morrowan",
"Morrowan only"),
      bty="n", pch=c(21,15,25), inset=0.03)
text(x=40, y=100, labels="Spearman rank correlation (95% CI)", adj=1,
cex=1.6)
text(x=35, y=40, labels=paste(round(rhoBoot.ci[1],3), " ≥ "), adj=1, cex=1.5)
text(x=35.25, y=40, labels=expression(paste(rho, " ≤ ")), adj=0, cex=1.5)
text(x=40, y=40, labels=round(rhoBoot.ci[2],3), adj=1, cex=1.5)
```

```
text(x=40, y=15, labels="Kolmogorov-Smirnov test", adj=1, cex=1.6)
text(x=40, y=6, labels=paste("D = ",round(ksData$statistic,3), "; p-value = 
",round(ksData$p.value,3)), adj=1, cex=1.5)


quartz(height=7, width=7)
layout(matrix(c(1,2,3,3), nrow=2, ncol=2, byrow=TRUE), widths = rep(0.5,2),
heights=rep(0.5,2))
par(cex.lab=0.75, cex.axis=0.75, las=1, mar=c(3.5, 3, 1, 0.00) + 0.1, mgp=c
(2.25, 1, 0))
plot(missPct[1,missPct[1,]>0], type="n", xlim=c(0,maxRank), ylim=c(minPct,
100), log="y", xaxt="n", yaxt="n",
      main="Chesterian", xlab="genus rank in abundance", ylab="percent
abundance", bty="n")
points(missPct[4,missPct[1,]>0 & missPct[3,]==1], missPct[1,missPct[1,]>0 &
missPct[3,]==1], pch=21)
points(missPct[4,missPct[1,]>0 & missPct[3,]==2], missPct[1,missPct[1,]>0 &
missPct[3,]==2], pch=15)
axis(side=1, at=c(0,10,20,30,40), labels=TRUE)
axis(side=2, at=c(0.01,0.1,1,10,100), labels=c(0.01,0.1,1,10,100))
text(x=c(1:7)+3, y=missPct[1,1:7]+c(35, 17, 10, 2, 0,-1,1.75),
labels=missAbundTaxa, cex=0.75, font=3, adj=0)
arrows(x0=c(1:7)+2.75, y0=missPct[1,1:7]+c(35, 17, 10, 2, 0,-1,1.75), x1=c
(1:7)+0.5, y1=missPct[1,1:7]+c(5,2,1,0.5,0,-0.5,0.7),
      length = 0.1, angle = 10, lwd=0.5)
legend(x="bottomleft", legend=c("Chesterian genera", "Chesterian and Morrowan
genera"), bty="n", pch=c(21,15), inset=0.03)
text(x=0, y=100, labels="A", adj=c(0,1), cex=2)


plot(pennPct[2,pennPct[2,]>0], type="n", xlim=c(0,maxRank), ylim=c(minPct,
100), log="y", xaxt="n", yaxt="n",
      main="Morrowan", xlab="genus rank in abundance", ylab="", bty="n")
points(pennPct[4,pennPct[2,]>0 & pennPct[3,]==1], pennPct[2,pennPct[2,]>0 &
pennPct[3,]==1], pch=25)
points(pennPct[4,pennPct[2,]>0 & pennPct[3,]==2], pennPct[2,pennPct[2,]>0 &
pennPct[3,]==2], pch=15)
      axis(side=1, at=c(0,10,20,30,40), labels=TRUE)
axis(side=2, at=c(0.01,0.1,1,10,100), labels=FALSE)
text(x=c(1:6)+rep(3,6), y=pennPct[2,1:6]+c(18, 8, 4, 2, 0,-0.5),
labels=pennAbundTaxa[1:6], cex=0.75, font=3, adj=0)
text(x=9, y=pennPct[7]+0.35, labels=pennAbundTaxa[7], cex=0.75, font=3,
adj=1)
arrows(x0=c(1:7)+c(rep(2.75,6),-2.5), y0=pennPct[2,1:7]+c(18, 8, 4, 2,
0,-0.5,-1.5), x1=c(1:7)+c(rep(0.8,6),-0.2), y1=pennPct[2,1:7]+c
(5,2,1,0.5,0,0,-0.5),
      length = 0.1, angle = 10, lwd=0.5)
legend(x="bottomleft", legend=c("Morrowan genera", "Chesterian and Morrowan
genera"), bty="n", pch=c(25,15), inset=0.03)
text(x=0, y=100, labels="B", adj=c(0,1), cex=2)

missX <- c(1:nMiss)
pennX <- c(1:nPenn)
```

```
# mississippian curve
par(cex.lab=0.75, cex.axis=0.75, las=1, mar=c(3.5, 3, 0.5, 0.00) + 0.1, mgp=c
(2.25, 1, 0))
plot(c(1:nMiss)/nMiss, missBootData[1,missBootData[1,]>0], type="n", xlim=c
(0,maxRank), ylim=c(minPct,100), log="y", xaxt="n", yaxt="n",
      xlab="genus rank in abundance", ylab="percent abundance", bty="n")
polygon(c(missX,rev(missX)), c(missPlus,rev(missMinus)), col=rgb(0.2, 0.2,
0.2, 0.2), border=NA)
polygon(c(pennX,rev(pennX)), c(pennPlus,rev(pennMinus)), col=rgb(0.2, 0.2,
0.2, 0.2), border=NA)

points(missX, missBootData[1,missBootData[1,]>0], type="l")
points(missBootData[6,missBootData[1,]>0 & missBootData[3,]==1], missBootData
[1,missBootData[1,]>0 & missBootData[3,]==1], pch=21, bg="white")
points(missBootData[6,missBootData[1,]>0 & missBootData[3,]==2], missBootData
[1,missBootData[1,]>0 & missBootData[3,]==2], pch=15)

# pennsylvanian curve
points(pennX, pennBootData[2,pennBootData[2,]>0], type="l")
points(pennBootData[6,pennBootData[2,]>0 & pennBootData[3,]==1], pennBootData
[2,pennBootData[2,]>0 & pennBootData[3,]==1], pch=25, bg="white")
points(pennBootData[6,pennBootData[2,]>0 & pennBootData[3,]==2], pennBootData
[2,pennBootData[2,]>0 & pennBootData[3,]==2], pch=15)

axis(side=1, at=c(0,10,20,30,40), labels=TRUE)
axis(side=2, at=c(0.01,0.1,1,10,100), labels=c(0.01,0.1,1,10,100))
legend(x="bottomleft", legend=c("Chesterian genera", "Chesterian and Morrowan
genera", "Morrowan genera"),
      bty="n", pch=c(21,15,25), inset=0.03)
text(x=0, y=100, labels="C", adj=c(0,1), cex=2)


### rank abund genera
sharedMiss <- c(missPct[1,missPct[1,]>0 & missPct[3,]==2])
missOnly <- c(missPct[1,missPct[1,]>0 & missPct[3,]==1])
sharedPenn <- c(pennPct[2,pennPct[2,]>0 & pennPct[3,]==2])
pennOnly <- c(pennPct[2,pennPct[2,]>0 & pennPct[3,]==1])

missInfo <- cbind(taxonInfo[match(names(sharedMiss), rownames(taxonInfo)),],
Genus=names(sharedMiss))
pennInfo <- cbind(taxonInfo[match(names(sharedPenn), rownames(taxonInfo)),],
Genus=names(sharedPenn))


######## analysis of genus ranges and where they are coming from

t1 <- Sys.time()
difftime(t1,t0)
```

```
##############################
#####  Similarity analysis
##############################

setwd("/Users/noelheim/Documents/Papers/OzarkPaper")
t0 <- Sys.time()

nBootstraps <- 1000
runBootstrap <- FALSE

# read in data
collections <- remove.rare(na2zero(as.matrix(read.csv(file="countData.csv",
header=TRUE, row.names=1))),1)[-60,] # 60 is a single collection,
monospecific bed
collInfo <- read.csv(file="collectionInfo.csv", header=TRUE, row.names=1)
[-60,]

columnNames <- colnames(collInfo)
for (i in 1:length(columnNames)) {
      if (columnNames[i]=="Lat") {
            lat <- i
      } else if (columnNames[i]=="Long") {
            long <- i
      } else if (columnNames[i]=="Age") {
            age <- i
      }
}

nColl <- nrow(collections)
nTaxa <- ncol(collections)
taxa <- colnames(collections)
nInt <- 2
xNames <- c("Chesterian", "Morrowan")

mississippian <- collections[collInfo$Age==0,]
missInfo <- collInfo[collInfo$Age==0,]
pennsylvanian <- collections[collInfo$Age==1,]
pennInfo <- collInfo[collInfo$Age==1,]

missBedNo <- unique(missInfo$Bed_num)
pennBedNo <- unique(pennInfo$Bed_num)

missData <- matrix(nrow=length(missBedNo), ncol=nTaxa, dimnames=list(c
(1:length(missBedNo)), taxa))
pennData <- matrix(nrow=length(pennBedNo), ncol=nTaxa, dimnames=list(c
(1:length(pennBedNo)), taxa))
for (i in 1:length(missBedNo)) {
      missData[i,] <- colSums(mississippian[missInfo[,2]==missBedNo[i],])
}
for (i in 1:length(pennBedNo)) {
      pennData[i,] <- colSums(pennsylvanian[pennInfo[,2]==pennBedNo[i],])
}

nMiss <- nrow(missData)
```

```
nPenn <- nrow(pennData)
n <- c(nMiss^2/2-(nMiss/2), nPenn^2/2-(nPenn/2))

if (runBootstrap==TRUE) {
      missBoot <- matrix(nrow=nBootstraps, ncol=n[1])
      pennBoot <- matrix(nrow=nBootstraps, ncol=n[2])
      for (i in 1:nBootstraps) {
            missMorisita <- matrix(nrow=nMiss, ncol=nMiss)
            pennMorisita <- matrix(nrow=nPenn, ncol=nPenn)

            for (j in 1:nMiss) {
                  for (k in (j+1):nMiss) {
                        x1 <- vector(mode="numeric", length=nTaxa); names(x1)
<- taxa
                        x2 <- x1
                        if(k > nMiss) {
                              break
                        } else {
                              y1 <- as.count(sample(census(missData[j,]), sum
(missData[j,]), replace=TRUE))
                              x1[match(names(y1), names(x1))] <- y1
                              y2 <- as.count(sample(census(missData[k,]), sum
(missData[k,]), replace=TRUE))
                              x2[match(names(y2), names(x2))] <- y2
                              missMorisita[j,k] <- morisita.horn(x1,x2)
                        }
                  }
            }

            for (j in 1:nPenn) {
                  for (k in (j+1):nPenn) {
                        x1 <- vector(mode="numeric", length=nTaxa); names(x1)
<- taxa
                        x2 <- x1
                        if(k > nPenn) {
                              break
                        } else {
                              y1 <- as.count(sample(census(pennData[j,]), sum
(pennData[j,]), replace=TRUE))
                              x1[match(names(y1), names(x1))] <- y1
                              y2 <- as.count(sample(census(pennData[k,]), sum
(pennData[k,]), replace=TRUE))
                              x2[match(names(y2), names(x2))] <- y2
                              pennMorisita[j,k] <- morisita.horn(x1,x2)
                        }
                  }
            }
            missBoot[i,] <- as.vector(missMorisita[is.na(missMorisita)
==FALSE])
            pennBoot[i,] <- as.vector(pennMorisita[is.na(pennMorisita)
==FALSE])
      }
      save(missBoot, pennBoot, nBootstraps, file="morisitaBooted")
} else {
```

```
      load("morisitaBooted")
}


morisitaData <- c(mean(apply(missBoot,2,mean)), mean(apply(pennBoot,2,
mean)));names(morisitaData) <- xNames
sdMorisita <- c(sqrt(sum(apply(missBoot,2,var))/nBootstraps), sqrt(sum(apply
(pennBoot,2, var))/nBootstraps))

n <- nBootstraps

alpha <- 0.05
degrees.freedom <- n-1
t.crit <- abs(qt(p=(alpha/2), df=degrees.freedom))
z.crit <- abs(qnorm(p=(alpha/2)))

ciMorisita <- t.crit * sdMorisita

morisitaMean <- morisitaData
morisitaPlus <- morisitaMean + ciMorisita
morisitaMinus <- morisitaMean - ciMorisita



quartz(height=3.5, width=7)
par(mfrow=c(1,2), cex.axis=0.75, cex.lab=0.75, las=1, mar=c(2.5,3.5,0.5,0),
mgp=c(2.5, 1, 0), las=1)
x <- barplot(morisitaMean, xlab=xNames, ylab="Morisita-Horn index", ylim=c
(0,0.4))
for (i in 1:2) {
      lines(rep.int(x[i],2), c(morisitaPlus[i], morisitaMinus[i]))
}
text(x=0.4, y=0.4, labels="A", adj=c(1,1), cex=2)

par(mar=c(2, 2.75, 0, 0) + 0.1, mgp=c(2, 0.75, 0))
boxplot(log(apply(missBoot,2,mean)/(1-apply(missBoot,2,mean))), log(apply
(pennBoot,2,mean)/(1-apply(pennBoot,2,mean))),
      range=1.5, ylim=c(-9,3), yaxt="n", varwidth=TRUE, frame.plot=FALSE,
notch=FALSE, xaxt="n", ylab="logit(Morisita-Horn index)")
axis(side=1, at = c(1,2), labels=xNames, tick = FALSE, line = NA)
axis(side=2, at = seq(-9,3,3), labels = TRUE)
text(x=0.65, y=3, labels="B", adj=c(1,1), cex=2)

morisitaCollMiss <- vector(mode="numeric", length=nMiss)
morisitaCollPenn <- vector(mode="numeric", length=nPenn)

missMeta <- colSums(missData)
pennMeta <- colSums(pennData)

for (i in 1:nMiss) {
      morisitaCollMiss[i] <- morisita(missData[i,], missMeta)
}
for (i in 1:nPenn) {
      morisitaCollPenn[i] <- morisita(pennData[i,], pennMeta)
```

```
}

meanMeta <- c(mean(morisitaCollMiss), mean(morisitaCollPenn)); names
(meanMeta) <- c("Ch. (M)", "Mor. (|P)")
sdMeta <- c(sd(morisitaCollMiss), sd(morisitaCollPenn))
degrees.freedom <- c(nMiss, nPenn)-1
t.crit <- abs(qt(p=(alpha/2), df=degrees.freedom))
ciMeta <- t.crit * sdMeta/sqrt(c(nMiss, nPenn))

quartz(height=3.5, width=7)
par(mfrow=c(1,2), cex.axis=0.75, cex.lab=0.75, las=1, mar=c(2.5,3.5,0.5,0),
mgp=c(2.5, 1, 0), las=1)
x <- barplot(meanMeta, ylab="Morisita index", ylim=c(0,0.8))
for (i in 1:2) {
      lines(rep.int(x[i],2), c(meanMeta[i] +ciMeta[i], meanMeta[i] - ciMeta
[i]))
}

par(mar=c(2, 2.75, 0, 0) + 0.1, mgp=c(2, 0.75, 0))
boxplot(morisitaCollMiss, morisitaCollPenn, range=1.5, ylim=c(0,1),
      varwidth=TRUE, frame.plot=FALSE, notch=FALSE, xaxt="n", ylab="Morisita
index")
axis(side=1, at = c(1,2), labels = c("Ch. (M)", "Mor. (|P)"), tick = FALSE,
line = NA)

missRC <- 1-vegdist(remove.rare(missData,1), method="raup", binary=TRUE)
pennRC <- 1-vegdist(remove.rare(pennData,1), method="raup", binary=TRUE)

missDist <- matrix(nrow=nMiss-1, ncol=nMiss-1, dimnames=list(c(2:nMiss), c(1:
(nMiss-1))))
pennDist <- matrix(nrow=nPenn-1, ncol=nPenn-1, dimnames=list(c(2:nPenn), c(1:
(nPenn-1))))

for (i in 1:(nMiss-1)) {
      for (j in 1:(nMiss-1)) {
            if(j > i) {
                  break
            } else {
                  missDist[i,j] <- sqrt((missInfo[i,lat]-missInfo[i+1,lat])^2
+ (missInfo[i,long]-missInfo[1+1,long])^2)
            }
      }
}

for (i in 1:(nPenn-1)) {
      for (j in 1:(nPenn-1)) {
            if(j > i) {
                  break
            } else {
                  pennDist[i,j] <- sqrt((pennInfo[i,lat]-pennInfo[i+1,lat])^2
+ (pennInfo[i,long]-pennInfo[1+1,long])^2)
            }
      }
}
```

```
quartz(width=7, height=3)
par(mfrow=c(1,2), las=1, cex.lab=0.75, cex.axis=0.75, mar=c(3,2.75,1,0),
mgp=c(2, 0.75, 0), bty="n")
plot(as.vector(missDist[is.na(missDist)==FALSE]), as.vector(missRC), pch=21,
xlim=c(0,1.5), ylim=c(0,1),
      xlab="distance in degrees", ylab="Raup-Crick index")
plot(as.vector(pennDist[is.na(pennDist)==FALSE]), as.vector(pennRC), pch=16,
xlim=c(0,2), ylim=c(0,1),
      xlab="distance in degrees", ylab="")

missFreq <- hist(missRC, breaks=20, plot=FALSE)$counts
pennFreq <- hist(pennRC, breaks=20, plot=FALSE)$counts

yMax <- 25
sigColors <- c("darkgray", "black")
barColors <- c(sigColors[1], rep(NA,18), sigColors[2])
barplot(missFreq/sum(missFreq)*100, ylim=c(0,yMax), yaxt="n",
main="Chesterian (M)", ylab="percent collections", space=0, col=barColors)
axis(side=1, at=seq(0,20,4), labels=seq(0,1,.2))
axis(side=2, at=seq(0,yMax, 5))
mtext("Raup-Crick Index", side=1, cex=0.75, line=1.75)
legend(x="topleft", bty="n", cex=0.75, fill=sigColors,
      legend=c(expression(paste("significantly dissimilar at ", alpha, " =
0.05")),
               expression(paste("significantly similar at ", alpha, " =
0.05"))))
barplot(pennFreq/sum(pennFreq)*100, ylim=c(0,yMax), yaxt="n", main="Morrowan
(|P)", space=0, col=barColors)
mtext("Raup-Crick Index", side=1, cex=0.75, line=1.75)
axis(side=1, at=seq(0,20,4), labels=seq(0,1,.2))
axis(side=2, at=seq(0,yMax, 5), labels=FALSE)

t1 <- Sys.time()
difftime(t1,t0)
```

```
##############################
#####  Range analysis of PBDB genera
##############################

setwd("/Users/noelheim/Documents/Papers/OzarkPaper/PBDB_MyData")

t0 <- Sys.time()

# read in raw output matrix from PBDB
      # col 1 = genus resolution
      # col 2 = genus name
      # last two cols are class and order
      # rest of columns are collection numbers (preceeded by X)
      # rows at end are collection info

### find mean paleolat and paleolong for my field data
load("collectionInfo")
meanLat <- mean(as.numeric(collectionInfo[,colnames(collectionInfo)
=="collections.paleolatdec"]))
meanLong <- mean(as.numeric(collectionInfo[,colnames(collectionInfo)
=="collections.paleolngdec"]))


setwd("/Users/noelheim/Documents/Papers/OzarkPaper/PBDB_09April2008")


###################################
##                               ##
##      Mississippian Taxa       ##
##                               ##
###################################
load("fauna_M")
load("taxa_M")
load("collectionInfo_M")

missTaxa <- c
("Echinoconchus","Inflatia","Ovatia","Spirifer","Diaphragmus","Orthotetes","E
umetria","Buxtonia",

"Reticulariina","Athyris","Torynifer","Schuchertella","Tetracamera","Productu
s","Streptorhynchus",

"Schellwienella","Chonetes","Camarophoria","Girtyella","Adectorhynchus","Brac
hythyris","Terebratuloid_indet")

for (i in 1:ncol(collectionInfo)) {
      columnNames <- colnames(collectionInfo)
      if (columnNames[i] == "collections.paleolatdec") {
            lat <- i
      } else if (columnNames[i] == "collections.paleolngdec") {
            long <- i
      } else if (columnNames[i] == "collections.stage") {
            stage <- i
      } else if (columnNames[i] == "collections.10mybin") {
```

```
            bin <- i
      } else if (columnNames[i] == "collections.period") {
            period <- i
      } else if (columnNames[i] == "collections.ma_min") {
            minInt <- i
      } else if (columnNames[i] == "collections.ma_max") {
            maxInt <- i
      }
}

collectionsHolder <- cull.rareAndDepaup(faunaData[collectionInfo[,period] ==
"Carboniferous" & as.numeric(collectionInfo[,minInt]) >= 339.4,],1,1)

# sort collections columns from most abundant to least
collections <- collectionsHolder[,match(missTaxa, colnames
(collectionsHolder))[is.na(match(missTaxa, colnames(collectionsHolder)))
==FALSE]]
collInfo <- collectionInfo[match(rownames(collections), rownames
(collectionInfo)),]

taxa <- colnames(collections)
nTaxa <- length(taxa)

missDistanceMean <- vector(mode="numeric", length=nTaxa); names
(missDistanceMean) <- taxa
missDistanceMedian <- vector(mode="numeric", length=nTaxa); names
(missDistanceMedian) <- taxa

quartz(height=7, width=7)
pointShading <- rgb(0.2, 0.2, 0.2, 0.2)
xLabs <- c(rep("",12), rep("paleolongitude",4))
yLabs <- c("paleolatitude", rep("",3), "paleolatitude", rep("",3),
"paleolatitude", rep("",3), "paleolatitude", rep("",3))
par(mfrow=c(4,4), bty="n", mar=c(4, 3.5, 1, 0.5) + 0.1, mgp=c(2.7, 1, 0),
las=1, font.main=3)
for (i in 1:nTaxa) {
      coordinates <- cbind(paleolong=as.numeric(collInfo[collections[,i]
==1,long]), paleolat=as.numeric(collInfo[collections[,i]==1,lat]))
      plot(coordinates, xlim=c(-80,160), ylim=c(-40,40), xlab=xLabs[i],
ylab=yLabs[i], main=colnames(collections)[i], xaxt="n", type="n")
      abline(h=0, lwd=0.75)
      points(meanLong, meanLat, cex=3, pch=4)
      points(coordinates, xlim=c(-80,160), ylim=c(-40,40), col=pointShading,
cex=1.5, pch=16)
      axis(side=1, at=seq(-80,160,80))

      distance <- sqrt((coordinates[,1]-meanLong)^2 + (coordinates[,2]-
meanLat)^2)
      missDistanceMean[i] <- mean(distance)
      missDistanceMedian[i] <- median(distance)

      text(x=160, y=40, labels=paste("d = ", round(missDistanceMean[i],2)),
font=3, adj=c(1,1))
}
```

```
###################################
##                               ##
##      Pennsylvanian Taxa       ##
##                               ##
###################################
load("fauna_P")
load("taxa_P")
load("collectionInfo_P")

pennTaxa <- c
("Antiquatonia","Tesuquea","Phricodothyris","Sandia","Plicochonetes","Desmoin
esia","Echinaria","Derbyia",

"Krotovia","Beecheria","Leptaena","Zia","Pulchratia","Neochonetes")

for (i in 1:ncol(collectionInfo)) {
      columnNames <- colnames(collectionInfo)
      if (columnNames[i] == "collections.paleolatdec") {
            lat <- i
      } else if (columnNames[i] == "collections.paleolngdec") {
            long <- i
      } else if (columnNames[i] == "collections.stage") {
            stage <- i
      } else if (columnNames[i] == "collections.10mybin") {
            bin <- i
      } else if (columnNames[i] == "collections.period") {
            period <- i
      } else if (columnNames[i] == "collections.ma_min") {
            minInt <- i
      } else if (columnNames[i] == "collections.ma_max") {
            maxInt <- i
      }
}

collectionsHolder <- cull.rareAndDepaup(faunaData[collectionInfo[,period] ==
"Carboniferous" & as.numeric(collectionInfo[,minInt]) >= 318.1,],1,1)

# sort collections columns from most abundant to least
collections <- collectionsHolder[,match(pennTaxa, colnames
(collectionsHolder))[is.na(match(pennTaxa, colnames(collectionsHolder)))
==FALSE]]
collInfo <- collectionInfo[match(rownames(collections), rownames
(collectionInfo)),]

taxa <- colnames(collections)
nTaxa <- length(taxa)

pennDistanceMean <- vector(mode="numeric", length=nTaxa); names
(pennDistanceMean) <- taxa
pennDistanceMedian <- vector(mode="numeric", length=nTaxa); names
(pennDistanceMedian) <- taxa
```

```
quartz(height=3.5, width=7)
xLabs <- c(rep("",4), rep("paleolongitude",4))
yLabs <- c("paleolatitude", rep("",3), "paleolatitude", rep("",3))
par(mfrow=c(2,4), bty="n", mar=c(4, 3.5, 1, 0.5) + 0.1, mgp=c(2.7, 1, 0),
las=1, font.main=3)
for (i in 1:nTaxa) {
      coordinates <- cbind(paleolong=as.numeric(collInfo[collections[,i]
==1,long]), paleolat=as.numeric(collInfo[collections[,i]==1,lat]))
      plot(coordinates, xlim=c(-80,160), ylim=c(-40,40), xlab=xLabs[i],
ylab=yLabs[i], main=colnames(collections)[i], xaxt="n", type="n")
      abline(h=0, lwd=0.75)
      points(meanLong, meanLat, cex=3, pch=4)
      points(coordinates, xlim=c(-60,180), ylim=c(-60,40), col=pointShading,
cex=1.5, pch=16)
      axis(side=1, at=seq(-80,160,80))

      distance <- sqrt((coordinates[,1]-meanLong)^2 + (coordinates[,2]-
meanLat)^2)
      pennDistanceMean[i] <- mean(distance)
      pennDistanceMedian[i] <- median(distance)

      text(x=160, y=40, labels=paste("d = ", round(pennDistanceMean[i],2)),
font=3, adj=c(1,1))
}

###################################
##                               ##
##          Shared Taxa          ##
##                               ##
###################################
load("fauna_S")
load("taxa_S")
load("collectionInfo_S")

sharedTaxa <- c
("Cleiothyridina","Composita","Anthracospirifer","Dielasma","Orbiculoidea","S
chizophoria","Punctospirifer",

"Rhipidomella","Lingula","Rhynchopora","Hustedia","Linoproductus","Spiriferel
lina")

for (i in 1:ncol(collectionInfo)) {
      columnNames <- colnames(collectionInfo)
      if (columnNames[i] == "collections.paleolatdec") {
            lat <- i
      } else if (columnNames[i] == "collections.paleolngdec") {
            long <- i
      } else if (columnNames[i] == "collections.stage") {
            stage <- i
      } else if (columnNames[i] == "collections.10mybin") {
            bin <- i
      } else if (columnNames[i] == "collections.period") {
            period <- i
      } else if (columnNames[i] == "collections.ma_min") {
```

```
			minInt <- i
		} else if (columnNames[i] == "collections.ma_max") {
			maxInt <- i
		}
}

collectionsHolder <- cull.rareAndDepaup(faunaData[collectionInfo[,period] ==
"Carboniferous" & as.numeric(collectionInfo[,minInt]) >= 318.1,],1,1)

# sort collections columns from most abundant to least
collections <- collectionsHolder[,match(sharedTaxa, colnames
(collectionsHolder))[is.na(match(sharedTaxa, colnames(collectionsHolder)))
==FALSE]]
collInfo <- collectionInfo[match(rownames(collections), rownames
(collectionInfo)),]

taxa <- colnames(collections)
nTaxa <- length(taxa)

sharedDistanceMean <- vector(mode="numeric", length=nTaxa); names
(sharedDistanceMean) <- taxa
sharedDistanceMedian <- vector(mode="numeric", length=nTaxa); names
(sharedDistanceMedian) <- taxa

quartz(height=7, width=7)
xLabs <- c(rep("",9), rep("paleolongitude",4))
yLabs <- c("paleolatitude", rep("",3), "paleolatitude", rep("",3),
"paleolatitude", rep("",3), "paleolatitude")
par(mfrow=c(4,4), bty="n", mar=c(4, 3.5, 1, 0.5) + 0.1, mgp=c(2.7, 1, 0),
las=1, font.main=3)
for (i in 1:nTaxa) {
	coordinates <- cbind(paleolong=as.numeric(collInfo[collections[,i]
==1,long]), paleolat=as.numeric(collInfo[collections[,i]==1,lat]))
	plot(coordinates, xlim=c(-80,160), ylim=c(-40,40), xlab=xLabs[i],
ylab=yLabs[i], main=colnames(collections)[i], xaxt="n", type="n")
	abline(h=0, lwd=0.75)
	points(meanLong, meanLat, cex=3, pch=4)
	points(coordinates, xlim=c(-60,180), ylim=c(-60,40), col=pointShading,
cex=1.5, pch=16)
	axis(side=1, at=seq(-80,160,80))

	distance <- sqrt((coordinates[,1]-meanLong)^2 + (coordinates[,2]-
meanLat)^2)
	sharedDistanceMean[i] <- mean(distance)
	sharedDistanceMedian[i] <- median(distance)
	text(x=160, y=40, labels=paste("d = ", round(sharedDistanceMean[i],2)),
font=3, adj=c(1,1))
}

t1 <- Sys.time()
difftime(t1, t0)
```