DOES ECOLOGICAL CHANGE SCALE WITH PERCENT EXTINCTION? QUANTIFYING THE DIFFERENCE BETWEEN TAXONOMIC LOSS AND FUNCTIONAL ECOLOGY

by

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(Under the Direction of Steven M. Holland)

ABSTRACT

Extinction in the fossil record is most often measured in terms of the percent of taxa (species, genera, families, etc.) that go extinct across a certain time interval. While this measures the taxonomic effects of extinction, previous work has indicated that these may be decoupled from the ecological effects of an extinction. In order to understand the role extinction plays in ecological change, extinction needs to be measured in terms of functional diversity as well.

This study quantifies whether the ecological intensity of extinction scales with the taxonomic intensity across the M4/M5 extinction in the Late Ordovician, the Late Devonian mass extinction, and the Ordovician-Silurian mass extinction. Taxonomic and ecological signals are measured by classifying organisms into genera and guilds, a method of grouping organisms based on their ecological function, not their evolutionary history. The taxonomic and ecological effects of each extinction are evaluated with additive diversity partitioning, detrended correspondence analysis, and relative abundance distributions.

The results of this study show that the largest taxonomic changes occur across the Ordovician-Silurian extinction and the largest ecological changes occur across the Late Devonian extinction. In terms of ecological selectivity, both the Late Devonian and M4/M5

were more selective than the Ordovician-Silurian. These results suggest taxonomic intensity of an extinction is a poor predictor of the ecological disruption caused by that extinction.

INDEX WORDS: Extinction, Ecology, Guild

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DEDICATION

To L. J. C.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

This thesis is written as a manuscript intended for submission to the academic journal *Paleobiology* and is therefore best read as a single chapter. The second chapter discusses the previous literature, background, methods, results, and conclusions in depth.

Extinction is typically measured in terms of the percentage of taxonomic loss (species, genera, families, etc.) across a given time interval. One of the most pervasive images in paleobiology is the plot of familial diversity through time identifying the "Big Five" mass extinctions (Raup and Sepkoski 1982). However, studies like this often do not consider the ecological function of organisms or measure the ecological loss experienced in an extinction event. While many authors have investigated the taxonomic effects of extinction (e.g. Raup and Sepkoski 1982, Raup 1991, Olszewski and Erwin 2004) and many have investigated the ecological effects (e.g. Droser et al. 1997, Layou 2009, Todd et al. 2002), few have quantitatively compared the two (but see Droser et al. 2000, McGhee et al. 2004).

Such comparisons are important because previous work has shown that the taxonomic and ecological signals of an extinction may be decoupled (Droser et al. 1997, 2000, McGhee 2004). Using a ranked, ordinal scale, Droser et al. (2000) showed that the ecological effects of the Late Devonian extinction were greater than those of the Ordovician-Silurian extinction, even though the Late Devonian exhibited less taxonomic extinction. Because Droser et al.'s (2000)

approach uses ordinal ecological data and continuous taxonomic data, it is difficult to test how ecological effects scale with taxonomic loss.

This study quantified ecological change by using the concept of ecological guilds (Root 1967) to classify taxa into functional groups. This is contrasted with taxonomic change as measured with genera. Three extinction events of varying magnitude and geographic scale are studied: the M4/M5 extinction in the early Late Ordovician, the Late Devonian mass extinction, and the Ordovician-Silurian mass extinction. The taxonomic and ecological changes are evaluated with additive diversity partitioning (ADP), detrended correspondence analysis (DCA), and relative abundance distributions (RAD), all performed on genera and guilds.

The results of this study suggest that ecological change does not necessarily increase with taxonomic loss. Taxonomic analyses show the least change across the M4/M5 for ADP, DCA, and RAD, and the greatest change across the Ordovician-Silurian for DCA and RAD. The Late Devonian shows the greatest change for ADP. Ecologically, analyses show the least change across the M4/M5 for DCA and RAD and the Ordovician-Silurian for ADP, and the greatest change across the Late Devonian for ADP and DCA. The Late Devonian and Ordovician-Silurian show similar ecological change for RAD. Thinking about extinction in terms of functional diversity is important because ecosystems will respond non-linearly to extinction. Understanding how ecosystems changed functionally in the past may lead to insight on how to better protect them in the future.

CHAPTER 2

DOES ECOLOGICAL CHANGE SCALE WITH PERCENT EXTINCTION? QUANTIFYING THE DIFFERENCE BETWEEN TAXONOMIC LOSS AND FUNCTIONAL ECOLOGY[1]

[1] Christie, M., S.M. Holland and A.M. Bush. To be submitted to *Paleobiology*.

Introduction

At least five mass extinctions that stand out relative to normal or background have occurred during the Phanerozoic (Raup and Sepkoski 1982). In addition, many smaller extinction events have also been recorded, such as the Oligocene-Miocene extinction (Edinger and Risk 1994), the Late Silurian event (Calner 2005), the Pliensbachian-Toarcian event in the Late Jurassic (Zakharov et al. 2006), and the early Late Ordovician event (Holland and Patzkowsky 1996, Layou 2009, Patzkowsky and Holland 1996, Patzkowsky and Holland 1997). Most extinction studies are concerned primarily with measuring changes in the taxonomic diversity of organisms across these time intervals (e.g. Alroy 2008, Benton 1995, Foote 2003, Jablonski 1986, Raup and Sepkoski 1982, Sepkoski 1993). In doing so, they measure the degree of taxonomic change during an extinction event, but not necessarily changes in ecosystem functioning (Droser et al. 1997, Ricklefs and Schluter 1993). Many authors have investigated ecological changes across extinction events (e.g. Boucot 1983, Bottjer and Ausich 1986, Jackson and Erwin 2006, Sheehan 1996, Todd et al. 2002, Watkins 1993), but few have explicitly contrasted taxonomic and ecological effects (Droser et al. 2000, McGhee et al. 2004). Of those, several have shown that ecological changes may not always mirror the level of taxonomic loss experienced after an extinction event (Droser et al. 1997, 2000, Plotnick and McKinney 1993, Roy 1996).

Changes in ecology are not as easily measured by taxonomic loss. Droser (2000) used four ordered levels to rank paleoecological changes, but this method lacks a quantitative framework. One way to quantify the ecological composition of a community is with the use of ecological guilds. These were first defined as "groups of species that exploit the same class of environmental resources in a similar way" (Root 1967). The importance of this approach is that

guild analysis groups similar functioning organisms regardless of taxonomic relation (Simberloff and Dayan 1991). Because of this structure, guild-level analyses can be readily compared to taxonomic-level analyses. However, it is often difficult to determine how extinct organisms partition environmental resources, especially without modern analogues. In the fossil record, the ecological function of extinct organisms is inferred from morphology. A morphological guild concept was introduced by Bambach (1983), and further refined by Bush et al. (2007). Several authors have used these guild concepts to identify and determine ecological diversity using consistently applied morphological criteria (e.g. Aberhan 1994, Fagerstrom 1988, Layou 2009, Wagner et al. 2006, Watkins 1991, 1993). By comparing differences in patterns between genera and guilds, we can determine how the ecological changes of extinction events compare to the taxonomic turnover during these events.

This study tests whether ecological changes increase with taxonomic loss for three extinction events of varying magnitude. In order of increasing taxonomic loss, this study examines the M4/M5, a regional early Late Ordovician extinction, the Late Devonian mass extinction, and the Ordovician-Silurian mass extinction. Taxonomic changes are measured in this study in terms of genera, while ecological changes are measured in terms of guilds. To compare changes among genera and guilds, additive diversity partitioning, detrended correspondence analysis, and relative abundance metrics are used. If taxonomic turnover is an adequate proxy for the ecological effects of an extinction, then the Ordovician-Silurian even should exhibit the greatest ecological change, and the M4/M5 should exhibit the least ecological change (Figure 1).

Background

The nature and effects of the extinctions in this study are covered from the smallest event (M4/M5) to the largest event (Ordovician-Silurian).

M4/M5.-The M4/M5 extinction occurred during the Mohawkian Stage of the Late Ordovician, roughly 455 million years ago (Patzkowsky and Holland 1993). The M4/M5 was a regional extinction limited to the Appalachian Basin of the eastern United States (Patzkowsky and Holland 1993, Patzkowsky and Holland 1997). Brachiopods were greatly reduced in diversity by this extinction regionally, but did not exhibit a strong global extinction (Patzkowsky and Holland 1993, Patzkowsky et al. 1997). In addition, corals, algae, gastropods and bryozoans were all affected regionally across this event (Layou 2009).

Major changes in sedimentation driven by the Taconic Orogeny occurred throughout the Appalachian basin, and these coincided with the M4/M5 extinction (Holland and Patzkowsky 1996). These changes resulted in a shift from tropical-type to temperate-type carbonate deposition, an increase in phosphate deposition, and an increase in siliciclastic sediment supply (Holland and Patzkowsky 1996). In addition, an increase in $\delta^{13}C$ of micrite and organic carbon occurred throughout the basin (Hatch et al. 1987, Railsback et al. 2003). Collectively, these features suggest regional upwelling, which resulted in a shift to cooler-water carbonates and increased nutrient supply (Holland and Patzkowsky 1996, 1997). Faunal turnover may have been caused by this regional cooling and increased water turbidity (Layou 2009).

Late Devonian.-The Late Devonian (approximately 385-359 Myr) was an interval of elevated faunal turnover, culminating in the Frasnian/Famennian event roughly 374 million years ago

(Gradstein et al. 2004, McGhee 1996, Racki 2005). The Late Devonian is described as a pulsed extinction with multiple events occurring throughout the epoch (McGhee 1996). The Late Devonian extinction occurred globally and resulted in an extinction of 50-60% of marine genera (Boucot 1975, Sepkoski 1986). Most major taxonomic groups were affected across this boundary, particularly colonial tabulate and rugose corals (McGhee 1996). Approximately 74% of reef building genera went extinct throughout the Late Devonian at a time when reef ecosystems were an order of magnitude more extensive than today (Copper 2002, McGhee 1996). In addition, nearly 75% of brachiopod genera went extinct across this boundary (McGhee 1996). Estimates of origination during the Late Devonian are greater than the Lower or Middle Devonian while estimates of extinction reach their peak in the Frasnian, before the beginning of the Famennian (Foote 2001).

Several causes for the Late Devonian extinction have been cited, including global cooling, global warming, and bolide impacts. Isotopic evidence has been found for both cooling (Joachimski and Buggisch 2002) and warming events (Brand 1989), in addition to nutrient cycle changes (Murphy et al. 2000). Authors have proposed that the extinction was caused by global cooling generated by the reduction of atmospheric CO_2 by land plants (Algeo and Scheckler 1998, Algeo et al. 2001) and through multiple bolide impacts (McLaren 1982). The Late Devonian was also a time of sea-level highstand and ocean anoxia has also been proposed as a potential cause of extinction (Joachimski and Buggisch 1993).

Ordovician-Silurian.-The Ordovician-Silurian extinction occurred approximately 443 to 444 million years ago and is the second largest mass extinction known (Sheehan 2001). The Ordovician-Silurian event occurred in two pulses associated with global climate change

(Brenchley et al. 2003). The extinction affected almost all major taxonomic groups. Brachiopods, tabulate and rugose corals, and crinoids all decreased greatly in diversity. The extinction event occurred globally, and 49-60% of marine genera and nearly 85% of marine species go extinct across this event (Jablonski 1991, Erwin 1998, Sheehan 2001). This diversity loss is thought to be driven primarily by elevated extinction intensity (Bambach et al. 2004), and high extinction rates are estimated for the Ordovician-Silurian; however, origination rates are low throughout this interval (Foote 2001). The fauna in the Silurian was largely similar to the fauna that existed during the Ordovician, suggesting that functional ecology did not change greatly across this boundary (Berry and Boucot 1973, Droser et al. 2000, McGhee et al. 2004, Sheehan 2001).

The Ordovician world exhibited greenhouse conditions with CO_2 levels several times greater than today and vast epicontinental seas (Sheehan 2001). Although climate was warmer, a brief glacial interval during the Late Ordovician affected both temperature and habitat area (Berry and Boucot 1973, Brenchley et al. 1994). Glaciation caused marine regression sufficient to drain epicontinental seas (Sheehan 2001). Fauna that lived in these shallow oceans was severely affected by the extinction (Johnson 1974). As glaciation subsided, flooding and anoxia resulted in the second extinction pulse.

Methods

Data.-The data for this study encompass three extinction events and draws on three different sources. Data from Layou (2009) are used to characterize the M4/M5 extinction. A new data set collected by the author of this study and supplemented by data from the Paleobiology database is used for the Late Devonian mass extinction. Data from Patzkowsky and Holland (2007) and

Zaffos and Holland (in review) are used for the Ordovician-Silurian mass extinction. All data sets consist of census data of individual bedding planes, with identifications made to the genus level where possible and then converted into a guild data set. For some groups (e.g. bryozoans) higher taxonomic units were used because genus level identification was not possible. Because these organisms will belong to the same guild, using higher taxonomic units should have the effect of dampening taxonomic patterns while maintaining the same patterns among guilds.

Data for the M4/M5 extinction was obtained from Layou (2009), who performed faunal counts from the M3 through M6 depositional sequences of Holland and Patzkowsky (1996) of the Mohawkian Stage in the Late Ordovician. These data were collected throughout Virginia, Tennessee, and Kentucky (Figure 2). Layou sampled both deep subtidal and shallow subtidal facies from all time intervals. Because limited exposure of some of these facies precluded the collection of similar numbers of samples from deep and shallow subtidal facies, data from the M3 and M4 sequences were combined to create a pre-extinction data set and the M5 and M6 sequences were combined to create a post-extinction data set. Collectively, the M3 and M4 sequences span approximately 1.5 Myr, and the combined M5 and M6 span approximately 2.0 Myr.

For the Late Devonian, a new data set was collected across the Frasnian-Famennian boundary in western New York by the author of this study and Dr. Andrew Bush (Figure 2). Late Devonian sediments in New York preserve a prograding delta with progressively deeper water facies westward (Sutton and McGhee 1985). Frasnian samples were collected from the Java Formation in the West Falls Group, and Famennian samples were collected from the Canadaway Group. All samples were collected *in situ* or were traced to their source beds. Samples were identified as distal delta front or proximal delta front based on their

sedimentological properties. Distal and proximal delta front are bathymetrically comparable to shoreface and transition zone (lower shoreface) facies and to deep subtidal and shallow subtidal facies (Holland and Patzkowsky 2007). Approximately the same number of samples from proximal delta front and distal delta front facies were collected pre- and post-extinction.

For the Ordovician-Silurian extinction, data were compiled from two sources, Ordovician data was obtained from Patzkowsky and Holland (2007) and Silurian data from Zaffos and Holland (in review). Ordovician samples were collected from the C5 sequence of the Richmondian Stage in Ohio, Kentucky, and Indiana (Figure 2). Silurian samples were collected from the Brassfield Formation in Ohio and Kentucky (Figure 2). Samples from the Ordovician was classified into deep subtidal and shallow subtidal facies based on sedimentological properties; however, facies were difficult to determine in the Brassfield Formation, so data from the Silurian were grouped into a single facies.

Ecological Guilds.-This study uses the guild framework of Bush et al. (2007) to produce two data sets from the same sets of faunal counts, with one organized by genera and the other by guilds. Bush et al. (2007) define a theoretical ecospace cube where each axis of the cube represents a different morphological or behavioral measures associated with ecological function: tiering, motility, and feeding strategy. Each of these characters has six different traits (Table 1). An organism can only express one trait on each axis, wherever these three traits overlap is defined as a guild. There are 216 possible guild combinations, although only a maximum of 17 combinations was seen in any data set of this study.

For each time interval, a list of genera was compiled. Tiering, motility, and feeding strategy was determined for each genus, based on their morphology. These characters were

assessed with taxonomic literature (e.g. The Treatise on Invertebrate Paleontology) and with the previously compiled guild data sets of Layou (2009) and Bush et al. (2007). All individuals belonging to the same guild in each sample were then summed, creating a guild data set from the original taxonomic data, in which each sample is counted in terms of guild membership instead of taxonomic membership.

Additive Diversity Partitioning.-To test for changes in diversity among genera and guilds, additive diversity partitioning was used. Additive diversity partitioning (ADP) defines β as the difference between diversity at a larger spatial scale (γ) and average diversity at a smaller scale ($\overline{\alpha}$; Lande 1996). The advantage of this approach over traditional multiplicative definitions of β (Whittaker 1960) is that comparisons within and among communities have the same units and can be compared to each other (Lande 1996, Veech et al. 2002). This method also allows for direct comparisons at multiple spatial scales (Gering et al. 2003). ADP is well suited to the fossil record because collections can be partitioned by sample and depositional environment to calculate changes in β diversity through time (Holland 2010).

In this study, α diversity is defined as local diversity, or the number of genera or guilds within a sample. Alpha is expressed as the average number of genera or guilds in a sample ($\overline{\alpha}$). Because samples can be grouped into facies, diversity within and among habitats can be investigated. Within-facies $\overline{\beta}$ is defined as the average diversity gained by examining multiple samples within a facies ($\overline{\beta}_{WF}$) and among-facies β is defined as the average diversity gained by examining multiple facies (β_{AF}) within a time interval (Figure 3). In addition to the entire data set, ADP analyses were also performed with originators and immigrants removed. An originator is any genus or guild present in at least one post-extinction sample, but absent in all pre-

extinction samples. Limiting analyses to survivors and extinct organisms isolates faunal change resulting from extinction alone to characterize the effect of an extinction on the ecosystem.

Gradient Ecology.-To characterize spatial and temporal gradients among pre- and post-extinction samples, detrended correspondence analysis (DCA) was applied to genera and to guilds. DCA is an ordination technique used to reduce distortions created by ecologically dissimilar samples that both lack large numbers of taxa (Hill and Gauch 1980). As for any ordination technique, samples and taxa that are similar in composition will plot closely in ordination space. DCA reduces the "arch effect" of correspondence analysis, a mathematical artifact produced when higher axes are not independent of lower axes, which can obscure underlying gradients (Peet et al. 1988). DCA works by dividing the ordination axis into segments, then subtracting the mean axis 2 segment score from each site, making the mean value of axis 2 in any segment zero (Jackson and Somers 1991), flattening the arch.

The degree of taxonomic and ecological changes can be compared between extinctions by calculating the degree of separation of pre- and post-extinction samples in ordination space. Greater values of separation indicate greater faunal differences between time intervals. DCA separation values were calculated by finding the centroids of pre- and post extinction samples, determining the slope of the line between those two points, and rotating samples in ordination space so that temporal variation is expressed on axis 1. DCA separation values were then calculated as:

$$\frac{D_{centroids}}{\overline{SD}}$$

where $D_{centroids}$ is the Euclidian distance between pre- and post-extinction centroids and is the average standard deviation of pre- and post-extinction samples along the axis of separation.

Relative Abundance Distribution.-To capture changes in the relative abundances of genera and guilds across each extinction event, relative abundance distributions were calculated. Relative abundances were calculated for all genera and guilds, and were ordered from most abundant to least abundant during the pre-extinction state for all extinction events.

To quantitatively examine relative abundance distributions, the total change in abundance for each genus and guild was measured. Relative abundance distribution change (*ΔRAD*) is defined as:

$$\Delta RAD = \sum_{i=1}^{n} \left| RA_{pre} - RA_{post} \right|$$

where RA_{pre} is the relative abundance of a genus or guild during the pre-extinction interval, RA_{post} is the relative abundance of that genus or guild during the post-extinction interval and n is the number of genera or guilds. *ΔRAD* ranges from 0 (no change in relative abundance across a time interval) to 2 (all pre-extinction organisms go extinct and are replaced by originating organisms).

Resampling.-Because samples vary in size, resampling was used to standardize the number of individuals per sample. In this procedure, all samples containing fewer than 20 individuals were removed, and every sample in a time interval was resampled to the fewest number of individuals in any one collection in that time interval. Analyses were performed on the resampled data set, with 1000 iterations of resampling and analysis. Results were averaged to produce the final

results. All resampling and subsequent analyses were done in the R programming language (R Core Development Team). The M4/M5 analyses contained 100 samples, the Late Devonian analyses contained 101 samples, and the Ordovician-Silurian analyses contained 77 samples.

Error estimates on DCA sample scores were obtained with a bootstrap routine. A DCA was performed for each of 1000 iterations of the resampled data set, and site and taxon scores were calculated. A Procrustes analysis was then used to rotate these 1000 sets of site and taxon scores to the same ordination configuration. Final site and taxon scores were then calculated by averaging the rotated scores. Standard error was also calculated based on these rotated scores.

Results

Additive Diversity Partitioning

M4/M5.-Beginning with the taxonomically least severe event, the M4/M5 shows relatively little extinction among genera (22.6%) (Figure 4A). Changes occur largely in within-facies $\overline{\beta}$ (38%) with a small decrease in $\overline{\alpha}$ (approximately 2.5 genera) and a small increase in among-facies β (approximately 3 genera). Taxonomic turnover in the M4/M5 therefore occurred primarily within habitats, leaving local diversity and diversity among habitats relatively unchanged.

Viewed ecologically, guild diversity does not change substantially across the M4/M5 extinction (Figure 4B). Alpha diversity largely remains constant at 3 guilds per sample. Within-facies $\overline{\beta}$ decreases slightly, but a corresponding increase in among-facies β maintains overall diversity to pre-extinction levels. This suggests that local ecological diversity was unchanged, but that ecological differences among habitats increased slightly.

When taxa that originate or immigrate in the M5 and M6 are removed, taxonomic extinction increases to 44.8% (Figure 4C). Post-extinction $\overline{\alpha}$ decreases slightly without these

organisms; however, the majority of extinction in these samples occurs in within-facies $\overline{\beta}$ and among-facies β. Ecologically, guild extinction increases to 14.2% when originators and immigrants are removed (Figure 4D). Diversity decreases at all hierarchical levels, although the greatest loss occurs in among-facies $\overline{\beta}$. This suggests that ecological change driven by extinction across the M4/M5 boundary occurred at all spatial scales, locally, within habitats, and among habitats, but with the greatest changes in diversity occurring among habitats.

Late Devonian.-Taxonomically, the Late Devonian event resulted in an overall extinction of 62% of genera (Figure 5A). This occurred in a major pulse across the Givetian-Frasnian boundary (51.2%) and a minor pulse across the Frasnian-Famennian boundary (22.2%). Alpha diversity remains similar across each time interval at approximately 5 genera and most extinction is accounted for by decreases in within-facies $\overline{\beta}$ (45.1%) and among-facies β (73.9%). Similarly, across the Frasnian-Famennian boundary diversity decreases within-facies (24.5%) and among-facies (58.1%). This suggests that while taxonomic diversity was unaffected at the local level, diversity within a habitat and especially among different habitats decreased. These diversity changes are more pronounced across the Givetian-Frasnian boundary than the Frasnian-Famennian boundary.

Ecologically, 51% of guilds go extinct across the two pulses of the Late Devonian event (Figure 5B). Guild extinction occurs across the Givetian-Frasnian boundary (52.4% of guilds), but not across the Frasnian-Famennian, with guild diversity increasing slightly (4.0%). The majority of guild loss occurs in within-facies $\overline{\beta}$ (57.7%) across the Givetian-Frasnian interval with smaller losses occurring in among-facies β (36.3%) and $\overline{\alpha}$ (approximately 1 guild). This suggests that while ecological diversity was stable to slightly depressed at the local level, far less

ecological diversity is found within habitats and among habitats across the first pulse of the extinction. Ecological diversity remained largely similar across the second extinction pulse.

When originators and immigrants are removed from the data, overall extinction across the Late Devonian increases to 92% of genera (Figure 5C) and 84% of guilds (Figure 5D). The same two-pulsed extinction pattern is preserved with a major pulse for both genera (85.4%) and guilds (76.5%). The secondary, minor pulse is also present, but accounts for the extinction of only 3 genera and 1 guild. Diversity decreases at all hierarchical levels across the Late Devonian extinction with originators and immigrants removed. This suggests that the extinction considerably decreases the taxonomic and ecological diversity of communities at the local level, within habitats, and among different habitats from the Givetian to Frasnian. While diversity decreased from the Frasnian to the Famennian, communities had already been affected by a major extinction, and were not substantially altered taxonomically or ecologically in terms of diversity.

Ordovician-Silurian.-Taxonomic diversity increases by 10.1% across the Ordovician-Silurian boundary (Figure 6A). Alpha diversity remains constant across this interval at roughly 6 genera. Taxonomic diversity increases primarily in terms of β diversity, although it is not possible to distinguish within-facies $\overline{\beta}$ and among-facies β.

Ecologically, guild diversity decreases by 28.7% across the extinction boundary, with $\overline{\alpha}$ diversity remaining constant at approximately three guilds and a decrease in β diversity of two to three guilds (Figure 6B). This suggests that while taxonomic diversity increased at larger spatial scales, post-extinction samples became more ecologically homogenous after the extinction.

When originators and immigrants are removed, taxonomic diversity decreases markedly for both $\overline{\alpha}$ and β diversity, exhibiting an overall extinction of 83.5% of genera (Figure 6C). In contrast, guild extinction is much lower (41.7%) (Figure 6D). Alpha diversity decreases by two guilds in the culled data set, but β diversity remains constant at roughly 5 guilds before and after the extinction. This suggests that when originators and immigrants are removed, ecological diversity is reduced substantially at the local level, but not in habitats. These organisms comprise a large component of taxonomic diversity, but only a small component of ecological diversity. This suggests that few ecological roles went extinct across the boundary, and that the originators and immigrants in the Silurian filled similar ecological roles as taxa in the Ordovician.

Detrended Correspondence Analysis

M4/M5 Event.-For genera, separation between pre- and post-extinction samples occurs primarily along a combination of axis 1 and 2, both with significant overlap (Figure 7A). Pre-extinction samples tend to plot towards lower values of axis 1 and 2 while post-extinction samples plot at greater values of axis 1 and 2. When samples are considered in terms of facies instead of time period, separation between deep subtidal and shallow subtidal facies also occurs along a combination of axis 1 and 2, perpendicular to the separation that occurs across the extinction boundary (Figure 8A). This suggests that faunal variation caused by the extinction is similar in scale to the variation caused by a depth gradient.

For guilds, pre- and post-extinction samples are separated primarily along axis 1, albeit with significant overlap (Figure 7B). Post-extinction samples tend to plot at positive values of axis 1 while pre-extinction samples plot at negative values. Guild scores indicate that pre-

extinction samples are dominated by surficial, freely fast motile, grazers and surficial, freely slow motile, grazers, while post-extinction samples are dominated by surficial, non-motile attached, suspension feeders, and erect, non-motile attached, suspension feeders. All of these guilds, however, are present in both time intervals. Samples classified by facies do not separate clearly along either axis 1 or 2 (Figure 8B).

Late Devonian.-For genera, Frasnian and Famennian samples show no separation along axis 1 or 2, but both separate from Givetian samples along axis 2 (Figure 9A). Axis 1 separates Givetian samples, suggesting that taxonomic variation within the Givetian is greater than taxonomic change across the Late Devonian extinction.

For guilds, most Frasnian and Famennian samples fall on a linear trend on axes 1 and 2; however, Givetian samples show greater variation ecologically (Figure 9B). Givetian samples have similar ecological compositions to Frasnian and Famennian samples at negative values of axis 2, but separate along axis 1 at positive values of axis 2. This indicates that some Givetian samples have ecological compositions similar to Frasnian and Famennian samples, but others are more ecologically diverse. Guilds that create more diverse Givetian communities plot at positive values of axes 1 and 2 (erect, non-motile attached, suspension feeders; shallow infaunal, freely slow motile, miners; and surficial, non-motile attached, predators), and go extinct or greatly reduce in abundance in the Frasnian. The linear pattern of Frasnian and Famennian samples suggests communities are dominated by two guilds, surficial attached and unattached non-motile suspension feeders, mainly made up of attached and unattached brachiopods. Frasnian samples are uniformly distributed along this axis suggesting that, overall, samples are not dominated by surficial attached or unattached non-motile suspension feeders. Famennian samples have mostly positive values axis 2 scores, suggesting Famennian communities are dominated by surficial

attached suspension feeders. Givetian samples, however, group near surficial unattached suspension feeders. This suggests that communities shifted through the Late Devonian from surficial unattached suspension feeder assemblages to surficial attached suspension feeder assemblages with an intermediate in the Frasnian.

Ordovician-Silurian.-For genera, pre- and post-extinction samples separate distinctly along axis 1 with no overlap (Figure 10A). In addition, axis 1 scores span a greater range than axis 2, suggesting most of the variation in these data is explained by taxonomic differences across this boundary.

In contrast, pre-extinction and post-extinction samples based on guilds separate along axis 1 with some overlap (Figure 10B). Along axis 1, Silurian site scores group near surficial, non-motile unattached, predators, while Ordovician site scores plot nearer to the erect, non-motile attached, suspension feeder and semi-infaunal, facultative mobile attached, suspension feeder guilds. Samples separate on axis 2 with surficial, non-motile unattached, suspension feeders dominant at negative values and surficial, non-motile attached, suspension feeders and surficial, freely fast motile, predators dominant at positive values. However, few of these guilds go extinct or originate across the boundary, and there is much more overlap among samples counted by guilds than among samples counted by genera. This suggests that while some ecological compositions shifted across Ordovician-Silurian boundary, taxonomic changes were much larger than ecological changes.

Relative Abundance Distribution

M4/M5.-Figure 11A shows a relative abundance distribution of genera prior to the extinction, with taxa in the same positions following the extinction (right). Genera appearing only in post-extinction samples (originators/immigrants) are sorted in descending rank order after genera that are present in pre-extinction samples. Changes in the shapes of these plots are another way to evaluate changes in relative abundance following an extinction.

Taxonomically, the abundance distribution for the M5 remains right-skewed, suggesting that genera that persist from the M4 remain the dominant members of the community after the extinction (Figure 11A). While many taxa do go extinct across this boundary, originators and immigrants are a minor component of total abundance.

Ecologically, the abundance distribution for guilds also remains right-skewed after the extinction, suggesting that surviving guilds remained dominant after the M4/M5 extinction (Figure 11B). The three dominant guilds before extinction, erect, non-motile attached, suspension feeders – surficial, non-motile attached, suspension feeders – and surficial, non-motile unattached, suspension feeders, remain dominant after the extinction, although their relative abundances do vary. While one guild, surficial, freely fast motile, grazers, is severely reduced in abundance in the M5 and M6, the abundance of most guilds does not change greatly. Both taxonomically and ecologically, the M4/M5 extinction had a minor impact on relative abundance of these faunas.

Late Devonian.-Taxonomically, large changes in the relative abundance of genera occur across the Late Devonian event (Figure 12A). Few genera present in the Givetian are present in the

Frasnian, and only one survivor (the brachiopod *Ambocoelia*) contributes significantly to total abundance. The contribution of these taxa is furthermore diminished from the Frasnian to Famennian. Only a few genera go extinct across this interval and the abundance rank of the surviving taxa is generally similar (except for three brachiopod genera: *Ambocoelia, Cupularostrum* and *Tylothyris*). Few genera originate in the Famennian, suggesting taxonomic compositions in the Famennian were similar to the Frasnian.

Ecologically, the relative abundance of guilds also shows large changes across the Givetian-Frasnian boundary (Figure 12B). While the two most abundant guilds (attached and unattached surficial suspension feeders) are still dominant after the extinction event, their relative abundance switches, and all other guilds go extinct or are severely reduced in abundance. The paucity of guilds continues into the Famennian. Taxonomically relative abundance across the Late Devonian interval reflects a shift to new genera, while ecologically, relative abundance was reduced in all guilds but one. This suggests that the Late Devonian extinction not only greatly changed taxonomic compositions, but greatly changed guild composition.

Ordovician-Silurian.-Taxonomically, the relative abundance of genera across the O/S boundary exhibits an abrupt change in taxonomic composition. Almost all of the taxa present in the Ordovician go extinct, and none of the surviving genera contribute substantially to overall abundance (Figure 13A).

Guilds show some shifts in rank abundance across the O/S boundary, but comparatively little given the taxonomic changes seen among genera (Figure 13B). The extinction results in a switch of the two dominant guilds: erect, non-motile attached, suspension feeders and surficial, non-motile attached, suspension feeders, as well as the addition of surficial, non-motile

unattached, predators. Although some guilds go extinct, the relative abundances of those guilds are a small percentage of total abundance. With the exception of surficial non-motile predators, guilds that had low abundances in the Ordovician and survived the extinction event remained at low abundances. While the taxonomic changes in relative abundance were intense across the Ordovician/Silurian boundary, the ecological changes due to extinction were relatively mild, although rugose corals increase substantially in abundance. This suggests that although the taxonomic compositions of the Ordovician and Silurian were different, changes in relative abundance of guilds were much greater than changes in diversity.

Discussion

Raup and Sepkoski's (1982) standing familial diversity through time and the identification of the "Big Five" have profoundly influenced how paleontologists think about extinction. Identifying and ordering events based on taxonomic loss serves as one descriptor of the severity of an extinction. Taxonomic loss is readily compared across events, but does not necessarily capture all of the effects an extinction on an ecosystem (Droser et al. 2000). If taxonomic loss characterizes all aspects of an extinction, one would predict that increasing taxonomic loss should drive progressively greater ecological changes. If this is true, then the M4/M5 would be expected to exhibit the least ecological change and the Ordovician-Silurian the most ecological change (Figure 1).

However, taxonomic measures of extinction do not necessarily capture the function of organisms within their ecosystem (Droser 2000, McGhee 2004). Two extinction events may have the same taxonomic signal, but if one results in the extinction of all groups of erect filter feeders while the other is distributed more evenly across guilds, then taxonomic loss is not

sufficient to explain this more complex pattern. Modern ecologists have recognized the importance of species characteristics and function in the maintenance of an ecosystem (Hooper et al. 2005 and references within). Because more than one species often performs the same or similar ecological functions, ecosystems have functional redundancies which may explain why some modern ecosystems exhibit initial insensitivity to extinction (Thébault et al. 2007). In the paleontological literature, authors have suggested that taxonomic diversity can be used as a proxy for ecological diversity (Sepkoski 1992), but to understand how extinction has affected ecological change throughout the Phanerozoic, we must consider organisms in terms of how they function in the ecosystem, and this should be assessed quantitatively.

Changes in Diversity.-Taxonomic and ecological effects can quantitatively be compared by using the percent extinction among genera and guilds. Here γ (total) diversity calculated for the ADP analyses is contrasted, and the percent extinction for genera and guilds is compared to determine if ecological changes scale with taxonomic loss. In order to isolate the effects of the extinction, the data set with originators and immigrants removed is used in this analysis.

Taxonomically, the M4/M5 extinction causes the least local taxonomic loss (44.8% of genera) while the Late Devonian causes the most (92% of genera). This conflicts with previous work that shows the Ordovician-Silurian extinction resulted in greater taxonomic loss, but this conflict may reflect differences in sampling and time frame. The Late Devonian extinction is sampled across three intervals, the Givetian, Frasnian, and Famennian, while the Ordovician-Silurian event is sampled only before and after the extinction. This gives organisms across the Late Devonian extinction more opportunities to become extinct. If the Late Devonian is

considered as two pulses, the major Givetian-Frasnian event (85.4%) is similar in magnitude to the Ordovician-Silurian event (83.5%), at least in these two regions.

Ecologically, the extinction events are ordered in the same way; the M4/M5 shows the least regional extinction among guilds (14.2%) and the Late Devonian shows the greatest regional extinction among guilds (84%) (Figure 14A). The Ordovician-Silurian event experiences little regional guild loss compared to the large amount of taxonomic loss observed. This suggests that ecological change does not increase with taxonomic loss as expected (Figure 1).

To assess the relative ecological effects of each extinction, the amount of taxonomic loss must be controlled. The amount of ecological extinction can be scaled by the amount of taxonomic extinction to determine which event had the greatest relative ecological effects (Figure 15). Positive values indicate a greater degree of ecological extinction relative to taxonomic extinction and more negative values indicate greater taxonomic extinction relative to ecological extinction. The Late Devonian (and both Givetian-Frasnian and Frasnian-Famennian) exhibits the greatest relative ecological change while the M4/M5 shows the least. Although ecological change increases with taxonomic loss, the magnitude of ecological changes during the Late Devonian far surpasses that of the Ordovician-Silurian or M4/M5 extinctions, suggesting that the relationship between ecological and taxonomic loss is non-linear.

Another way to assess the relative ecological change and ecological selectivity is to determine the ratio of genera that go extinct to guilds that go extinct. These results show that more genera went extinct per guild during the M4/M5 than the Ordovician-Silurian or Late Devonian extinctions (Figure 16A). Dividing these ratios by the average number of genera per guild prior to the extinction indicates the ecological selectivity of the extinction (Figure 16B).

Positive values indicate greater ecological selectivity and negative values indicate less ecological selectivity. These results indicates that the ecological impact of the Late Devonian extinction was much greater than either the M4/M5 or Ordovician-Silurian extinctions, suggesting that functional loss does not increase linearly with taxonomic loss.

Changes in Faunal Composition.-Comparing the separation of pre- and post-extinction samples in ordination space quantifies differences in faunal composition across the three extinction events. Taxonomically, the M4/M5 shows the least separation (2.22) while the Ordovician-Silurian shows the greatest separation (8.44). The Late Devonian (3.45 Givetian to Famennian) has greater separation for the Givetian-Frasnian boundary (2.63) than the Frasnian-Famennian boundary (1.04).

Ecologically, the M4/M5 shows the least separation among the guild data set (0.75) while the Late Devonian shows the most separation (1.72). The two pulses of the Late Devonian exhibit the opposite pattern in the guild data set then they do in the taxonomic data set. Separation among Givetian and Frasnian samples is 0.63 while Frasnian-Famennian samples is 1.64. This is likely because Givetian samples are more ecologically diverse than Frasnian or Famennian samples, and therefore Givetian samples have a larger standard deviation.

These results suggest that pre- and post-extinction communities were ecologically less similar across the Late Devonian than the Ordovician-Silurian, even though Late Devonian communities were much more alike taxonomically (Figure 14B). This indicates that differences in functional faunal compositions do not increase with differences in taxonomic faunal composition. The M4/M5 extinction shows less difference in pre- and post-extinction samples

taxonomically or ecologically and variation within samples is primarily driven by differences in habitat.

Changes in Relative Abundance.-Changes in relative abundance may not be captured by richness if organisms do not go extinct, comparing ΔRAD values quantifies changes in abundance patterns due to abundance increases, decreases, or extinctions. Taxonomically, the M4/M5 witnessed the least change in relative abundance (ΔRAD = 1.38) while the Ordovician-Silurian exhibits the greatest change (1.94). This indicates that across the M4/M5 interval, the majority of total abundance shifted to new genera, but overall a large proportion of abundance among taxa was similar in pre- and post-extinction samples. However, the larger values of ΔRAD during the Ordovician-Silurian and Late Devonian (1.82) indicate that the relative abundance for most genera changed drastically. Because the values are nearing 2, nearly all taxa exhibited major changes in relative abundance in each extinction event.

Ecologically, the M4/M5 extinction also exhibits the least change (0.48), while the Late Devonian (0.80) and Ordovician-Silurian (0.81) extinctions are almost identical. This indicates that the relative abundance distributions of guilds did not change greatly across the M4/M5 extinction and that the changes in relative abundance for both the Late Devonian and Ordovician-Silurian were similar in magnitude.

To some extent, ecological effects do increase with taxonomic loss (Figure 14C). For example, the Late Devonian and Ordovician-Silurian mass extinctions exhibit similar ΔRAD values both taxonomically and ecologically. This likely occurs because while more guilds go extinct across the Late Devonian, those guilds do not account for a large proportion of total abundance. The major shift in abundance occurs between surficial unattached and attached

suspension feeder guilds, which both survive the Late Devonian extinction. During the Ordovician-Silurian event, in contrast, large changes in relative abundance occur within surficial, non-motile unattached, predators; erect, non-motile attached, suspension feeders; and surficial, non-motile unattached, suspension feeders, but few guilds go extinct. The presence or absence of rare taxa or guilds would be detected by ADP or DCA, but are less influential in a ΔRAD analysis. This suggests that from the standpoint of ecological relative abundance, the Late Devonian and Ordovician-Silurian extinctions had similar effects. The relative abundance analysis shows the greatest relationship between increasing ecological and taxonomic changes.

Why is Function Important?.-Many authors have considered extinction events taxonomically (e.g. Alvarez et al. 1984, Jablonski 1991, Olszewski and Erwin 2004, Raup 1991, Raup and Sepkoski 1982, Sepkoski et al. 1981) and many have done so ecologically (e.g. Bambach 1983, Bambach et al. 2007, Bush et al. 2007, Droser et al. 1997, Layou 2009, Todd et al. 2001), but few have explicitly contrasted the two (but see Droser et al. 2000, McGhee et al. 2004). In addition, many paleoecological studies describe ecological patterns in terms of taxa (Bush and Brame 2010, Holland and Patzkowsky 2007, Patzkowsky and Holland 2007). These patterns are important to explain and have led to the understanding of how taxa are distributed globally and within habitats, and the controls resulting in different ecosystems; however, far fewer paleontological studies focus on the function of organisms in a quantitative way (but see Bambach et al. 2007, Boucot 1983, Bush et al. 2007, Droser and Bottjer 1989, Kowalewski et al. 2006, Sheehan 1996, Watkins 1991, 2000).

Sepkoski (1992) quantified ecological diversity as "the number of species, etc. at a given place." This measure is readily comparable to taxonomic diversity, and allows workers to

investigate patterns of taxonomic and ecological diversity quantitatively. However, this measure does not consider the function of organisms in a community. Eldridge (1992) in the same volume suggests that ecological diversity is the different "*sorts* of organisms present in a local ecosystem" (italics mine). Those organisms that have the same function are treated in the same way. Classifying organisms into functional groups this way allows researchers to examine ecological patterns in the same way as taxonomic patterns.

Functional traits have been recognized in the ecological literature as an important factor in ecosystem properties (Hooper and Vitousek 1997, Hooper et al. 2005, Van Valkenburgh 1999). Research has shown that in some systems, functional diversity is the primary driving factor in ecosystem change (Tilman 1997). These systems might initially be insensitive to taxonomic extinction because many taxa perform similar functions in an ecosystem, but once those taxa are extinct, the ecosystem may change drastically (Schwartz et al. 2000, Solan et al. 2004). A functional approach can identify ecological redundancy as well as functions that are performed by only a small group of taxa. The difficulty with this approach is determining the function of an organism in the community. This is especially true in the fossil record where they may be no modern analogues for extinct taxa. In contrast, taxonomic relationships are often well worked out and can be applied to fossil taxa easily. In paleontology, the Bambachian guilds used in this study (Bambach 1983, Bush et al. 2007) address the function of fossil organisms through the use of morphological traits; however, other systems also describe function in the fossil record (Novack-Gottshall 2007). Because function can be more difficult to assess than phylogeny, multiple methods of classifying functional groups should be considered.

The advantage of functional groups is the ability to quantify ecological change. Droser et al. (1997) described a method to rank the ecological effects of extinction based on an ordinal

scale. These rankings base loosely on the appearance or disappearance of different community types and guilds. They provide a framework to rank the ecological consequences of extinction. However, this ordinal classification system is not easily comparable with continuous taxonomic results. It allows workers to rank events, not describe quantitatively how much ecological change occurs over a time interval. Droser et al. (2000) addresses the relative rankings of taxonomic and ecological extinction signals across the Late Devonian and Ordovician-Silurian events. Their findings are similar to this study; Late Devonian ecological communities were more severely affected than Ordovician-Silurian communities. But because this measure of ecology is ordinal, it is difficult to test how ecological change scales with taxonomic change.

The importance of these methods is that they classify organisms into a system independent of taxonomy, organized by function. Though these two are almost certainly linked, measuring both allows workers to assess the relative importance of evolutionary history and biological function. This may be important in determining selectivity across an extinction boundary. The loss of particular functional groups may indicate ecological selection. Functional groups could also be used to determine ecological extinctions and radiations throughout the Phanerozoic, similar to Raup and Sepkoski (1982). By classifying taxa into functional groups, we can also explain patterns of ecology in the fossil record in a quantitative way.

Conclusions

1) Taxonomically and ecologically, diversity changes are greatest for the Late Devonian extinction and least for the M4/M5 extinction. However, when controlling for the amount of taxonomic loss, ecological change is much greater across the Late Devonian extinction. In

addition, taxonomic and ecological diversity changes occur mainly within and among habitats (within-facies $\overline{\beta}$ and among-facies β) leaving local diversity (α) untouched.

2) Ordination of taxonomically counted samples shows the greatest taxonomic change due to extinction across the Ordovician-Silurian boundary, and the least taxonomic change across the M4/M5 boundary. Ordination of ecologically counted samples shows the greatest ecological change across the Late Devonian boundary, and the least ecological change across the M4/M5 boundary. Taxonomically, the M4/M5 extinction exhibits a depth gradient along axis 1, suggesting that faunal variation due to depth changes is greater than faunal changes due to extinction.

3) Taxonomically, relative abundances of genera change the greatest across the Ordovician-Silurian extinction and least across the M4/M5 extinction. Ecologically, relative abundances of guilds are almost indistinguishable between the Late Devonian and Ordovician-Silurian extinctions, and least for the M4/M5 extinction. This suggests that in terms of relative abundance changes, the Late Devonian and Ordovician-Silurian extinctions had similar effects.

4) As previously argued, this study shows that the ecological changes associated with an extinction event do not scale with taxonomic loss (cf. Boucot 1983, Droser et al. 2000, McGhee et al. 2004). Combining the results of all three measures of taxonomic and ecological change, the M4/M5 extinction resulted in moderate taxonomic changes and mild ecological changes, the Ordovician-Silurian extinction resulted in large taxonomic changes and moderate ecological changes, and the Late Devonian resulted in large taxonomic changes and large ecological changes.

CHAPTER 3

CONCLUSIONS

The effects of extinction on communities have been measured as a function of taxonomic loss in the fossil record (Raup and Sepkoski 1982, Raup 1991, Olszewski and Erwin 2004); however, few studies have quantitatively measured the ecological effects of extinction. Here, the ecological effects of three extinctions, the M4/M5 extinction in the Late Ordovician, the Late Devonian mass extinction, and the Ordovician-Silurian mass extinction, were measured through the use of ecological guilds. Guilds are a method of classifying organisms based on their ecological functions, not their evolutionary history. To assess changes in genera and guilds, additive diversity partitioning, detrended correspondence analysis, and relative abundance distributions were then used.

A comparison of the three extinction events shows that the ecological intensity of an extinction does not scale with the taxonomic intensity of that event. In this study, the Ordovician-Silurian event showed the greatest taxonomic differences, while the Late Devonian event showed the greatest ecological differences. When controlling for taxonomic extinction intensity, the Ordovician-Silurian exhibited the least ecological selectivity. This suggests that greater guild loss during the Ordovician-Silurian (as opposed to the M4/M5) was a result of the magnitude of the extinction event, not selectivity against certain guilds. When investigating relative abundance, the Ordovician-Silurian shows a similar amount of total relative abundance change (ΔRAD) to the Late Devonian extinction, suggesting that while few guilds went extinct across this boundary, large changes in the abundance of guilds occurred in the Silurian.

These results support the findings of Droser et al. (2000) and McGhee et al. (2004) that the ecological and taxonomic effects of extinction are decoupled, and that the Late Devonian exhibits greater ecological effects than the Ordovician-Silurian, even though it the taxonomic intensity was less. Furthermore, these results suggest that to understand the ecological effects of extinction, functional ecology must be considered.

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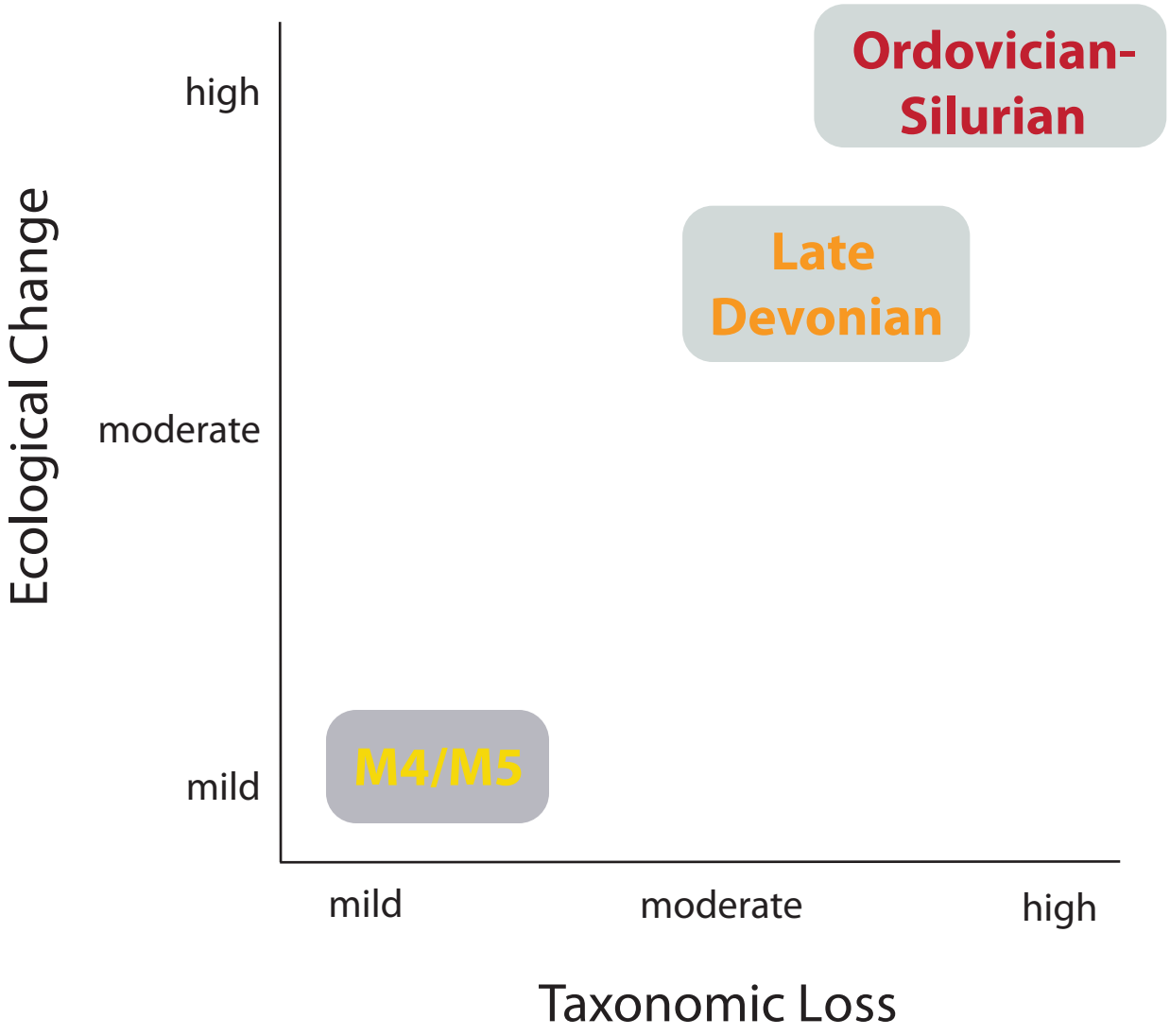

Ordovician-
Silurian
Late
Devonian
M4/M5
high
moderate
mild
Ecological Change
mild
moderate
high
Taxonomic Loss

Figure 1 – Null hypothesis of extinction intensity. As taxonomic loss increases, ecological changes should increase linearly.

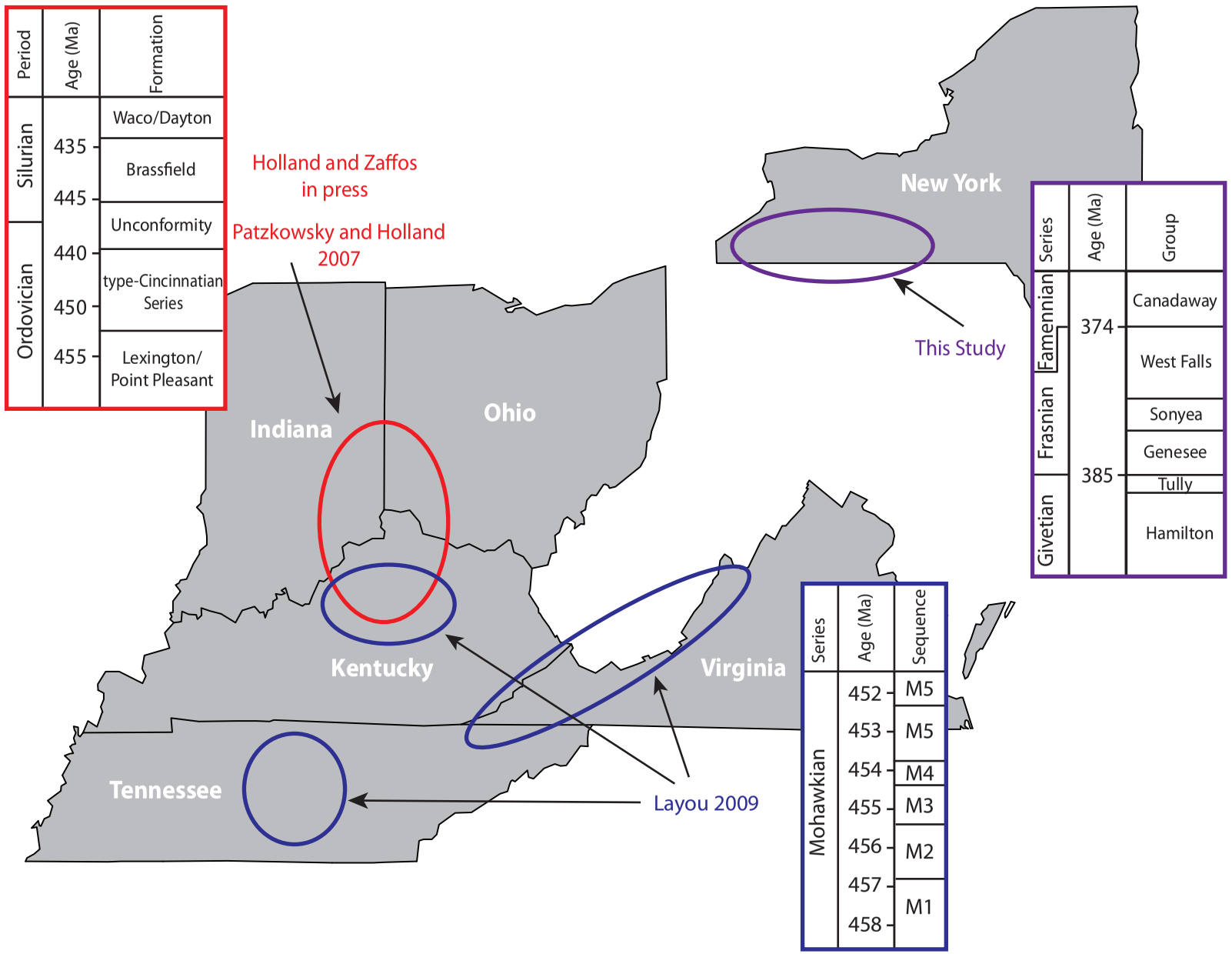
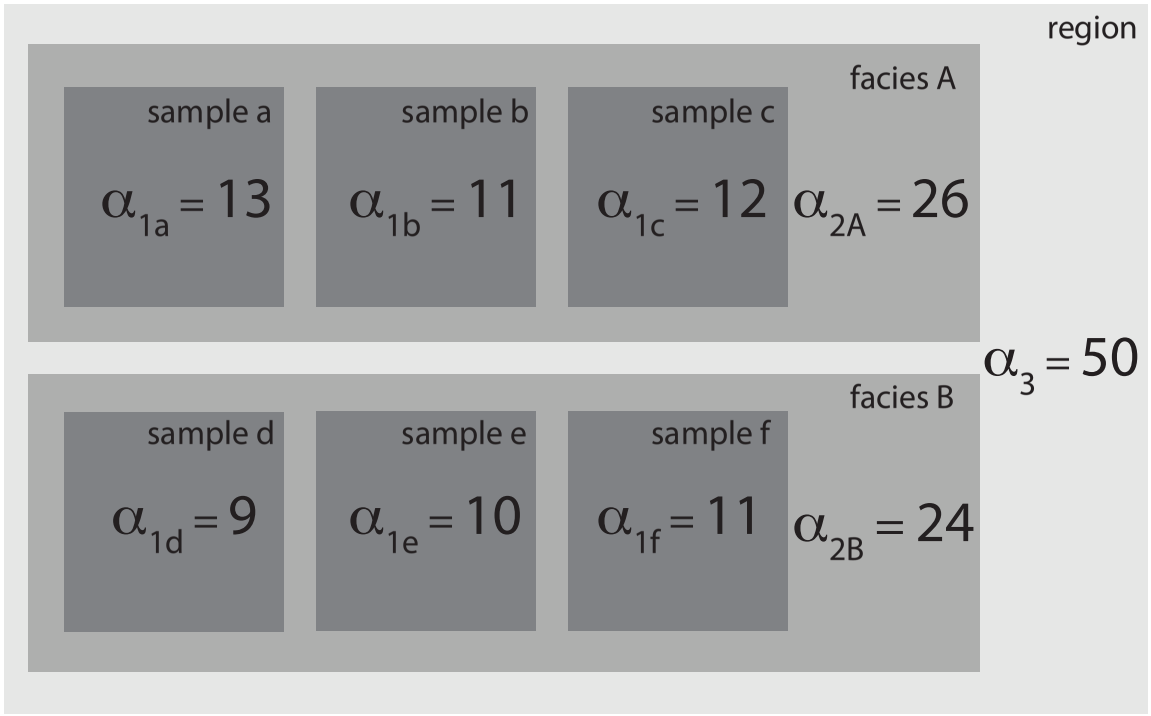
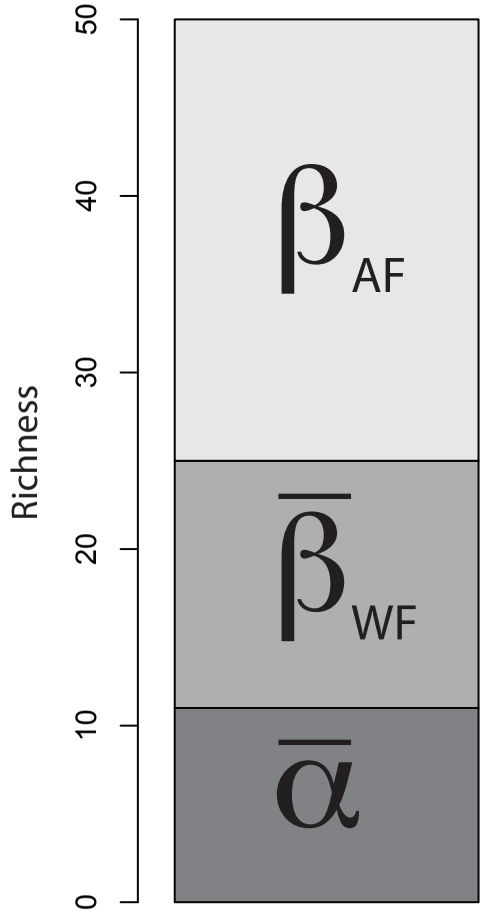

Period
Age (Ma)
Formation
Silurian
Ordovician
435
445
440
450
455
Waco/Dayton
Brassfield
Unconformity
type-Cincinnatian Series
Lexington/ Point Pleasant
Holland and Zaffos in press
Patzkowsky and Holland 2007
Indiana
Ohio
Kentucky
Virginia
Tennessee
New York
This Study
Layou 2009
Series
Age (Ma)
Group
Famennian
Frasnian
Givetian
374
385
Canadaway
West Falls
Sonyea
Genesee
Tully
Hamilton
Series
Age (Ma)
Sequence
Mohawkian
452
453
454
455
456
457
458
M5
M5
M4
M3
M2
M1

Figure 2 - Map of study areas. Field areas from Layou (2009) are circled in blue, field areas from Patzkowsky and Holland (2007) and Zaffos and Holland (in press) are circled in red, and field areas from this study are circled in purple. Accompanying each circled field area is a regional column showing stratigraphic units.

Ecologic Category	Description	Example
Tiering		
1. Pelagic	In the water column	Nautiloids
2. Erect	Benthic, extending into the water mass	Crinoids
4. Semi-infaunal	Benthic, not extending significantly upward	Lingulid
5. Shallow infaunal	Partly infaunal, partly exposed	Many bivalves
3. Surficial	Living in the top 5 cm of the sediment	Articulate brachiopods (e.g. *Floweria*)
6. Deep infaunal	Living in the bottom 5 cm of the sediment	None in this study
Motility Level		
1. Freely, fast	Regularly moving, unencumbered	Nautiloids, trilobites
2. Freely, slow	As above, but strong bond to the substrate	Gastropods
3. Facultative, unattached	Moving only when necessary, free-lying	Many bivalves (e.g. *Edmondia*)
4. Facultative, attached	Moving only when necessary, attached	Some clams (e.g. *Modiamorpha*)
5. Non-motile, unattached	Not capable of movement, free-lying	Reclining brachiopods (e.g. *Sowerbyella*)
6. Non-motile, attached	Not capable of movement, attached	Pedunculate brachiopods (e.g. *Tylothyris*)
Feeding Mechanism		
1. Suspension	Capturing food particles from the water	Brachiopods
2. Surface deposit	Capturing loose particles from a substrate	Some gastropods (e.g. *Cyclonema*)
3. Mining	Recovering buried food	Many bivalves (e.g. *Ctenodonta*)
4. Grazing	Scraping or nibbling food from a substrate	Many gastropods (e.g. *Liospira*)
5. Predatory	Capturing prey capable of resisitance	Cephalopods
6. Other	e.g., photo- or chemosymbiosis, parasites	

Table 1 – Classification of guild traits. Ecological traits from Bush et al. (2007). Each genus is assigned an ecologic category from tiering, motility level, and feeding mechanism. Each unique combination is a potential guild.





$$\overline{\alpha} = \overline{\alpha}_1 = \frac{13 + 11 + 12 + 9 + 10 + 11}{6} = 11$$

$$\overline{\beta}_{WF} = \overline{\alpha}_2 - \overline{\alpha}_1 = \frac{24 + 26}{2} - \overline{\alpha} = 14$$

$$\overline{\beta}_{AF} = \alpha_3 - \overline{\alpha}_2 = 50 - \overline{\beta}_{WF} - \overline{\alpha} = 25$$

Figure 3 – Additive diversity partitioning. Nested hierarchy for additive diversity partitioning analysis. Alpha represents the number of units (genera or guilds) in a certain spatial level (sample or α_1, facies or α_2, and region or α_3). $\overline{\alpha}$ is the average diversity from all samples. $\overline{\beta}_{WF}$ is the average diversity gained by examining multiple samples in the same facies. β_{AF} is the diversity gained by examining multiple facies in the same region. Adapted from Holland (2010).

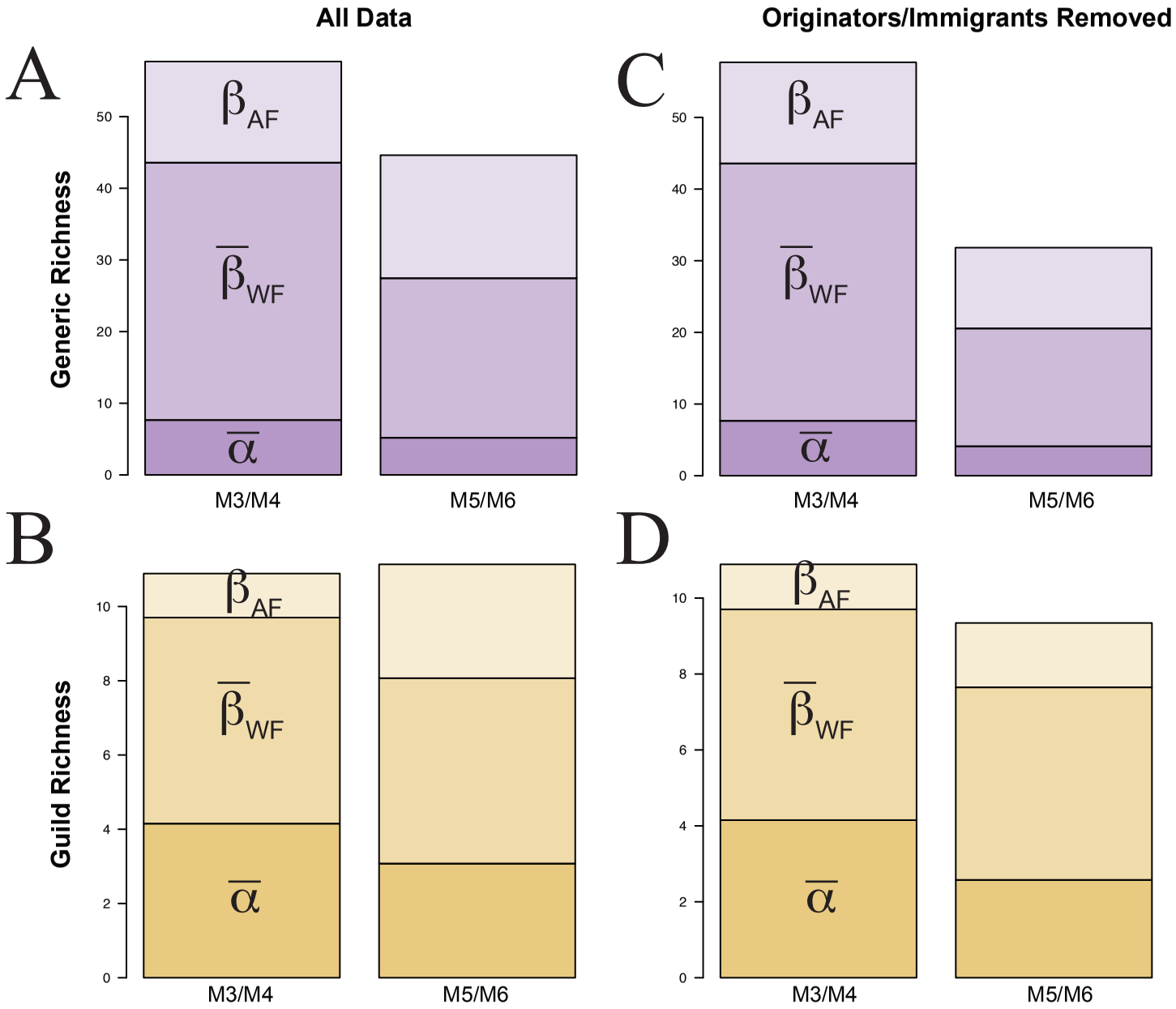

All Data
Originators/Immigrants Removed
A
B
C
D
Generic Richness
Guild Richness
β_{AF}
$\overline{\beta}_{WF}$
$\overline{\alpha}$
M3/M4
M5/M6
0
10
20
30
40
50
2
4
6
8

Figure 4 – ADP for the M4/M5 extinction. Showing $\overline{\alpha}$ diversity, within-facies $\overline{\beta}$, and among-facies β. A) Taxonomic diversity for the entire data set B) Guild diversity for the entire data set C) Taxonomic diversity with originators removed D) Guild diversity with originators removed.

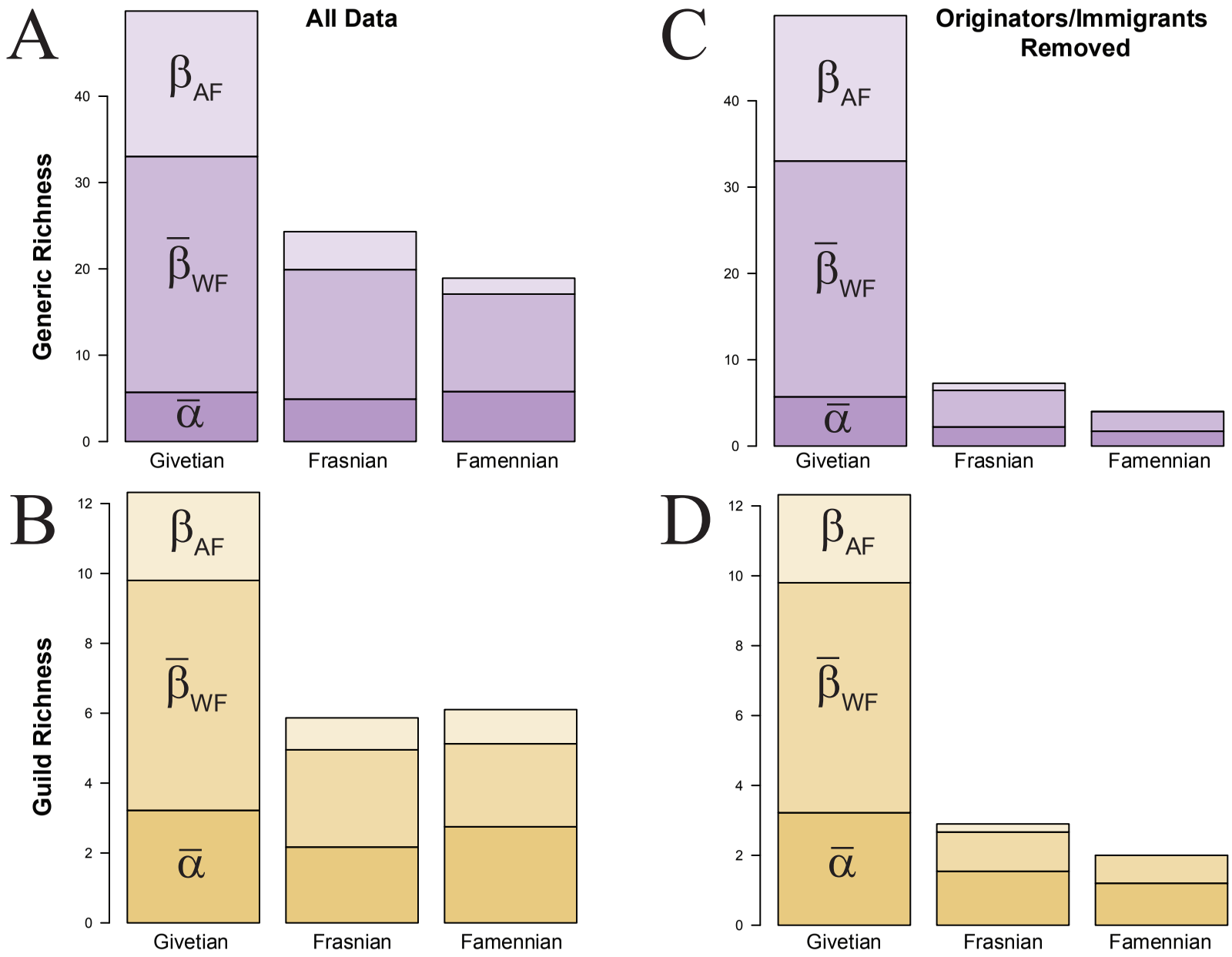

A
All Data
Generic Richness
β_{AF}
$\bar{\beta}_{WF}$
$\bar{\alpha}$
0
10
20
30
40
Givetian
Frasnian
Famennian
B
Guild Richness
0
2
4
6
8
10
12
C
Originators/Immigrants Removed
D

Figure 5 - ADP for the Late Devonian extinction. Showing $\overline{\alpha}$ diversity, within-facies $\overline{\beta}$ and among-facies β. A) Taxonomic diversity for the entire data set B) Guild diversity for the entire data set C) Taxonomic diversity with originators removed D) Guild diversity with originators removed.

Additive Diversity Partitioning among Taxa

Additive Diversity Partitioning among Guilds

Figure 6 - ADP for the Ordovician-Silurian extinction. Showing $\overline{\alpha}$ diversity, within-facies $\overline{\beta}$, and among-facies β. A) Taxonomic diversity for the entire data set B) Guild diversity for the entire data set C) Taxonomic diversity with originators removed D) Guild diversity with originators removed. Because facies could not be distinguished in the Silurian data set, β_{WF} and β_{AF} could not be calculated and are combined into a single β term reflecting both within-facies and among-facies heterogeneity.

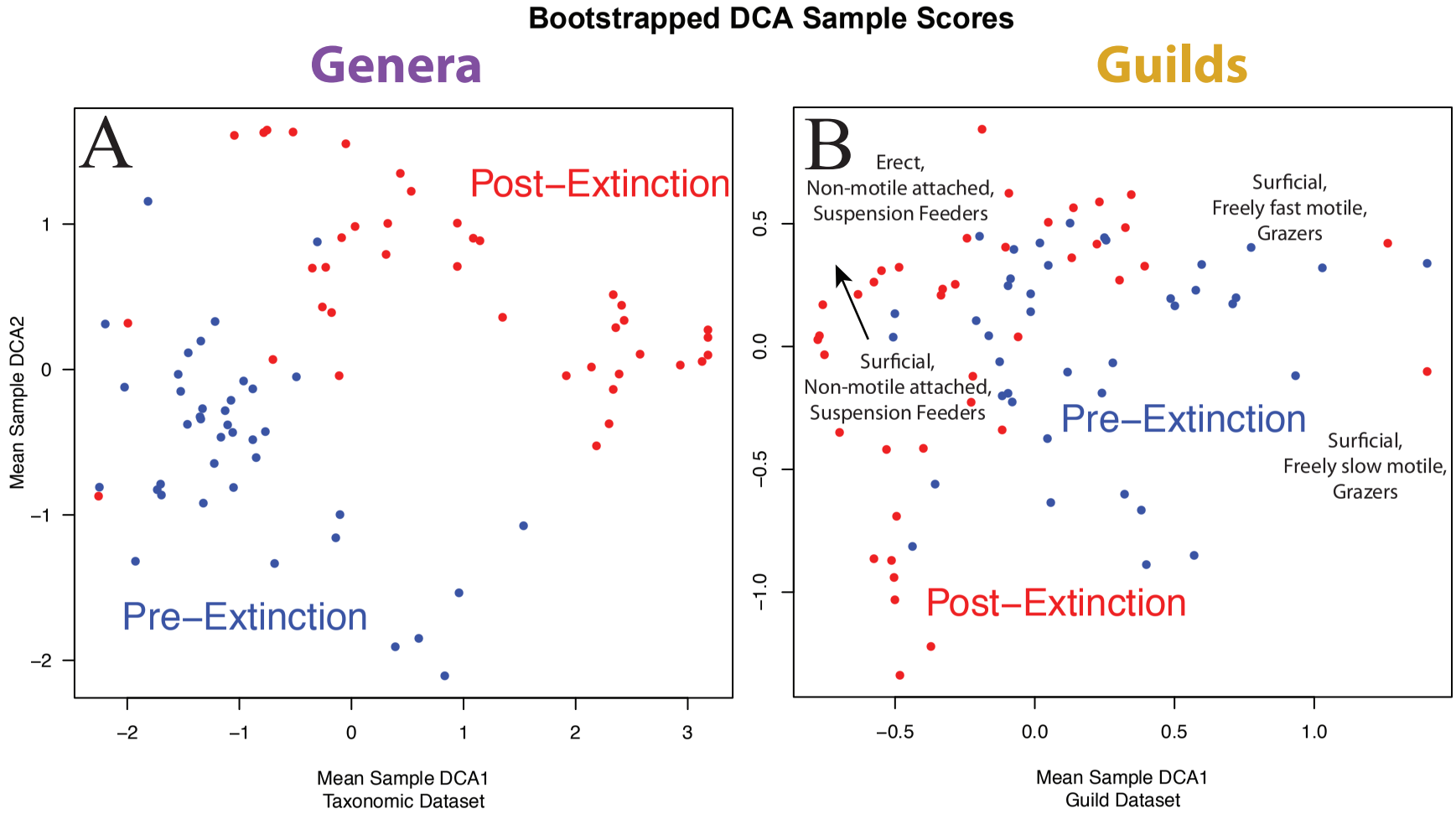

Bootstrapped DCA Sample Scores
Genera
Guilds
A
Post–Extinction
Pre–Extinction
Mean Sample DCA2
Mean Sample DCA1
Taxonomic Dataset
B
Erect,
Non-motile attached,
Suspension Feeders
Surficial,
Freely fast motile,
Grazers
Surficial,
Non-motile attached,
Suspension Feeders
Pre–Extinction
Surficial,
Freely slow motile,
Grazers
Post–Extinction
Mean Sample DCA1
Guild Dataset

Figure 7 – DCA for the M4/M5 extinction. Pre-extinction samples are shown in blue, post-extinction samples are shown in red. A) DCA for the taxonomic data set B) DCA for the guild data set.

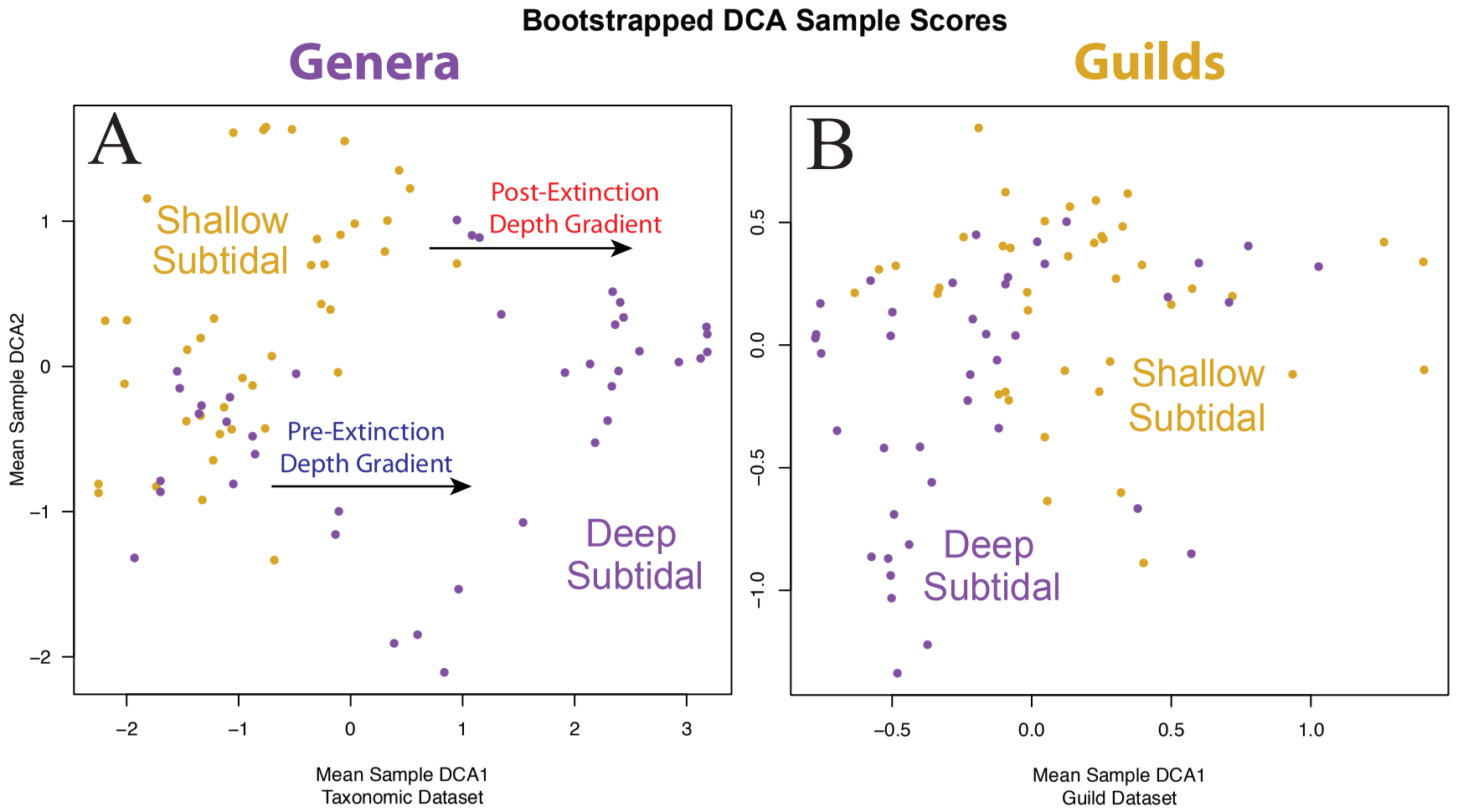

Bootstrapped DCA Sample Scores
Genera
Guilds
A
B
Shallow
Subtidal
Post-Extinction
Depth Gradient
Pre-Extinction
Depth Gradient
Deep
Subtidal
Shallow
Subtidal
Deep
Subtidal
Mean Sample DCA2
Mean Sample DCA1
Taxonomic Dataset
Mean Sample DCA1
Guild Dataset

Figure 8 - DCA for the M4/M5 extinction (Facies). Here samples are colored by their facies. Shallow subtidal facies appear in yellow, deep subtidal facies appear in purple. A) DCA for the taxonomic data set B) DCA for the guild data set.

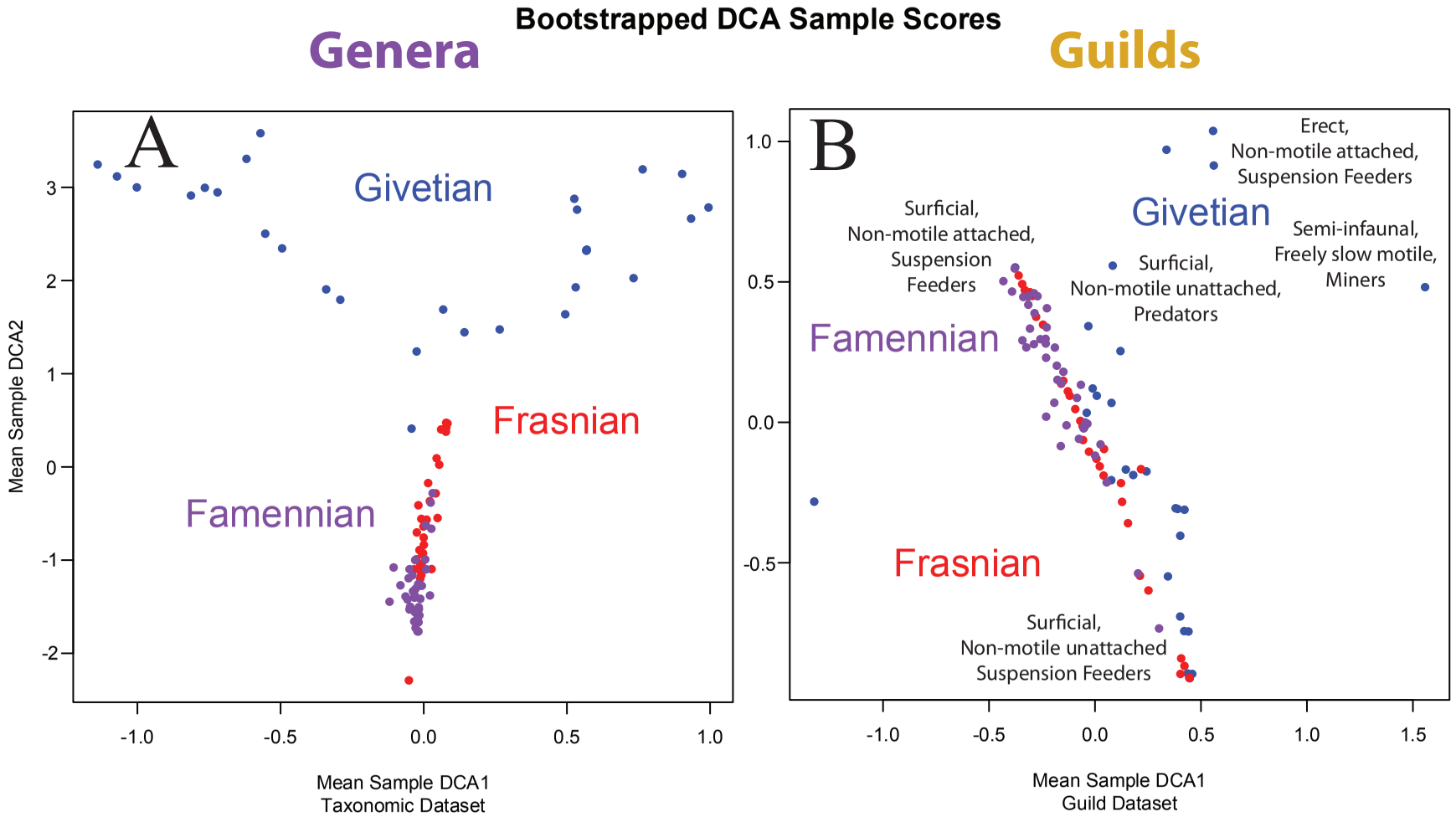

Bootstrapped DCA Sample Scores
Genera
Guilds
A
Givetian
Frasnian
Famennian
Mean Sample DCA2
Mean Sample DCA1
Taxonomic Dataset
B
Erect,
Non-motile attached,
Suspension Feeders
Surficial,
Non-motile attached,
Suspension
Feeders
Givetian
Semi-infaunal,
Freely slow motile,
Miners
Surficial,
Non-motile unattached,
Predators
Famennian
Frasnian
Surficial,
Non-motile unattached
Suspension Feeders
Mean Sample DCA1
Guild Dataset

Figure 9 - DCA for the Late Devonian extinction. Pre-extinction samples are shown in blue, post-extinction samples are shown in red. A) DCA for the taxonomic data set B) DCA for the guild data set.

Bootstrapped DCA Sample Scores

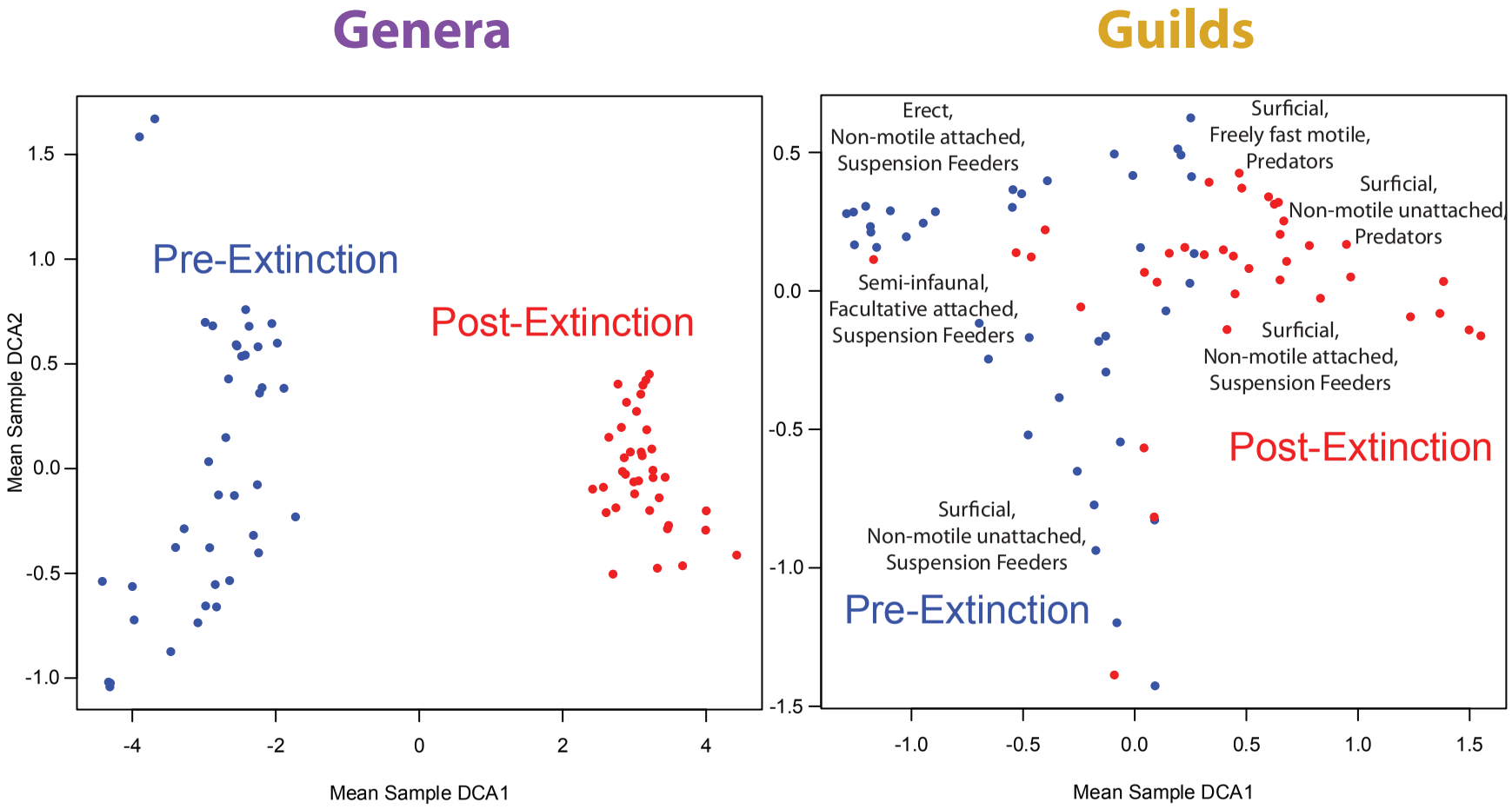


Figure 10 - DCA for the Ordovician-Silurian extinction. Pre-extinction samples are shown in blue, post-extinction samples are shown in red. A) DCA for the taxonomic data set B) DCA for the guild data set.

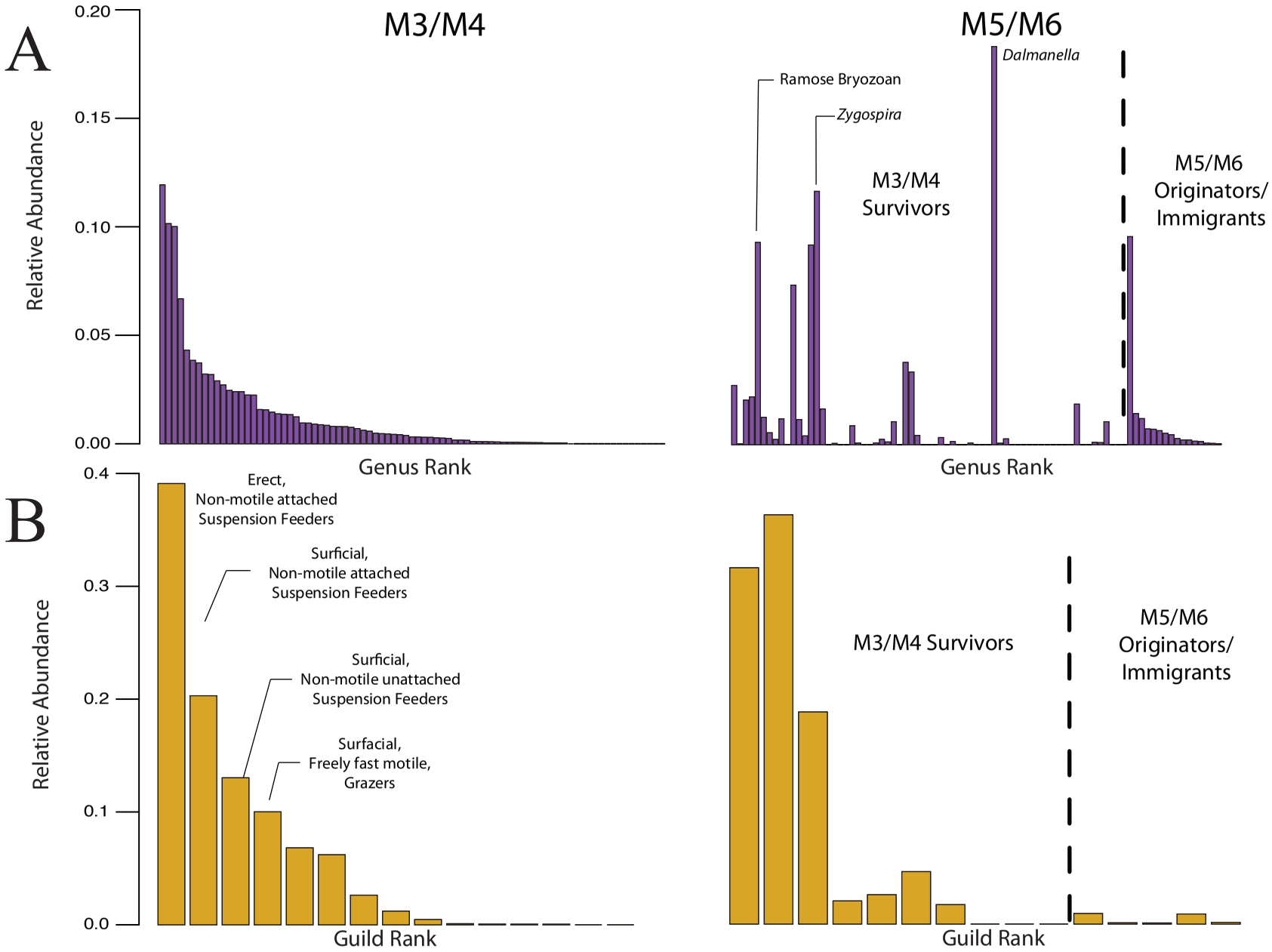

A
M3/M4
M5/M6
Relative Abundance
0.20
0.15
0.10
0.05
0.00
Ramose Bryozoan
Zygospira
Dalmanella
M3/M4
Survivors
M5/M6
Originators/
Immigrants
Genus Rank
Genus Rank
B
Relative Abundance
0.4
0.3
0.2
0.1
0.0
Erect,
Non-motile attached
Suspension Feeders
Surficial,
Non-motile attached
Suspension Feeders
Surficial,
Non-motile unattached
Suspension Feeders
Surfacial,
Freely fast motile,
Grazers
M3/M4 Survivors
M5/M6
Originators/
Immigrants
Guild Rank
Guild Rank

Figure 11 – RAD for the M4/M5 extinction. A) Pre-extinction (left) and post-extinction (right) relative abundance for each genus B) Pre-extinction (left) and post-extinction (right) relative abundance for each guild.

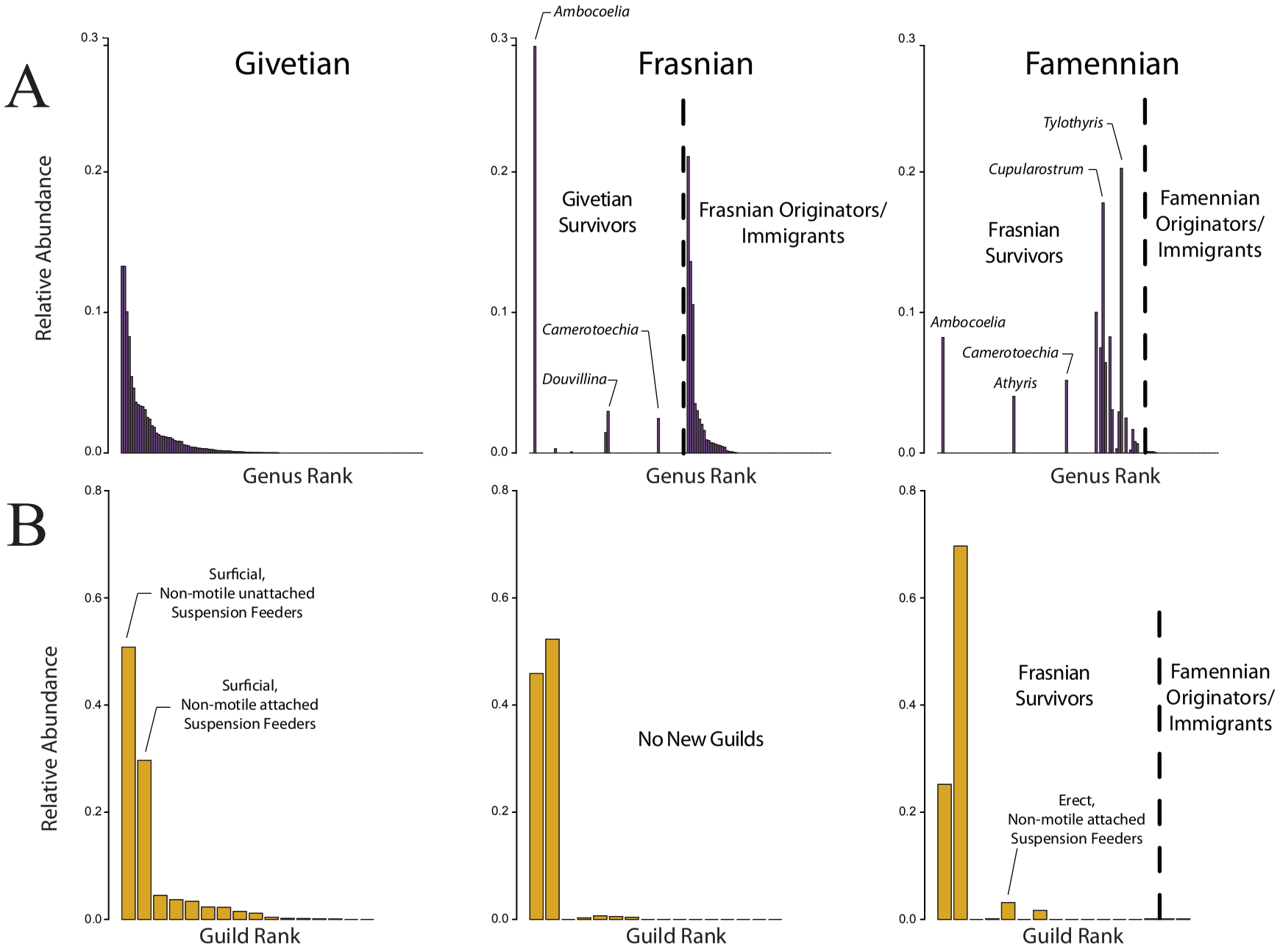

A
Givetian
Frasnian
Famennian
Relative Abundance
Genus Rank
Ambocoelia
Givetian Survivors
Frasnian Originators/ Immigrants
Camerotoechia
Douvillina
Tylothyris
Cupularostrum
Frasnian Survivors
Famennian Originators/ Immigrants
Athyris
B
Surficial, Non-motile unattached Suspension Feeders
Surficial, Non-motile attached Suspension Feeders
No New Guilds
Erect, Non-motile attached Suspension Feeders
Guild Rank

Figure 12 – RAD for the Late Devonian extinction. A) Givetian (left), Frasnian (middle) and Famennian (right) relative abundance for each genus B) Givetian (left), Frasnian (middle) and Famennian (right) relative abundance for each guild.

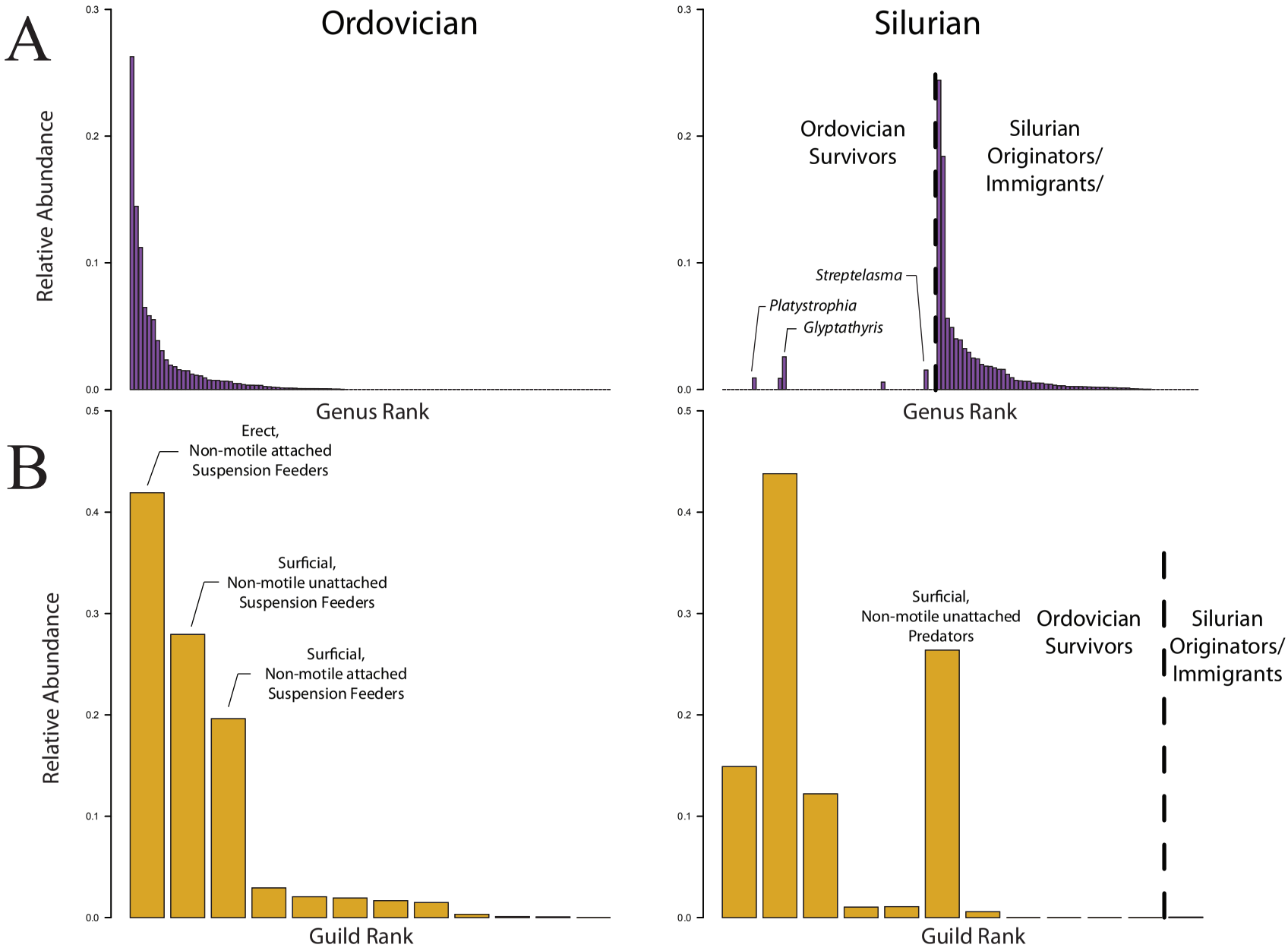
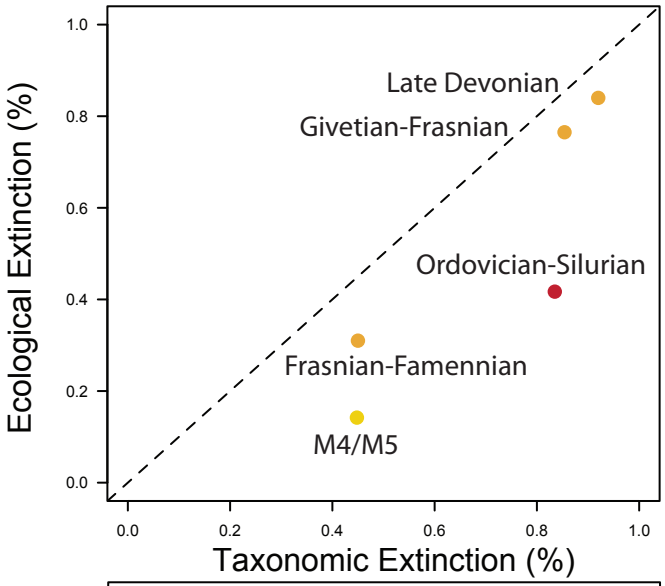
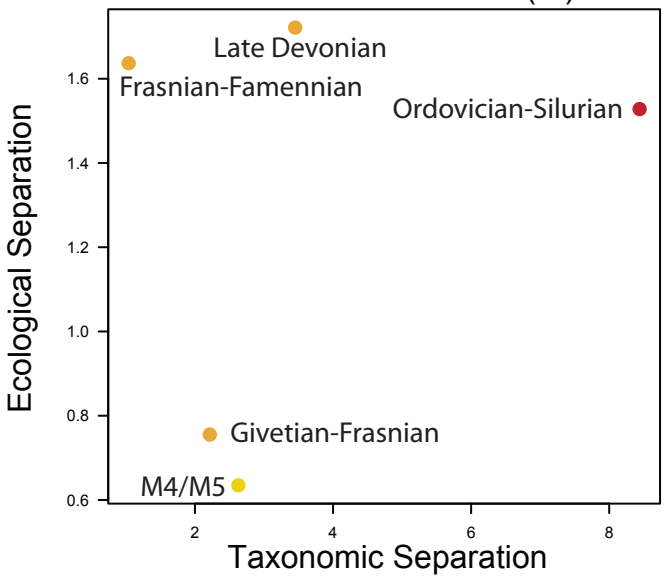

A
Ordovician
Silurian
Relative Abundance
Genus Rank
Ordovician
Survivors
Silurian
Originators/
Immigrants/
Streptelasma
Platystrophia
Glyptathyris
B
Erect,
Non-motile attached
Suspension Feeders
Surficial,
Non-motile unattached
Suspension Feeders
Surficial,
Non-motile attached
Suspension Feeders
Surficial,
Non-motile unattached
Predators
Ordovician
Survivors
Silurian
Originators/
Immigrants
Guild Rank

Figure 13 – RAD for the Ordovician-Silurian extinction. A) Pre-extinction (left) and post-extinction (right) relative abundance for each genus B) Pre-extinction (left) and post-extinction (right) relative abundance for each guild.


Ecological Extinction (%)
Taxonomic Extinction (%)
Late Devonian
Givetian-Frasnian
Ordovician-Silurian
Frasnian-Famennian
M4/M5
0.0
0.2
0.4
0.6
0.8
1.0


Ecological Separation
Taxonomic Separation
Late Devonian
Frasnian-Famennian
Ordovician-Silurian
Givetian-Frasnian
M4/M5
0.6
0.8
1.0
1.2
1.4
1.6
2
4
6
8

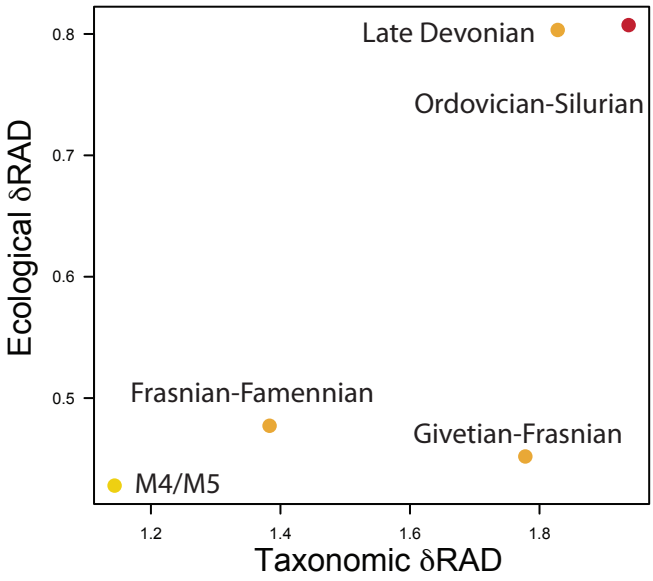

Ecological δRAD
Taxonomic δRAD
Late Devonian
Ordovician-Silurian
Frasnian-Famennian
Givetian-Frasnian
M4/M5
0.5
0.6
0.7
0.8
1.2
1.4
1.6
1.8

Figure 14 – Ecological vs. Taxonomic extinction intensity. Comparison of ecological and taxonomic metrics. A) Percent extinction among genera (taxonomic extinction), and guilds (ecological extinction) for each extinction event. The dotted line represents the null hypothesis, that taxonomic intensity scales directly with ecological intensity. B) DCA separation values for genera (Taxonomic Separation) and guilds (Ecological Separation). C) ΔRAD values for genera (Taxonomic ΔRAD) and guilds (Ecological ΔRAD).

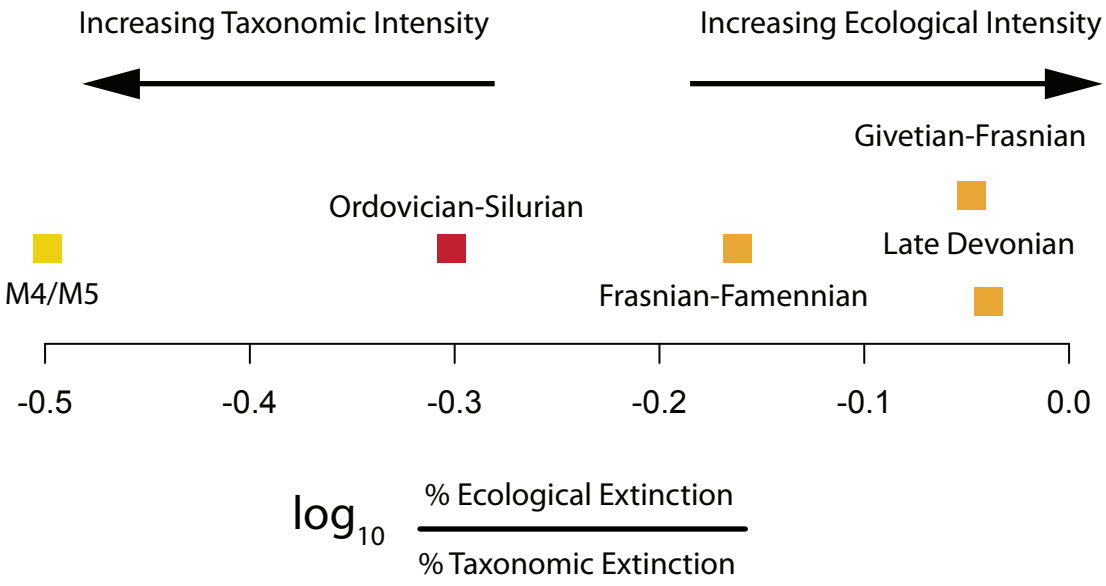

Increasing Taxonomic Intensity
Increasing Ecological Intensity
Givetian-Frasnian
Ordovician-Silurian
Late Devonian
M4/M5
Frasnian-Famennian
-0.5
-0.4
-0.3
-0.2
-0.1
0.0
log10 % Ecological Extinction / % Taxonomic Extinction

Figure 15 – Relative ecological intensity. Log percent ecological extinction divided by percent taxonomic extinction scales the ecological effects of the extinction by the taxonomic effects, and it measures the intensity of extinction of guilds relative to genera.

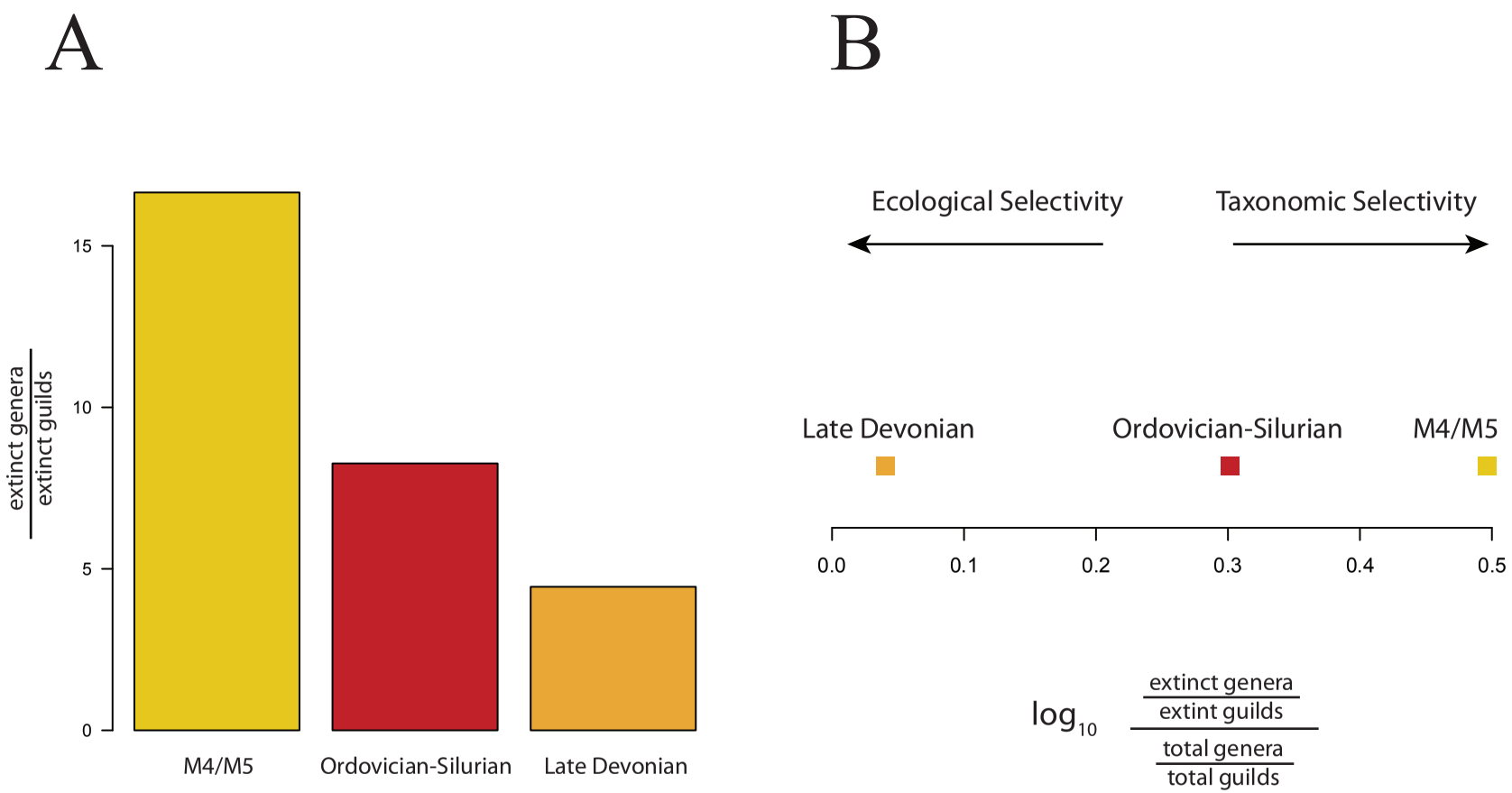

A
extinct genera / extinct guilds
15
10
5
0
M4/M5
Ordovician-Silurian
Late Devonian
B
Ecological Selectivity
Taxonomic Selectivity
Late Devonian
Ordovician-Silurian
M4/M5
0.0
0.1
0.2
0.3
0.4
0.5
log10 (extinct genera / extint guilds) / (total genera / total guilds)

Figure 16 – Ecological selectivity. A) Barplot showing the ratio of extinct genera to extinct guilds. B) Chart showing the number of genera that go extinct per guild divided by the total number of genera divided by the total number of guilds in a time interval.

APPENDIX A

Guilds Present in this Study

Guilds in this study were assigned a unique number based on their position in an ecospace cube (Bush et al., 2007) the axes of the cube represent traits for Tiering, Motility, and Feeding Strategy. Each guild number is a three digit code, the first number corresponds to Tiering, the second number corresponds to Motility, and the third number corresponds to Feeding Strategy as per Table 1. Guilds were assigned using the function: guildCube()

Guild Number	Tiering	Motility Level	Feeding Mechanism
261	Erect	Non-motile, attached	Suspension
361	Surficial	Non-motile, attached	Suspension
351	Surficial	Non-motile, unattached	Suspension
315	Surficial	Freely, fast	Predatory
324	Surficial	Freely, slow	Grazing
355	Surficial	Non-motile, unattached	Predatory
115	Pelagic	Freely, fast	Predatory
441	Semi-infaunal	Facultative, attached	Suspension
523	Shallow infaunal	Freely, slow	Mining
531	Shallow infaunal	Facultative, unattached	Suspension
346	Surficial	Facultative, unattached	Other
321	Surficial	Freely, slow	Suspension
314	Surficial	Freely, fast	Grazing
316	Surficial	Freely, fast	Other
126	Pelagic	Freely, fast	Other
266	Erect	Non-motile, attached	Other
431	Semi-infaunal	Facultative, unattached	Suspension
433	Semi-infaunal	Facultative, unattached	Mining
322	Surficial	Freely, slow	Surface Deposit
423	Semi-infaunal	Freely, slow	Mining
362	Surficial	Non-motile, attached	Surface Deposit
331	Surficial	Facultative, unattached	Suspension
312	Surficial	Freely, fast	Surface Deposit
241	Erect	Facultative, attached	Suspension
251	Erect	Non-motile, unattached	Predatory
532	Shallow infaunal	Facultative, unattached	Surface Deposit
431	Semi-infaunal	Facultative, unattached	Suspension
126	Surficial	Freely, slow	Other

APPENDIX B

Guild Assignments

M3M4 Guilds

Genus	Higher Taxon	Guild
Deceptrix	Bivalvia	423
Ctenodonta	Bivalvia	423
Cunemya	Bivalvia	431
Cyrtodonta	Bivalvia	431
Whitella	Bivalvia	531
Anazyga	Brachiopoda	361
Bilobia	Brachiopoda	361
Camerella	Brachiopoda	361
Christiana	Brachiopoda	361
Dinorthis	Brachiopoda	361
Doleroides	Brachiopoda	361
Eoplectodonta	Brachiopoda	361
Glyptorthis	Brachiopoda	361
Hesperorthis	Brachiopoda	361
Leptaena	Brachiopoda	351
Multicostella	Brachiopoda	361
Oepikina	Brachiopoda	351
Oxoplecia	Brachiopoda	361
Paucicrura	Brachiopoda	361
Paurorthis	Brachiopoda	361
Pionodema	Brachiopoda	361
Plectocamara	Brachiopoda	361
Rostricellula	Brachiopoda	361
Schizotreta	Brachiopoda	361
Strophomena	Brachiopoda	351
Sowerbyella	Brachiopoda	351
Zygospira	Brachiopoda	361
Inarticulata.indet.	Brachiopoda	361
rhynchonellid.indet.	Brachiopoda	361
Brachiopoda.indet.	Brachiopoda	361
Dalmanella	Brachiopoda	361
Hebertella	Brachiopoda	361
Rafinesquina	Brachiopoda	351
Rhynchotrema	Brachiopoda	361
Chasmatopora	Bryozoa	261
Escharopora	Bryozoa	261
Prasopora	Bryozoa	261
Rhindictya	Bryozoa	261
encrusting.bryozoan	Bryozoa	361
thick.ramose.bryozoan	Bryozoa	261

thin.ramose.bryozoan..morph.	Bryozoa	261
thin.ramose.bryozoan.indet.	Bryozoa	261
Heterotrypa	Bryozoa	261
massive.trepostome	Bryozoa	261
bifoliate.bryozoan	Bryozoa	261
orthoconic.nautiloids	Cephalopoda	116
cog.crinoid	Crinoidea	261
thin.ring.crinoid	Crinoidea	261
thick.ring.crinoid	Crinoidea	261
flower.crinoid	Crinoidea	261
pentagonal.crinoid	Crinoidea	261
stacked.crinoid	Crinoidea	261
inner.star.crinoid	Crinoidea	261
striped.crinoid	Crinoidea	261
striped.flower.crinoid	Crinoidea	261
star.crinoid	Crinoidea	261
striped.star.crinoid	Crinoidea	261
Hormotoma	Gastropoda	324
Lophospira	Gastropoda	324
Maclurites	Gastropoda	324
Gastropoda.indet.	Gastropoda	324
Cyclonema	Gastropoda	322
Liospira	Gastropoda	324
leperditid.ostracod	Ostracoda	314
Chondrites	Polychaeta	433
Diplocraterion	Polychaeta	433
alga.Hindia..	Porifera	362
rhombiferan.plate	Rhombifera	361
Streptelasma	Rugose Coral	266
Tetradium	Tabulate Coral	266
Cornulites	Tentaculita	331
Ceraurus	Trilobita	316
Isotelus	Trilobita	316
Pterygometopus	Trilobita	316
Trilobita.indet.	Trilobita	316
Isotelus.spines	Trilobita	316
Trilobita.A	Trilobita	316

M5M6 Guilds

Genus	Higher Taxon	Guild
Ambonychia	Bivalvia	341
Ctenodonta	Bivalvia	423
Cunemya	Bivalvia	431
Cyrtodonta	Bivalvia	431
Cyrtodontula	Bivalvia	531
Deceptrix	Bivalvia	423
Ischyrodonta	Bivalvia	431
modiomorphid	Bivalvia	431
Paleoneilo	Bivalvia	423
Whitella	Bivalvia	531
Bivalvia.indet.	Bivalvia	431
Lyrodesma	Bivalvia	431
Anazyga	Brachiopoda	361
Dalmanella	Brachiopoda	361
Dinorthis	Brachiopoda	361
Doleroides	Brachiopoda	361
Glyptorthis	Brachiopoda	361
Hebertella	Brachiopoda	361
Hesperorthis	Brachiopoda	361
Heterorthina	Brachiopoda	361
Lingulid	Brachiopoda	361
Platystrophia	Brachiopoda	361
Rafinesquina	Brachiopoda	351
Rhynchotrema	Brachiopoda	361
Rostricellula	Brachiopoda	361
Strophomena	Brachiopoda	351
Sowerbyella	Brachiopoda	351
Zygospira	Brachiopoda	361
Inarticulata.indet.	Brachiopoda	361
Orthorhyncula	Brachiopoda	361
Escharopora	Bryozoa	261
Prasopora	Bryozoa	261
Rhindictya	Bryozoa	261
massive.trepostome	Bryozoa	261
bifoliate.bryozoan	Bryozoa	261
bumpy.bryo..ramose.	Bryozoa	261
encrusting.bryozoan	Bryozoa	361
thick.ramose.bryozoan	Bryozoa	261
thin.ramose.bryozoan..morph.	Bryozoa	261
thin.ramose.bryozoan.indet.	Bryozoa	261

Chasmatopora	Bryozoa	261
Constellaria	Bryozoa	261
orthoconic.nautiloids	Cephalopoda	116
cog.crinoid	Crinoidea	261
thin.ring.crinoid	Crinoidea	261
thick.ring.crinoid	Crinoidea	261
flower.crinoid	Crinoidea	261
pentagonal.crinoid	Crinoidea	261
stacked.crinoid	Crinoidea	261
star.crinoid	Crinoidea	261
striped.crinoid	Crinoidea	261
crinoidea.indet.	Crinoidea	261
Echinodermata.indet.	Crinoidea	261
cog.star.crinoid	Crinoidea	261
inner.star.crinoid	Crinoidea	261
Bucania	Gastropoda	324
Cyclonema	Gastropoda	322
Lophospira	Gastropoda	324
Maclurites	Gastropoda	324
Gastropoda.indet.	Gastropoda	324
Bellerophon	Gastropoda	324
Hormotoma	Gastropoda	324
Cyclora	Gastropoda	324
graptolites	Hemichordata	116
leperditid.ostracod	Ostracoda	314
Chondrites	Polychaeta	433
Diplocraterion	Polychaeta	433
Stromatoporoidea	Porifera	361
Stromatoporoids	Porifera	361
algal.coating	Protista	362
Solenopora	Protista	362
Streptelasma	Rugose Coral	266
Columnaria	Rugose Coral	266
Tetradium	Tabulate Coral	266
Cornulites	Tentaculita	331
Sinuites	Tergomya	324
Ceraurus	Trilobita	316
Cryptolithus	Trilobita	311
Eomonorachus	Trilobita	316
Flexicalymene	Trilobita	316
Isotelus	Trilobita	316
Trilobita.indet.	Trilobita	316
Isotelus.spines	Trilobita	316

Gravicalymene	Trilobita	316

Brassfield Guilds

Genus	Higher Taxon	Guild
Pterinea	Bivalvia	361
Dalejina	Brachiopod	361
Dolerorthis	Brachiopod	361
Eospirifer	Brachiopod	361
Fardenia	Brachiopod	361
Glyptorthis	Brachiopod	351
Leptaena	Brachiopod	351
Platystrophia	Brachiopod	361
Plectatrypa	Brachiopod	361
Resserella	Brachiopod	361
Rhynchotreta	Brachiopod	361
Sowerbyella	Brachiopod	351
Stegerhynchus	Brachiopod	361
Strohonella	Brachiopod	351
Triplesia	Brachiopod	351
Aspidopora	Bryozoa	361
Chasmatopora	Bryozoa	261
Clathropora	Bryozoa	261
Fenestellid	Bryozoa	261
Hallopora	Bryozoa	261
Helopora	Bryozoa	351
Hemitrypa	Bryozoa	361
Pachydictya	Bryozoa	261
Phaenopora	Bryozoa	261
Ptilodictya	Bryozoa	261
Ramose.Bryozoan	Bryozoa	261
Rhinopora	Bryozoa	361
Thin.Ramose.Bryozoan	Bryozoa	261
Trepostome	Bryozoa	261
Nautiloid	Cephalopod	115
Conularida	Cnidaria	261
Bellerophontina	Gastropoda	324
Hormotoma	Gastropoda	324
Oxydiscus	Gastropoda	324
Platystoma	Gastropoda	324
Arachnophyllum	Rugose Coral	355
Cyathophyllum	Rugose Coral	355
Dinophyllum	Rugose Coral	355
Horn.Coral	Rugose Coral	355
Rhegmaphyllum	Rugose Coral	355

Streptelasma	Rugose Coral	355
Streptelasmiid	Rugose Coral	355
Alveolites	Tabulate Coral	351
Coenites	Tabulate Coral	351
Favosites	Tabulate Coral	351
Heliolites	Tabulate Coral	351
Lyellia	Tabulate Coral	351
Syringopora	Tabulate Coral	351
Cornulites	Tentaculita	261
Bumastus	Trilobita	312
Calymenid	Trilobita	315
Dalmanites	Trilobita	315
Encrinurus	Trilobita	315
Illaenus	Trilobita	315
Trimerus	Trilobita	315

C5 Guilds

Genus	Higher Taxon	Guild
Ambonychia	Bivalvia	361
Caritodens	Bivalvia	361
Deceptrix	Bivalvia	523
Modiomorpha	Bivalvia	441
Inarticulate	Brachiopoda	531
Petrocrania	Brachiopoda	361
Trematis	Brachiopoda	531
Dalmanella	Brachiopoda	361
Eochonetes	Brachiopoda	351
Glyptorthis	Brachiopoda	351
Hebertella	Brachiopoda	361
Hiscobeccus	Brachiopoda	361
Holtedahlina	Brachiopoda	351
Leptaena	Brachiopoda	351
Plaesiomys	Brachiopoda	361
Platystrophia	Brachiopoda	361
Rafinesquina	Brachiopoda	351
Rhynchotrema	Brachiopoda	361
Strophomena	Brachiopoda	351
Zygospira	Brachiopoda	361
bifoliate.trepostome.indet.	Bryozoa	261
Constellaria	Bryozoa	261
Cuffeyella	Bryozoa	261
encrusting.bryozoan.indet.	Bryozoa	361
Fenestella	Bryozoa	261
massive.trepostome.indet.	Bryozoa	261
Parvohallopora	Bryozoa	261
ramose.trepostome.indet.	Bryozoa	261
Ropalonaria	Bryozoa	361
thin.ramose.bryozoan.indet.	Bryozoa	261
Nautiloid	Cephalopoda	115
Cincinnaticrinus	Crinoidea	261
Cupulocrinus	Crinoidea	261
Ectenocrinus	Crinoidea	261
Glyptocrinus	Crinoidea	261
Iocrinus	Crinoidea	261
Lichenocrinus	Crinoidea	261
Xenocrinus	Crinoidea	261
Bellerophonta	Gastropoda	324
Cyclonema	Gastropoda	336

gastropod.indet.	Gastropoda	324
Hormotoma	Gastropoda	324
Liospira	Gastropoda	324
Lophospira	Gastropoda	324
Phragmolites	Gastropoda	324
Stromatoporoid	Porifera	361
Cyathophylloides	Rugose Coral	355
Grewingkia	Rugose Coral	355
Streptelasma	Rugose Coral	355
Calapoecia	Tabulate Coral	351
Foerstephyllum	Tabulate Coral	351
Protaraea	Tabulate Coral	351
Tetradium	Tabulate Coral	351
Tentaculites	Tentaculita	115
Cornulites	Tentaculita	261
Cyrtolites	Tergomya	324
Flexicalymene	Trilobita	315
Ceraurinus	Trilobita	315
Ceraurus	Trilobita	315
Isotelus	Trilobita	315
Odontopleurid	Trilobita	315
Tricopelta	Trilobita	315

Givetian Guilds

Genus	Higher Taxon	Guild
Actinopteria	Bivalvia	33
Allanella	Brachiopoda	33
Ambocoelia	Brachiopoda	33
Amplexiphyllu	Rugose Coral	171
Anamesocrinus	Crinoidea	20
Ancyrocrinus	Crinoidea	20
Athyris	Brachiopoda	27
Atrypa	Brachiopoda	33
Aulocystis	Tabulate Coral	27
Blotherophyllu	Rugose Coral	171
Botryllopora	Bryozoa	20
Botryocrinus	Crinoidea	20
Camarotoechia	Brachiopoda	33
Centronella	Brachiopoda	27
Chonetes	Brachiopoda	27
Cladochonus	Tabulate Coral	27
Cladopora	Tabulate Coral	32
Coenites	Tabulate Coral	27
Crania	Brachiopoda	33
Crurispina	Brachiopoda	33
Cryptonella	Brachiopoda	27
Cupularostrum	Brachiopoda	33
Cypricardella	Bivalvia	17
Cypricardinia	Bivalvia	17
Cyrtina	Brachiopoda	33
Cyrtinoides	Brachiopoda	33
Cystiphylloide	Rugose Coral	171
Cyttarocrinus	Crinoidea	20
Decadocrinus	Crinoidea	20
Dechenella	Trilobita	39
Deltacrinus	Crinoidea	20
Delthyris	Brachiopoda	33
Depasophyllun	Rugose Coral	171
Devonochonete	Brachiopoda	27
Dipleura	Trilobita	39
Douvillina	Brachiopoda	27
Echinocoelia	Brachiopoda	33
Elita	Brachiopoda	27
Emanuella	Brachiopoda	33
Eridophyllum	Rugose Coral	171

Eumetabolotoe	Brachiopoda	27
Eutaxocrinus	Crinoidea	20
Favosites	Tabulate Coral	27
Fenestella	Bryozoa	32
Fistulipora	Bryozoa	32
Gilbertsocrinus	Crinoidea	20
Greenops	Trilobita	39
Hadrophyllum	Rugose Coral	171
Hederella	Bryozoa	33
Heliophyllum	Rugose Coral	170
Heterophrentis	Rugose Coral	171
Hyperoblastus	Crinoidea	20
Kophinocrinus	Crinoidea	20
Leiorhynchus	Brachiopoda	27
Lingulid	Brachiopoda	17
Loculipora	Bryozoa	32
Logocrinus	Crinoidea	20
Longispina	Brachiopoda	27
Mediospirifer	Brachiopoda	33
Meristella	Brachiopoda	27
Modiomorpha	Bivalvia	22
Mourlonia	Gastropoda	117
Mucrospirifer	Brachiopoda	33
Naticonema	Gastropoda	189
Nucleocrinus	Crinoidea	20
Nucleospira	Brachiopoda	33
Nucula	Bivalvia	53
Nuculites	Bivalvia	83
Orbiculoides	Brachiopoda	27
Orthis	Brachiopoda	27
Palaeocaris	Crustacea	43
Palaeoneilo	Bivalvia	83
Palaeozygopleu	Gastropoda	15
Paleozygopleur	Gastropoda	15
Paracyclas	Bivalvia	17
Parazyga	Brachiopoda	27
Pentamerella	Brachiopoda	27
Petrocrania	Brachiopoda	33
Phacops	Trilobita	39
Pholadella	Bivalvia	17
Pholidops	Brachiopoda	33
Pholidostrophia	Brachiopoda	33
Pleurodictyum	Tabulate Coral	27

Ponticeras	Cephalopoda	145
Productella	Brachiopoda	27
Protoleptostrop	Brachiopoda	27
Pseudaviculope	Bivalvia	33
Pseudoatrypa	Brachiopoda	33
Pterinopecten	Bivalvia	33
Pterochaenia	Bivalvia	33
Ptilonaster	Asterozoa	153
Ptychopteria	Bivalvia	33
Receptaculites	Plantae	207
Retichonetes	Brachiopoda	27
Rhipidomella	Brachiopoda	27
Rhipidothyris	Brachiopoda	27
Rhombopora	Bryozoa	32
Schuchertella	Brachiopoda	27
Sphaerospongi	Porifera	213
Spinatrypa	Brachiopoda	27
Spinocyrtia	Brachiopoda	33
Spinulocosta	Brachiopoda	27
Stereolasma	Rugose Coral	171
Straparollus	Gastropoda	27
Strophodonta	Brachiopoda	27
Sulcoretepora	Bryozoa	32
Syaptocrinus	Crinoidea	20
Synaptocrinus	Crinoidea	20
Synbathocrinus	Crinoidea	20
Taeniopora	Bryozoa	32
Tentaculites	Mollusca	27
Thamnoptychi	Tabulate Coral	27
Tornoceras	Cephalopoda	145
Tropidocyph	Trilobita	39
Tropidoleptus	Brachiopoda	33
Truncalosia	Brachiopoda	27
Zoophycus	Annelida	16
Zostocrinus	Crinoidea	21

Frasnian Guilds

Genus	Higher Taxon	Guild
Edmondia	Bivaliva	531
Leptodesma	Bivaliva	361
Pectin	Bivaliva	361
Ambocoelia	Brachiopoda	361
Athyris	Brachiopoda	351
Camarotoechia	Brachiopoda	361
Carniferella	Brachiopoda	361
Chonetacea	Brachiopoda	351
Cupularostrum	Brachiopoda	361
Cyrtina	Brachiopoda	361
Cyrtospirifer	Brachiopoda	361
Devonoproductus	Brachiopoda	351
Douvillina	Brachiopoda	351
Eumetabolatoechia	Brachiopoda	351
Floweria	Brachiopoda	351
Lingulid	Brachiopoda	531
Nervostrophia	Brachiopoda	351
Orbiculoid	Brachiopoda	351
Praewaagenoconcha	Brachiopoda	351
Schizophoria	Brachiopoda	361
Spinatrypa	Brachiopoda	351
Spirifer	Brachiopoda	361
Striatochonetes	Brachiopoda	351
Strophoproductus	Brachiopoda	351
Thiemella	Brachiopoda	361
Tylothyris	Brachiopoda	361
Bryozoa.twig	Bryozoa	261
nautiloid	Cephalopoda	115
Crinoid.star	Crinoidea	241
Crinoid.wheel	Crinoidea	241
Rugosa	Rugose Coral	355

Famennian Guilds

Genus	Higher Taxon	Guild
Edmondia	Bivalvia	531
Leptodesma	Bivalvia	361
Modiamorpha	Bivalvia	441
Mytilarca	Bivalvia	341
Ambocoelia	Brachiopoda	361
Athyris	Brachiopoda	351
Camarotoechia	Brachiopoda	361
Carniferella	Brachiopoda	361
Cyrtospirifer	Brachiopoda	361
Cupularostrum	Brachiopoda	361
Schizophoria	Brachiopoda	361
Floweria	Brachiopoda	351
Spirifer	Brachiopoda	361
Striatochonetes	Brachiopoda	351
Thiemella	Brachiopoda	361
Tylothyris	Brachiopoda	361
Praewaagenoconcha	Brachiopoda	351
Bryozoa.twig	Bryozoa	261
Bryozoa.fen	Bryozoa	261
Crinoid.star	Crinoidea	241
Crinoid.wheel	Crinoidea	241
gastropod	Gastropoda	324

APPENDIX C

Devonian Localities

Givetian PBDB Collection Numbers

Collection numbers for all Givetian samples from New York at www.paleodb.org

5620	9370	76332	76376	76415	76695	76791	76830
5655	9371	76333	76377	76416	76696	76792	76831
5656	9372	76335	76378	76417	76697	76793	76832
5657	10101	76339	76379	76418	76698	76794	76833
5660	10107	76340	76380	76419	76699	76795	76834
5662	10108	76341	76381	76420	76700	76796	76835
5663	10109	76342	76382	76421	76701	76797	76836
5664	10110	76343	76383	76422	76702	76798	76837
5665	10119	76344	76384	76423	76703	76799	76838
5666	10518	76345	76385	76424	76704	76800	76839
5669	10519	76347	76386	76425	76705	76801	76840
5670	10520	76348	76387	76426	76706	76802	76841
5671	10523	76349	76388	76427	76707	76803	
8755	10525	76350	76389	76428	76764	76804	
8756	10535	76351	76390	76429	76765	76805	
8757	10536	76352	76391	76430	76766	76806	
8758	10537	76353	76392	76431	76767	76807	
8759	10538	76354	76393	76432	76768	76808	
8760	10539	76355	76394	76433	76769	76809	
8764	10540	76356	76395	76434	76770	76810	
8765	10541	76357	76396	76435	76771	76811	
8767	10542	76358	76397	76436	76772	76812	
8769	10543	76359	76398	76437	76773	76813	
8771	10544	76360	76399	76438	76774	76814	
8772	10546	76361	76400	76439	76775	76815	
8779	10552	76362	76401	76440	76776	76816	
8780	10553	76363	76402	76441	76777	76817	
8786	10556	76364	76403	76442	76778	76818	
8789	75223	76365	76404	76443	76779	76819	
8793	76104	76366	76405	76444	76780	76820	
8794	76137	76367	76406	76686	76782	76821	
8795	76162	76368	76407	76687	76783	76822	
8796	76194	76369	76408	76688	76784	76823	
8797	76210	76370	76409	76689	76785	76824	
8798	76213	76371	76410	76690	76786	76825	
8799	76214	76372	76411	76691	76787	76826	
9367	76215	76373	76412	76692	76788	76827	
9368	76263	76374	76413	76693	76789	76828	
9369	76266	76375	76414	76694	76790	76829	

Frasnian Localities List

Watson Creek Road. Road cut about ½ mile west of the intersection of US Route 15 and Watson Creek Road. Steuben County, New York. 42°00.670′ N, 77°08.248′ W

Route 417 and 100. Road cut about 0.1 mile south of the intersection of Route 417 and Steuben County Route 100, between South Addison and Borden. Steuben County, New York. 42°04.394′ N, 77°17.953′ W

Route 110 (2 Sites). Site 1: Road cut at the intersection of Steuben County Route 110 and Demun Road near Cameron Mills. Steuben County, New York. 42°10.275′ N, 77°21.697′ W
Site 2: Road cut along Steuben County Route 100, approximately 300 ft. southeast from the intersection of Steuben County Route 100 and Richtmeyer Road. Steuben County, New York. 42°10.586′ N, 77°21.904′ W

Route 119 and Hanyon Road. Road cut at the intersection of Steuben County Route 119 (Canisteo River Road) and Hanyon Road. Steuben County, New York. 42°15.378′ N, 77°29.957′ W

Route 119 W of Adrian. Road cut about 1 mile west of the intersection of Catatunk Road and Steuben County Road 119. Steuben County, New York. 42° 15.430′ N, 77°32.156′ W

Route 70 and 24, Swain. Road cut at the intersection of Route 70 and Allegany County Route 24. Allegany County, New York. 42°28.731′ N, 77°50.912′ W

CAM. Road cut just west of Cameron, near the intersection of Steuben County Route 119 and Bath Cameron Road. Steuben County, New York. Coordinates unknown.

Big Creek (BCP). Stream cut behind Peterson Farmhouse (as of summer 2010) at 7498 Old Big Creek Road, about 1 mile east of the intersection of Route 36 and Route 70A. Steuben County, New York. 42°22.069′ N, 77°38.493′ W

Famennian Locality List

Angelica Creek (ANC). Stream cut along Allegany Co. Route 16 about ¼ mile southeast from the intersection with Allegany Route 15 under the bridge. Allegany County, New York. 42°18.502′ N, 78°2.615′ W

Big Creek (BCP). Stream cut behind Peterson Farmhouse (as of summer 2010) at 7498 Old Big Creek Road, about1 mile east of the intersection of Route 36 and Route 70A. Steuben County, New York. 42°22.069′ N, 77°38.493′ W

Bryant Hill Creek (BHC). Stream cut near 5575 Bryant Hill Road Ellicottville, New York 14731. Locality at bridge ¼ mile east of intersection of Bryant Hill Road and Route 242. Cattaraugus County, New York. 42°18.454′ N, 78°37.283′ W

Caneadea Creek (CAN). Stream cut 1 mile south of the intersection of Route 19 and Route 243. Where Caneadea Creek meets Genesee River. Allegany County, New York. 42°23.004′ N, 78°09.281′ W

Crosby Creek near Hornell (CCH). Stream cut about ½ mile west from intersection of Route 36 and Crosby Creek Road. Steuben County, New York. 42°18.954′ N, 77°40.230′ W

Cunningham Creek (CHC). Stream cut about 1 mile west from the intersection of Cunningham Creek Road, and Steuben County Road 29. Steuben County, New York. 42°18.698′ N, 77°36.436′ W

Gowan Hollow Creek (GHC). Stream cut about ¾ mile west from the intersection of State Land Road and Gowan Gulf Road, New Albion. Cattaraugus County, New York. 42°18.285′ N, 78°50.614′ W

Hammer Creek (HAC). Stream cut 0.8 mile northeast from the intersection of Hammer Creek Road and Steuben Route 29. Steuben County. 42°17.727′ N, 77°35.923′ W

Hathaway Hollow Road (HAT). Road cut about ¼ mile northwest from the intersection of Hathaway Hollow Road and Steuben Route 29. Steuben County, New York. 42°15.070′ N, 77°27.149′ W

Kurtz Hollow Creek (KHC). Stream cut on Kurtz Hollow Road, South of Dansville, ¾ mile east of the intersection of Ryder Road and Kurtz Hollow Road. Steuben County, New York. 42°28.895′ N, 77°39.203′ W

Mud Hollow Creek (MHC). Stream cut 0.6 mile south from the intersection of Catatuck Road and Roosa Road, along Roosa Road. Steuben County, New York. 42°14.650′ N, 77°29.614′ W

McHenry Valley Creek (MHV). Stream cut about ½ mile southwest from the intersection of Route 21 and McHenry Valley Road, along McHenry Valley Road. Under the 1st bridge. Allegany County, New York. 42°18.544′ N, 77°45.203′ W

McHenry Valley Creek 2 (MHV2). Stream cut about 2.5 miles southwest from the intersection of Route 21 and McHenry Valley Road, along McHenry Valley Road. Allegany County, New York. 42°17.682′ N, 77°46.628′ W

Rushford Creek (RFC). Stream cut along North Valley Road. About ¼ mile southwest from the intersection of Barber Road and North Valley Road near Rushford Conservation Camp. Allegany County, New York. 42°20.723′ N, 78°13.984′ W

Roosa School (RSC). Stream cut on McChesney Road about 1.5 miles northeast from the intersection of McChesney Road and Steuben County Road 30. Steuben County, New York. 43°14.038′ N, 77°72.956′ W

Shamrock Pines (SRP). Outcrop at Shamrock Pines campground along Route 98 in Franklinville. Outcrop is in the northwest corner of the campground. Cattaraugus County, New York. 42°18.008′ N, 78°31.551′ W

Tuscarora Creek (TAC). Stream cut at the intersection of Route 417 and Steuben County Route 85. Steuben County, New York. 42°4.267′ N, 77°16.174′ W

White Creek (WHC). Stream cut along Allegany County Route 17 about ½ mile south from the intersection of Allegany Route 17 and Route 19. Allegany County, New York. 42°19.311′ N, 78°06.416′ W

APPENDIX D

Devonian Faunal Counts

Faunal counts made for this study from the Frasnian and Famennian of New York

	Ambocoelia	Athyris	Bryozoa-twig	Camarotoechi	Carniferella
CAM-138	8	5	0	1	1
BCP-005	0	0	0	0	0
119/Hanyan R	20	0	1	0	0
KHC02	0	0	0	0	0
DAN21	33	0	0	0	0
CAM89	13	0	0	1	0
Swain 1	22	1	0	0	2
CAM-144	20	2	0	0	4
CAM-141	13	2	0	0	1
CAM104	1	0	0	0	6
BCP-019/020/	21	0	1	0	0
CAM-140	10	4	0	0	9
HAC02	3	0	0	0	1
DAN14	23	0	0	0	0
CAM116	11	1	20	2	0
Watson Creek	0	0	0	0	0
BCP-099	0	0	0	0	0
CAM-146	12	2	0	0	0
CAM96	3	7	0	0	3
CAM-145	5	3	0	0	16
119/Handen R	20	0	0	0	0
BCP-023	55	0	1	0	0
BCP-035	48	0	0	0	1
Cam Mills 1	6	0	0	104	7
BCP-016	1	0	1	0	1
CAM-143	2	0	0	0	5
CAM-148	3	0	0	2	2
CAM-087	1	0	0	2	1
CAM-139	4	2	0	0	2
BCP-106	217	0	0	0	0
KHC01	0	0	0	0	0
Cam Mills 2	0	0	0	0	0
BCP-024	85	0	0	0	0
BCP-040	106	0	0	0	0

Chonetacea	Crinoid-star	Crinoid-wheel	Cupularostrur	Cyrtina	Cyrtospirifer
0	0	0	6	0	24
0	0	0	0	0	0
0	0	0	0	0	13
0	0	0	0	0	0
0	0	0	0	0	0
0	0	1	2	1	4
0	0	4	8	0	2
10	0	0	1	0	15
4	0	0	0	0	5
0	0	1	4	0	2
0	0	0	0	0	0
0	0	0	5	0	10
0	1	0	4	0	0
0	0	0	0	0	0
0	0	5	0	0	5
0	0	0	0	0	0
0	0	1	0	0	0
0	0	0	11	0	4
0	0	2	4	0	37
0	0	0	8	0	35
0	0	0	0	0	3
0	0	0	0	0	0
0	0	1	0	0	0
0	1	3	0	0	0
0	0	0	0	0	0
0	0	0	0	0	7
2	0	0	6	0	98
0	0	0	5	0	17
0	0	0	7	0	14
0	0	1	0	1	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0

Devonoprodu	Douvillina	Edmondia	Eumetabolato	Floweria	Leptodesma
0	0	0	1	11	0
0	11	0	0	0	0
0	6	0	0	0	0
0	0	0	0	0	0
0	2	0	0	0	0
0	0	0	0	0	5
0	0	0	16	0	2
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	1	5	0
0	2	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	8	0
0	0	0	0	2	23
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	1
0	0	0	0	6	0
0	4	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	7	0	0	1	3
0	0	0	0	3	0
0	0	0	0	0	0
0	0	0	0	15	0
0	1	2	0	0	138
0	0	0	0	0	0
1	30	0	0	0	0
0	0	0	0	1	0
0	5	0	0	0	0
0	0	0	0	0	0
0	1	0	0	0	0

Lingula	nautiloid	Nervostrophia	Orbiculoid	Pectin	Praewaagenoc
0	0	0	0	0	5
0	0	0	0	0	8
0	0	0	0	1	0
0	0	0	0	0	40
0	0	0	0	0	0
0	0	0	0	0	19
3	0	0	0	0	25
0	0	0	0	0	11
0	0	0	0	0	0
0	0	0	0	0	43
1	0	0	0	0	20
0	0	0	0	0	0
0	0	0	0	0	19
0	0	0	0	0	1
0	0	0	0	0	31
0	1	0	0	0	0
0	0	20	0	0	5
0	0	0	0	0	2
0	0	0	0	0	18
0	0	0	0	0	5
0	0	0	0	0	0
0	0	0	0	0	1
0	0	0	0	0	19
0	0	0	0	0	0
1	0	1	0	0	7
0	0	0	0	0	2
0	0	0	0	0	20
1	0	0	1	0	0
0	0	0	0	0	5
0	0	0	0	0	0
0	0	0	0	0	35
0	0	0	0	0	8
0	0	0	0	0	0
0	0	0	0	0	0

Rugosa	Schizophoria	Spinatrypa	Spirifer	Striatochonet	Strophoprodu
0	4	23	0	0	0
0	0	14	1	0	0
3	1	28	0	0	0
0	0	0	0	0	1
0	0	0	0	0	0
0	0	6	0	0	0
0	1	12	0	1	0
0	6	6	0	0	0
0	0	4	0	0	0
0	0	0	0	0	0
0	0	7	2	0	0
0	0	16	0	0	0
0	0	8	0	0	0
0	0	0	0	0	0
0	0	0	0	2	0
0	0	0	0	0	0
0	0	3	0	0	0
0	1	0	0	0	0
0	2	0	0	12	0
0	6	18	0	0	0
0	1	5	0	0	0
0	0	2	0	1	0
0	0	0	0	0	0
9	9	0	0	2	0
1	2	2	5	0	0
0	1	11	0	0	0
0	0	12	0	0	0
0	0	0	0	0	0
0	2	20	0	0	0
6	0	4	0	3	0
0	0	1	0	0	0
0	0	24	0	0	0
0	0	0	0	0	0
0	0	0	0	1	0

Thiemella	Tylothyris
0	0
0	0
0	2
2	0
0	0
0	5
0	0
0	0
0	0
0	0
0	0
0	0
0	1
0	0
0	0
0	0
0	0
0	1
0	1
0	1
0	0
0	0
0	0
0	0
0	0
0	0
0	2
0	0
0	0
0	2
0	0
0	0
0	0
0	0

	Ambocoelia	Athyris	Bryozoa-twig	Bryozoa-fen	Camarotoechi
HAT01	0	4	0	0	1
CAN01	0	0	0	0	0
MHV07	14	1	0	0	0
MHV05	13	1	2	0	1
HAC03	3	3	2	0	2
HOC01	1	0	0	0	11
RSC04	0	5	2	0	0
CAN04	0	0	0	0	0
TAC01	1	0	7	0	0
CCH01	5	0	0	0	0
WHC02	2	0	2	0	8
MHV03	15	0	0	0	0
WHC04	0	0	0	0	0
HAT03	8	8	0	0	0
MHC03	10	0	7	1	0
GHC02	0	0	0	0	0
RFC01	4	1	0	0	0
CHC02	0	4	9	0	0
BHC01	0	0	0	0	0
BCP03	0	0	0	0	0
KHC03	0	2	0	0	0
BAC01	2	0	0	0	0
BHC02	6	0	4	0	0
RSC07	0	15	0	0	0
MHV04	3	13	9	0	9
ANC01	0	0	0	0	0
CHC03	110	2	3	0	37
CHC04	1	3	0	0	0
BCP04	0	0	4	0	0
GHC05	0	0	0	0	2
SRP03	3	1	3	0	0
GHC04	9	4	3	0	13
MHC02	0	0	0	0	0
WHC01	3	0	0	0	24
HAT02	1	5	9	0	0
HAC04	13	6	12	0	0
MHV202	0	3	0	0	0
CCH03	8	2	21	0	0
GHC01	0	1	0	0	5
CCH02	0	1	0	0	0
RSC08	3	4	1	0	0

Carniferella	Crinoid-star	Crinoid-wheel	Cyrtospirifer	Cupularostrur	Edmondia	
0	0	48	0	5	0	
0	0	0	0	22	0	
2	0	3	0	2	0	
2	0	3	0	2	0	
0	0	1	1	3	0	
0	0	0	1	2	0	
1	0	0	18	6	0	
0	0	7	0	3	0	
5	6	0	5	0	0	
8	0	12	3	0	0	
0	0	0	0	29	0	
1	1	0	0	0	1	
0	0	0	5	1	0	
30	0	5	0	14	0	
5	0	37	0	54	0	
0	0	12	4	10	0	
0	7	5	4	4	0	
22	0	0	1	10	0	
2	1	0	18	1	0	
0	0	0	0	25	0	
5	0	15	0	1	0	
0	0	0	6	3	0	
2	0	6	11	1	0	
0	0	3	2	0	0	
8	0	0	0	13	0	
0	0	11	4	9	0	
3	0	0	0	2	0	
2	0	5	0	7	0	
0	4	0	0	25	0	
5	0	2	1	1	0	
2	0	0	24	21	0	
0	0	1	0	17	0	
6	0	0	3	15	0	
0	0	0	0	8	0	
1	0	14	0	5	0	
1	0	4	0	5	0	
0	7	0	13	6	1	
5	0	1	0	8	0	
11	0	1	3	3	0	
7	0	0	6	0	0	
0	4	0	0	14	0	

gastropod	Leptodesma	Modiamorpha	Mytilarca	Schizophoria	Floweria
0	0	0	0	1	0
0	0	0	0	0	2
0	0	0	0	0	0
0	0	0	0	0	0
0	1	0	0	0	4
0	0	0	0	0	1
0	0	0	0	11	20
0	0	0	0	0	0
0	0	0	0	9	15
0	0	0	0	0	0
0	0	0	0	0	1
0	0	0	0	1	0
0	0	0	0	0	5
0	0	0	0	3	1
0	0	0	0	0	0
0	0	0	0	1	3
0	0	0	0	9	4
1	0	0	0	9	34
0	0	0	0	10	0
0	1	0	0	1	1
0	0	0	0	1	0
0	0	0	0	0	15
0	0	0	0	0	0
0	0	0	0	0	27
0	0	0	0	0	0
0	0	0	0	4	18
0	0	0	0	0	0
0	0	0	0	1	2
0	0	0	1	0	4
0	0	0	0	0	6
0	0	0	0	0	0
0	1	1	0	0	0
1	0	0	0	1	5
0	0	0	0	0	3
0	0	0	0	0	2
0	0	0	0	0	2
0	0	1	0	0	3
0	0	0	0	0	7
0	0	0	0	0	2
0	0	0	0	1	0
0	0	0	1	7	1

Spirifer	Striatochonet	Thiemella	Tylothyris	Praewaagenoconcha
0	0	0	17	8
0	0	0	2	1
0	0	0	11	0
0	3	1	1	1
0	0	0	6	4
0	0	0	4	3
0	0	1	13	8
0	0	0	20	0
0	0	0	2	2
0	10	1	7	1
0	0	0	7	3
0	3	0	10	10
0	1	0	4	5
0	0	4	0	0
0	0	0	23	7
0	0	0	0	0
0	0	0	4	13
0	5	3	31	23
0	0	0	2	12
0	0	0	2	8
0	0	0	11	1
0	0	3	10	5
0	0	0	7	0
0	0	0	5	13
0	0	2	2	5
0	0	0	19	4
0	0	0	4	55
2	1	0	23	1
2	0	0	10	0
1	42	0	6	1
0	0	0	0	4
0	0	0	0	4
0	0	0	6	6
0	0	3	1	0
0	0	0	8	6
0	1	0	43	9
0	0	0	22	2
1	0	0	36	0
0	0	0	0	3
0	0	0	12	1
0	0	0	17	24

APPENDIX E

[R] Code

```
# myAlpha, myWFbeta, and myAFbeta calculate additive
diversity partitioning values


myAlpha <- function(myData, lithology) {

  PAMatrix <- myData > 0

#Calculate Alpha Diversity

  sampleshallowAlpha <- mean(apply(PAMatrix[lithology[ ,2]
== "shallow", ], MARGIN = 1, FUN = sum))

  sampledeepAlpha <- mean(apply(PAMatrix[lithology[ ,2] ==
"deep", ], MARGIN = 1, FUN = sum))

  meanAlpha <- c(sampleshallowAlpha, sampledeepAlpha)

}

##########################################################
####################
myWFbeta <- function (myData, lithology) {

#Calculate Alpha Diversity
  PAMatrix <- myData > 0

  sampleshallowAlpha <- mean(apply(PAMatrix[lithology[ ,2]
== "shallow", ], MARGIN = 1, FUN = sum))

  sampledeepAlpha <- mean(apply(PAMatrix[lithology[ ,2] ==
"deep", ], MARGIN = 1, FUN = sum))

#Calculate Beta Within Facies
  faciesshallow <- apply(myData[lithology[ ,2] ==
"shallow", ], MARGIN=2, FUN=sum)
  faciesshallowAlpha <- sum(faciesshallow > 0)
```

```
  faciesdeep <- apply(myData[lithology[ ,2] == "deep", ],
MARGIN = 2, FUN=sum)
  faciesdeepAlpha <- sum(faciesdeep > 0)

  WFbeta <- c(faciesshallowAlpha-sampleshallowAlpha,
faciesdeepAlpha - sampledeepAlpha)
}


##########################################################
####################
myAFbeta <- function (myData, lithology) {

  PAMatrix <- myData > 0

#Calculate Alpha Diversity
  sampleshallowAlpha <- mean(apply(PAMatrix[lithology[ ,2]
== "shallow", ], MARGIN = 1, FUN = sum))

  sampledeepAlpha <- mean(apply(PAMatrix[lithology[ ,2] ==
"deep", ], MARGIN = 1, FUN = sum))

  meanAlpha <- c(mean(sampleshallowAlpha),
mean(sampledeepAlpha))

#Calculate Beta Within Facies
  faciesshallow <- apply(myData[lithology[ ,2] ==
"shallow", ], MARGIN=2, FUN=sum)
  faciesshallowAlpha <- sum(faciesshallow > 0)

  faciesdeep <- apply(myData[lithology[ ,2] == "deep", ],
MARGIN = 2, FUN=sum)
  faciesdeepAlpha <- sum(faciesdeep > 0)

  WFbeta <- c(faciesshallowAlpha-sampleshallowAlpha,
faciesdeepAlpha - sampledeepAlpha)

#Calculate Gamma
  Ind <- apply(myData, MARGIN = 2, FUN = sum)
  Gamma <- sum(Ind > 0)

#Calculate Beta Among Facies
  AFbeta <- Gamma - mean(WFbeta) - mean(meanAlpha)
  AFbeta
}

##########################################################
####################
```

```
# combineArray combines 3 dimensional arrays for two time
intervals

combineArray <- function(array1, array2) {
     # arrays are set up so that rows and columns can be
different, but iterations must be the same value for both
arrays.


     finalData <- array(NA, dim = c((nrow(array1) +
nrow(array2)), length(unique(c(colnames(array1),
colnames(array2)))), dim(array1)[3]))



     # finalData is an array of all the species in the two
matrices in columns, and all the samples in rows and all
iterations.  This will be the final array with both data
sets.
     rowarray1 <- rownames(array1) #all the sample names of
the first matrix
     rowarray2 <- rownames(array2) #all the sample names of
the second matrix

     species <- unique(c(colnames(array1),
colnames(array2))) #names of all unique species between the
two data sets

     rownames(finalData) <- c(rowarray1,rowarray2)
     colnames(finalData) <- species
     #set the row and col names for the final data array to
be the samples as rows and species as cols

     array1Species <- colnames(array1)
     array2Species <- colnames(array2)

     for (i in 1:(nrow(array1) + nrow(array2))) {
          for (j in 1:dim(finalData)[3]) {
               if(i <= nrow(array1)) {
                    index <- which(array1[i, ,j] > 0,
arr.ind = TRUE)
                    speciesUrn  <-
rep(array1Species[index], times = array1[i,array1[i, ,j] >
0, j]) #species urn creates a vector of the names of all
```

```
the species in a sample, repeated for nIndividuals in the
sample
                    finalData[i, ,j] <-
table(factor(speciesUrn, levels = species))
                    # tables the data with all the of the
unique species between the two data sets and puts them into
the corresonding row in the final matrix
               }
               if(i > nrow(array1)) {
                    index <- which(array2[(i-nrow(array1)),
,j] > 0)
                    speciesUrn <- rep(array2Species[index],
times = array2[(i-nrow(array1)),array2[(i-nrow(array1)),
,j] > 0, j])
                    finalData[i, ,j] <-
table(factor(speciesUrn, levels = species))
               }
          }
          # need to hold onto i to put the samples in the
right spot in the finalData matrix but need to subtract the
number of samples from the first matrix to get the correct
positions in the second matrix
     }
     list(finalData,nrow(array1), nrow(array2))
     # this list gives the finalData matrix, the number of
rows in the first matrix, and the number of rows in the
second matrix
}
```

#guildCube creates a theoretical ecospace where each genus present in the data set is assigned a guild number

```
guildCube <- function(guildMatrix, fileName) {
#fileName in " "
     genera <- colnames(guildMatrix)

     index <- which(guildMatrix == TRUE) # find the index
of the guild matrix where the number is positive, this
represents a positive in that category
     guildRaw <- matrix(index, nrow = 3) # puts it into a
matrix form
     scalar <- 0:(ncol(guildRaw)-1) *18 # as we increase
columns we increase the number of each guild by 18, we need
to subtract 18 * the row number - 1
```

```
     guildMatrix <- array(NA, dim = dim(guildRaw)) # set a
blank matrix
     for (i in 1:ncol(guildMatrix)) {
          guildMatrix[ ,i] <- guildRaw[ ,i] - scalar[i]
     }
     # this loop gets makes every column match the index of
where it is 1 in the guild Matrix
     guildMatrix[2, ] <- guildMatrix[2, ] - 6 # subtracts 6
to get us from the guild matrix to axis 2 of the
theoretical morphospace
     guildMatrix[3, ] <- guildMatrix[3, ] - 12 # subtract
12 to get us from the guild matrix to axis 3 of the
theoretical morphospace

     guilds <- vector(length = ncol(guildMatrix))

     for (z in 1:ncol(guildMatrix)) {
          guilds[z] <- (guildMatrix[1,z] * 100) +
(guildMatrix[2,z] * 10) + guildMatrix[3,z]
     }

     guildList <- matrix(NA, ncol = ncol(guildMatrix), nrow
= 2)
     guildList[1, ] <- genera
     guildList[2, ] <- guilds
     #converts the guilds to a list with colnames = genera
and values = theoretical guild

     write.csv(guildList, file = fileName, row.names =
FALSE) # write the output to a .csv file

     return(guildList)
}
```

 # convert2guild uses the output of guildCube to count all individuals in the taxonomic data set and sum them into a comparable array with counts of guilds

```
convert2guild <- function(taxaArray, guildCalls) {
     nTaxa          <- length(guildCalls[ ,1])
     nGuilds        <- length(unique(guildCalls[ ,2]))
     nSamples  <- length(taxaArray[ ,1,1])
     nResamples     <- length(taxaArray[1,1, ])

     guildArray <- array(0, dim =
c(nSamples,nGuilds,nResamples))
     colnames(guildArray) <- unique(guildCalls[,2])
```

```
     rownames(guildArray) <- rownames(taxaArray)
     for (i in 1:nTaxa) {
          guild <-
as.numeric(guildCalls[colnames(taxaArray)[i] == guildCalls[
, 1], 2])
          #get the guild number
          guildArray[ ,which(colnames(guildArray) ==
guild), ] <- guildArray[ ,which(colnames(guildArray) ==
guild), ] + taxaArray[ ,i, ]
          #use the guild number, which is stored as a
character, to match the column names of the guild matrix,
then add the number in that cell plus the number in the
taxa array, summing the number of individuals in the guild
     }
     return(guildArray)
}
```

 # myStand is used to create a matrix of relative abundances of genera or guilds

```
myStand <- function(myData, meth) {
     # meth is decostand method, must be in " "
     library(vegan)
     dimen <- dim(myData)
     iterations <- dimen[3]
     finalData <- array(NA, dim = dimen)
     for (i in 1:iterations) {
          mySample <- decostand(myData[ , ,i], method =
meth)
          finalData[ , ,i] <- mySample
     }
     finalData
}
```

 # myBootDCA performs the DCA bootstrap on a standardized (for relative abundance) generic or guild data set

```
myBootDCA <- function(myData){
#myBootDCA will perform a Detrended Corespondance Analysis
on a resampled data set, then use a procrustes
transformation to orient the points.

# myBootDCA returns a list with two procGPA objects, with
site scores and species scores, each procrustes transformed
```

```
# to call site and species scores from these objects use:
$rawscores

     library(vegan)
     library(shapes)

     iterations <- dim(myData)[3]
     finalSiteScores <- array(NA, c(nrow(myData),
4,iterations))
     finalSpeciesScores <- array(NA, c(ncol(myData), 4,
iterations))
     for (i in 1:iterations) {
          index <- which(apply(myData[ , ,i], MARGIN = 2,
FUN = sum) > 0)
          myDCA <- decorana(myData[ ,index, i])
          speciesScores <- scores(myDCA, display =
"species")
          siteScores <- scores(myDCA, display = "sites")
          finalSiteScores[,,i] <- siteScores
          finalSpeciesScores[index, ,i] <- speciesScores
     }

     index <- matrix(NA, ncol = ncol(myData), nrow =
iterations)
     for (j in 1:iterations) {
          index[j, ] <- apply(myData[ , ,j], MARGIN = 2,
FUN = sum)
     }
     index <- index == 0

     finalSpeciesScores[is.na(finalSpeciesScores)] <- 0

     mySpeciesProc <- procGPA(finalSpeciesScores)
     mySiteProc <- procGPA(finalSiteScores)

     for (k in 1:dim(mySpeciesProc$rotated)[3]) {
          mySpeciesProc$rotated[index[k, ], ,k] <- NA
     }

     list(mySiteProc, mySpeciesProc)
}


# baird determines organisms that go extinct, survive, or
originate in a data set

baird <- function(myData1, myData2) {
```

```
     sp1 <- colnames(myData1)
     sp2 <- colnames(myData2)

          survivors <- intersect(sp1, sp2)
          originators <- setdiff(sp2, sp1)
          extinction <- setdiff(sp1, sp2)
          survivorIndexPre <- NULL
          survivorIndexPost <- NULL
          originatorIndex <- NULL
          extinctionIndex <- NULL



     for (i in 1:length(survivors)){
          survivorIndexPre <- c(survivorIndexPre, which(sp1
== survivors[i]))
          survivorIndexPost <-
c(survivorIndexPost,which(sp2 == survivors[i]))
          }


     for (i in 1:length(originators)){
          originatorIndex <- c(originatorIndex, which(sp2
== originators[i]))


          }
     for (i in 1:length(extinction)){
          extinctionIndex <- c(extinctionIndex,which(sp1 ==
extinction[i]))
          }

     list(survivorIndexPre, survivorIndexPost,
originatorIndex, extinctionIndex)

}

# guildAbundance calculates relative abundance
distributions for genera or guild data sets

guildAbundance <- function(guildData1, guildData2 = NULL,
guildData3 = NULL, guildData4 = NULL, method = "total",
lithology1 = NULL, lithology2 = NULL, lithology3 = NULL,
lithology4 = NULL) {

     # guildAbundance is a function which will output nHist
histograms (default 2) depicting the relative abundance of
a guild within a community.  It will combine the relative
```

```
abundance of taxa in guilds and present that data sorted by
descending relative abundnace during the pre-extinction.
     #
     # guildData1 though guildData 4 = data sets, can be
taxa or guilds (named guilds because that was the original
intention)  Must be a 3 dimensional array, though one of
those dimensions may be 1 (?)
     #
     # method = "total" or "facies".  Total will average
all abundances over all iterations for a single taxon.
Facies will break that out based on facies (deep or
shallow)
     #
     # lithology1 though lithology4 = lithology calls
matrix.  must be in "shallow" or "deep" with row names
corresponding to the length of the guildData arrays
     # History
     # written as a guild abundance calculator, can also be
used for taxa
     #
     # 2/17/2011
     # first cut
     #
     # 2/18/2011
     # adding error bars
     #
     #



     nHist <- 1
     if(sum(guildData2) > 0) nHist <- 2
     if(sum(guildData3) > 0) nHist <- 3
     if(sum(guildData4) > 0) nHist <- 4

     # nHist will let us know how many histograms to
create.  Taken from how many data sets we input.

     uniqueGuilds <- unique(c(colnames(guildData1),
colnames(guildData2), colnames(guildData3),
colnames(guildData4)))
     # will find all the unique guilds


     if (method == "total") {
          finalMatrix <- matrix(NA, ncol = nHist, nrow =
length(uniqueGuilds))
          rownames(finalMatrix) <- uniqueGuilds
```

```
          finalSD <- matrix(NA, ncol = nHist, nrow =
length(uniqueGuilds))
          rownames(finalSD) <- uniqueGuilds
     }
     # if method = "total" we only need one matrix to hold
our final data, it will be nrow = the number of data sets
(time slices), and ncol = the number of unique guilds

     if (method == "facies") {
          shallowMatrix <- matrix(NA, ncol = nHist, nrow =
length(uniqueGuilds))
          rownames(shallowMatrix) <- uniqueGuilds
          shallowSD <- matrix(NA, ncol = nHist, nrow =
length(uniqueGuilds))
          rownames(shallowSD) <- uniqueGuilds

          deepMatrix <- matrix(NA, ncol = nHist, nrow =
length(uniqueGuilds))
          rownames(deepMatrix) <- uniqueGuilds
          deepSD <- matrix(NA, ncol = nHist, nrow =
length(uniqueGuilds))
          rownames(deepSD) <- uniqueGuilds
     }

     #See above.  We need 2 matricies of the same size to
hold different facies information (shallow and deep)

     guilds <- colnames(guildData1)
     iterations <- dim(guildData1)[3]
     nrows <- dim(guildData1)[1]
     relativeAbundance1 <- array(NA, c(nrows,
length(guilds), iterations))
     colnames(relativeAbundance1) <- guilds
     rownames(relativeAbundance1) <- rownames(guildData1)
     for (j in 1:iterations) {
          for (i in 1:nrows) {
               nInd <- sum(guildData1[i, ,j])
               relAbun <- guildData1[i, ,j] / nInd
               relativeAbundance1[i, ,j] <- relAbun
          }
     }

     # each of the sections with this construction first
save the guilds from the original data set, save the
iterations (z axis of the array), and the nubmer of rows
from the array.  The double loop finds the number of
individuals of all taxa in a sample (rows) in 1 iteration
```

(z axis). The number of individuals of a single taxon is divided by this to find its relative abundance.

```
     i <- NULL
     j <- NULL

     if (sum(guildData2) > 0) {
          guilds <- colnames(guildData2)
          iterations <- dim(guildData2)[3]
          nrows <- dim(guildData2)[1]
          relativeAbundance2 <- array(NA, c(nrows,
length(guilds), iterations))
          colnames(relativeAbundance2) <- guilds
          rownames(relativeAbundance2) <-
rownames(guildData2)
          for (j in 1:iterations) {
               for (i in 1:nrows) {
                    nInd <- sum(guildData2[i, ,j])
                    relAbun <- guildData2[i, ,j] / nInd
                    relativeAbundance2[i, ,j] <- relAbun
               }
          }

     i <- NULL
     j <- NULL
     }


     if (sum(guildData3) > 0) {
          guilds <- colnames(guildData3)
          iterations <- dim(guildData3)[3]
          nrows <- dim(guildData3)[1]
          relativeAbundance3 <- array(NA, c(nrows,
length(guilds), iterations))
          colnames(relativeAbundance3) <- guilds
          rownames(relativeAbundance3) <-
rownames(guildData3)
          for (j in 1:iterations) {
               for (i in 1:nrows) {
                    nInd <- sum(guildData3[i, ,j])
                    relAbun <- guildData3[i, ,j] / nInd
                    relativeAbundance3[i, ,j] <- relAbun
               }
          }

          i <- NULL
          j <- NULL
```

```
     }


          if (sum(guildData4) > 0) {
          guilds <- colnames(guildData4)
          iterations <- dim(guildData4)[3]
          nrows <- dim(guildData4)[1]
          relativeAbundance4 <- array(NA, c(nrows,
length(guilds), iterations))
          colnames(relativeAbundance4) <- guilds
          rownames(relativeAbundance4) <-
rownames(guildData4)
          for (j in 1:iterations) {
               for (i in 1:nrows) {
                    nInd <- sum(guildData4[i, ,j])
                    relAbun <- guildData4[i, ,j] / nInd
                    relativeAbundance4[i, ,j] <- relAbun
               }
          }

          i <- NULL
          j <- NULL
     }


##############################################################
##############
     if (method == "total") {

          meanGuild1 <- matrix(NA, nrow =
nrow(relativeAbundance1), ncol = ncol(relativeAbundance1))
          colnames(meanGuild1) <-
colnames(relativeAbundance1)
          rownames(meanGuild1) <-
rownames(relativeAbundance1)
          stdDev1 <- vector(length =
ncol(relativeAbundance1))
          for (z in 1:ncol(relativeAbundance1)) {
               meanAbun <- apply(relativeAbundance1[ ,z, ],
MARGIN = 1, FUN = mean)
               meanGuild1[ ,z] <- meanAbun
               stdDev1[z] <-
sd(as.vector(relativeAbundance1[ ,z, ]))
          }

          guildMeans <- apply(meanGuild1, MARGIN = 2, FUN =
mean)
```

```
          for (i in 1:ncol(meanGuild1)) {
               index <- which(rownames(finalMatrix) ==
colnames(meanGuild1)[i])
               finalMatrix[index,1] <- guildMeans[i]
               finalSD[index, 1] <- stdDev1[i]
          }

          # if method = total this construction is used.
Each section creates a new matrix of samples x guilds, and
gets the mean relative abundance (from the above matrix)
for each taxon and each sample across all iterations.  The
second loop finds the average relative abundance for each
taxon across all samples and places them in the appropiate
place in the final matrix by finding where the rowname
occurs in the final matrix.  This is important because not
every guild will be represented in the final matrix.

          if (sum(guildData2) > 0) {
               i <- NULL
               meanGuild2 <- matrix(NA, nrow =
nrow(relativeAbundance2), ncol = ncol(relativeAbundance2))
               colnames(meanGuild2) <-
colnames(relativeAbundance2)
               rownames(meanGuild2) <-
rownames(relativeAbundance2)
               stdDev2 <- vector(length =
ncol(relativeAbundance2))
               for (z in 1:ncol(relativeAbundance2)) {
                    meanAbun <- apply(relativeAbundance2[
,z, ], MARGIN = 1, FUN = mean)
                    meanGuild2[ ,z] <- meanAbun
                    stdDev2[z] <-
sd(as.vector(relativeAbundance2[ ,z, ]))
               }

               guildMeans <- apply(meanGuild2, MARGIN = 2,
FUN = mean)
               for (i in 1:ncol(meanGuild2)) {
                    index <- which(rownames(finalMatrix) ==
colnames(meanGuild2)[i])
                    finalMatrix[index,2] <- guildMeans[i]
                    finalSD[index, 2] <- stdDev2[i]
               }
          }


          if (sum(guildData3) > 0) {
               i <- NULL
```

```
               meanGuild3 <- matrix(NA, nrow =
nrow(relativeAbundance3), ncol = ncol(relativeAbundance3))
               colnames(meanGuild3) <-
colnames(relativeAbundance3)
               rownames(meanGuild3) <-
rownames(relativeAbundance3)
               stdDev3 <- vector(length =
ncol(relativeAbundance3))
               for (z in 1:ncol(relativeAbundance3)) {
                    meanAbun <- apply(relativeAbundance3[
,z, ], MARGIN = 1, FUN = mean)
                    meanGuild3[ ,z] <- meanAbun
                    stdDev3[z] <-
sd(as.vector(relativeAbundance3[ ,z, ]))
               }

               guildMeans <- apply(meanGuild3, MARGIN = 2,
FUN = mean)
               for (i in 1:ncol(meanGuild3)) {
                    index <- which(rownames(finalMatrix) ==
colnames(meanGuild3)[i])
                    finalMatrix[index,3] <- guildMeans[i]
                    finalSD[index, 3] <- stdDev3[i]
               }
          }



          if (sum(guildData4) > 0) {
               i <- NULL
               meanGuild4 <- matrix(NA, nrow =
nrow(relativeAbundance4), ncol = ncol(relativeAbundance4))
               colnames(meanGuild4) <-
colnames(relativeAbundance4)
               rownames(meanGuild4) <-
rownames(relativeAbundance4)
               stdDev4 <- vector(length =
ncol(relativeAbundance4))
               for (z in 1:ncol(relativeAbundance4)) {
                    meanAbun <- apply(relativeAbundance4[
,z, ], MARGIN = 1, FUN = mean)
                    meanGuild4[ ,z] <- meanAbun
                    stdDev4[z] <-
sd(as.vector(relativeAbundance4[ ,z, ]))
               }

               guildMeans <- apply(meanGuild4, MARGIN = 2,
FUN = mean)
```

```
               for (i in 1:ncol(meanGuild4)) {
                    index <- which(rownames(finalMatrix) ==
colnames(meanGuild4)[i])
                    finalMatrix[index,4] <- guildMeans[i]
                    finalSD[index, 4] <- stdDev4[i]
               }
          }
     }
##########################################################
##############
     if (method == "facies") {

          meanGuild1 <- matrix(NA, nrow =
nrow(relativeAbundance1), ncol = ncol(relativeAbundance1))
          colnames(meanGuild1) <-
colnames(relativeAbundance1)
          rownames(meanGuild1) <-
rownames(relativeAbundance1)
          stdDevS1 <- vector(length =
ncol(relativeAbundance1[lithology1[,2] == "shallow", , ]))
          stdDevD1 <- vector(length =
ncol(relativeAbundance1[lithology1[,2] == "deep", , ]))
          for (z in 1:ncol(relativeAbundance1)) {
               meanAbun <- apply(relativeAbundance1[ ,z, ],
MARGIN = 1, FUN = mean)
               meanGuild1[ ,z] <- meanAbun
               stdDevS1[z] <-
sd(as.vector(relativeAbundance1[lithology1[,2] ==
"shallow",z, ]))
               stdDevD1[z] <-
sd(as.vector(relativeAbundance1[lithology1[,2] == "deep",z,
]))
          }

          guildMeans <- apply(meanGuild1[lithology1[,2] ==
"shallow", ], MARGIN = 2, FUN = mean)
          for (i in 1:ncol(meanGuild1)) {
               index <- which(rownames(shallowMatrix) ==
colnames(meanGuild1)[i])
               shallowMatrix[index,1] <- guildMeans[i]
               shallowSD[index, 1] <- stdDevS1[i]
          }
          guildMeans <- apply(meanGuild1[lithology1[,2] ==
"deep", ], MARGIN = 2, FUN = mean)
          for (i in 1:ncol(meanGuild1)) {
               index <- which(rownames(deepMatrix) ==
colnames(meanGuild1)[i])
               deepMatrix[index,1] <- guildMeans[i]
```

```
                deepSD[index,1] <- stdDevD1[i]
          }

          # if method = facies the construction is similar
to method = total, except that the means are broken up by
facies, and the construction uses 2 loops to place them in
to shallow and deep facies.


          if (sum(guildData2) > 0) {
                meanGuild2 <- matrix(NA, nrow =
nrow(relativeAbundance2), ncol = ncol(relativeAbundance2))
                colnames(meanGuild2) <-
colnames(relativeAbundance2)
                rownames(meanGuild2) <-
rownames(relativeAbundance2)
                stdDevS2 <- vector(length =
ncol(relativeAbundance2[lithology2[,2] == "shallow", , ]))
                stdDevD2 <- vector(length =
ncol(relativeAbundance2[lithology2[,2] == "deep", , ]))
                for (z in 1:ncol(relativeAbundance2)) {
                     meanAbun <- apply(relativeAbundance2[
,z, ], MARGIN = 1, FUN = mean)
                     meanGuild2[ ,z] <- meanAbun
                     stdDevS2[z] <-
sd(as.vector(relativeAbundance2[lithology2[,2] ==
"shallow",z, ]))
                     stdDevD2[z] <-
sd(as.vector(relativeAbundance2[lithology2[,2] == "deep",z,
]))
                }

                guildMeans <-
apply(meanGuild2[lithology1[,2] == "shallow", ], MARGIN =
2, FUN = mean)
                for (i in 1:ncol(meanGuild2)) {
                     index <- which(rownames(shallowMatrix)
== colnames(meanGuild2)[i])
                     shallowMatrix[index,2] <- guildMeans[i]
                     shallowSD[index, 2] <- stdDevS2[i]
                }
                guildMeans <-
apply(meanGuild2[lithology1[,2] == "deep", ], MARGIN = 2,
FUN = mean)
                for (i in 1:ncol(meanGuild2)) {
                     index <- which(rownames(deepMatrix) ==
colnames(meanGuild2)[i])
                     deepMatrix[index,2] <- guildMeans[i]
```

```
                    deepSD[index,2] <- stdDevD2[i]
               }
          }



          if (sum(guildData3) > 0) {
               meanGuild3 <- matrix(NA, nrow =
nrow(relativeAbundance3), ncol = ncol(relativeAbundance3))
               colnames(meanGuild3) <-
colnames(relativeAbundance3)
               rownames(meanGuild3) <-
rownames(relativeAbundance3)
               stdDevS3 <- vector(length =
ncol(relativeAbundance3[lithology3[,2] == "shallow", , ]))
               stdDevD3 <- vector(length =
ncol(relativeAbundance3[lithology3[,2] == "deep", , ]))

               for (z in 1:ncol(relativeAbundance3)) {
                    meanAbun <- apply(relativeAbundance3[
,z, ], MARGIN = 1, FUN = mean)
                    meanGuild3[ ,z] <- meanAbun
               }

               guildMeans <-
apply(meanGuild3[lithology1[,2] == "shallow", ], MARGIN =
2, FUN = mean)
               for (i in 1:ncol(meanGuild3)) {
                    index <- which(rownames(shallowMatrix)
== colnames(meanGuild3)[i])
                    shallowMatrix[index,3] <- guildMeans[i]
                    shallowSD[index, 3] <- stdDevS3[i]

               }
               guildMeans <-
apply(meanGuild3[lithology1[,2] == "deep", ], MARGIN = 2,
FUN = mean)
               for (i in 1:ncol(meanGuild3)) {
                    index <- which(rownames(deepMatrix) ==
colnames(meanGuild3)[i])
                    deepMatrix[index,3] <- guildMeans[i]
                    deepSD[index,3] <- stdDevD3[i]
               }
          }
```

```
          if (sum(guildData4) > 0) {
               meanGuild4 <- matrix(NA, nrow =
nrow(relativeAbundance4), ncol = ncol(relativeAbundance4) )
               colnames(meanGuild4) <-
colnames(relativeAbundance4)
               rownames(meanGuild4) <-
rownames(relativeAbundance4)
               stdDevS4 <- vector(length =
ncol(relativeAbundance4[lithology4[,2] == "shallow", , ]))
               stdDevD4 <- vector(length =
ncol(relativeAbundance4[lithology4[,2] == "deep", , ]))

               for (z in 1:ncol(relativeAbundance4)) {
                    meanAbun <- apply(relativeAbundance4[
,z, ], MARGIN = 1, FUN = mean)
                    meanGuild4[ ,z] <- meanAbun
               }

               guildMeans <-
apply(meanGuild4[lithology1[,2] == "shallow", ], MARGIN =
2, FUN = mean)
               for (i in 1:ncol(meanGuild4)) {
                    index <- which(rownames(shallowMatrix)
== colnames(meanGuild4)[i])
                    shallowMatrix[index,4] <- guildMeans[i]
                    shallowSD[index, 4] <- stdDevS4[i]
               }
               guildMeans <-
apply(meanGuild4[lithology1[,2] == "deep", ], MARGIN = 2,
FUN = mean)
               for (i in 1:ncol(meanGuild4)) {
                    index <- which(rownames(deepMatrix) ==
colnames(meanGuild4)[i])
                    deepMatrix[index,4] <- guildMeans[i]
                    deepSD[index,4] <- stdDevD4[i]
               }
          }


     }
##############################################################
##############
```

```
# Plotting the Data and output the final matricies so we
can retrieve them from the function


     if (method == "total") {

          sortedMatrix <-
finalMatrix[order(finalMatrix[,1], decreasing = TRUE), ]
          sortedMatrix[is.na(sortedMatrix)] <- 0

          finalSD[is.na(finalSD)] <- 0
          sortedSD <- finalSD[order(finalMatrix[,1],
decreasing = TRUE), ]


               myStart <- min(which(sortedMatrix[,1] == 0))
               myEnd <- nrow(sortedMatrix)

          for (i in 2:nHist) {

               rownames(sortedSD) <-
c(rownames(sortedSD)[1:myStart-1],
rownames(sortedSD)[order(sortedMatrix[myStart:myEnd,i],
decreasing = TRUE) + myStart - 1])

               rownames(sortedMatrix) <-
c(rownames(sortedMatrix)[1:myStart-1],
rownames(sortedMatrix)[order(sortedMatrix[myStart:myEnd,i],
decreasing = TRUE) + myStart - 1])

               sortedSD[myStart:myEnd, i:nHist] <-
sortedSD[order(sortedMatrix[myStart:myEnd,i], decreasing =
TRUE) + myStart - 1, i:nHist]

               sortedMatrix[myStart:myEnd, i:nHist] <-
sortedMatrix[order(sortedMatrix[myStart:myEnd,i],
decreasing = TRUE) + myStart - 1, i:nHist]

               index <-
min(which(sortedMatrix[myStart:myEnd, i] == 0)) - 1

               myStart <- myStart + index
          }

          # get rid of rows where everything is 0
```

```
          if (min(apply(sortedMatrix,1,sum)) == 0){
               removeIndex <- which(apply(sortedMatrix, 1,
sum) == 0)
               sortedMatrix <- sortedMatrix[-
c(removeIndex), ]
          }
          par(mfrow = c(1,nHist))
          barplot(sortedMatrix[,1], ylim = c(0,1), las = 1)
          if(sum(guildData2) > 0) barplot(sortedMatrix[,2],
ylim = c(0,1), las = 1)
          if(sum(guildData3) > 0) barplot(sortedMatrix[,3],
ylim = c(0,1), las = 1)
          if(sum(guildData4) > 0) barplot(sortedMatrix[,4],
ylim = c(0,1), las = 1)


     }




     if (method == "facies") {
          sortedShallow <-
shallowMatrix[order(shallowMatrix[,1], decreasing = TRUE),
]
          sortedDeep <- deepMatrix[order(shallowMatrix[,1],
decreasing = TRUE), ]

          sortedShallow[is.na(sortedShallow)] <- 0
          sortedDeep[is.na(sortedDeep)] <- 0

          shallowSD[is.na(shallowSD)] <- 0
          deepSD[is.na(deepSD)] <- 0

          sortedShallowSD <-
shallowSD[order(shallowMatrix[,1], decreasing = TRUE), ]
          sortedDeepSD <- deepSD[order(shallowMatrix[,1],
decreasing = TRUE), ]

          par(mfrow = c(2,nHist))

          barplot(sortedShallow[,1], ylim = c(0,1), las =
1)
          if(sum(guildData2) > 0)
barplot(sortedShallow[,2], ylim = c(0,1), las = 1)
          if(sum(guildData3) > 0)
barplot(sortedShallow[,3], ylim = c(0,1), las = 1)
```

```
          if(sum(guildData4) > 0)
barplot(sortedShallow[,4], ylim = c(0,1), las = 1)

          barplot(sortedDeep[,1], ylim = c(0,1), las = 1)
          if(sum(guildData2) > 0) barplot(sortedDeep[,2],
ylim = c(0,1), las = 1)
          if(sum(guildData3) > 0) barplot(sortedDeep[,3],
ylim = c(0,1), las = 1)
          if(sum(guildData4) > 0) barplot(sortedDeep[,4],
ylim = c(0,1), las = 1)

     }



     if (method == "total") list(sortedMatrix, sortedSD)
else list(sortedShallow, sortedDeep, sortedShallowSD,
sortedDeepSD)


}
```

 # sepDCA calculates the separation between centroids in a DCA ordination

```
sepDCA <- function(dca1, dca2, nIntervals, rows1, rows2,
rows3 = NULL, myNames = 0) {

     # dca1 is all scores along axis 1
     # dca2 is all scores along axis 2
     # nIntervals is the number of time intervals or number
of centroids wanted
     # rows1 - 3 are the nubmer of rows in dca1 and dca2
for each time interval
     # myNames is an optional vector of names deliniating
the names of the intervals or centroids

     dca1mean <- vector(length= nIntervals)
     dca2mean <- vector(length= nIntervals)

     dca1mean[1] <- mean(dca1[1:rows1,])
     dca1mean[2] <- mean(dca1[(rows1+1):(rows1+rows2),])
     if (nIntervals > 2) dca1mean[3] <-
mean(dca1[(rows1+rows2+1):(rows1+rows2+rows3),])
```

```
     dca2mean[1] <- mean(dca2[1:rows1,])
     dca2mean[2] <- mean(dca2[(rows1+1):(rows1+rows2),])
     if (nIntervals > 2) dca2mean[3] <-
mean(dca2[(rows1+rows2+1):(rows1+rows2+rows3),])

     if(myNames == 0) myNames <- 1:nIntervals
     myCentroids <- data.frame(myNames, dca1mean, dca2mean)

     # Calculate RMA slope of centroids in axis 1 - axis 2
space
     slope <-
sd(myCentroids$dca2mean)/sd(myCentroids$dca1mean)

     # Rotate ordination so slope of centroids is zero
     rotateMatrix <- function(x, theta) {
     # rotates a 2-dimensional matrix clockwise by theta
radians
     rotationElements <- c(cos(theta), sin(theta), -
sin(theta), cos(theta))
     rotationDimensions <- c(2,2)
     rotationMatrix <- array(rotationElements,
rotationDimensions)
     theRotatedMatrix <- x %*% rotationMatrix
     theRotatedMatrix
     }

     # Rotate sample scores so slope of facies centroids is
zero
     int1DCA <-
data.frame(as.vector(dca1[1:rows1,]),as.vector(dca2[1:rows1
,]))
     int2DCA <-
data.frame(as.vector(dca1[(rows1+1):(rows1+rows2),]),as.vec
tor(dca2[(rows1+1):(rows1+rows2),]))
     if(nIntervals > 2) int3DCA <-
data.frame(as.vector(dca1[(rows1+rows2+1):(rows1+rows2+rows
3),]),
as.vector(dca2[(rows1+rows2+1):(rows1+rows2+rows3),]))

     int1DCARotated <- rotateMatrix(as.matrix(int1DCA),
atan(slope))
     int2DCARotated <- rotateMatrix(as.matrix(int2DCA),
atan(slope))
     if(nIntervals > 2) int3DCARotated <-
rotateMatrix(as.matrix(int3DCA), atan(slope))

     # DCA Separation Index
```

```
     if (nIntervals == 2) {
          cent <- myCentroids[ ,2:3]
          distCent <- dist(cent)
          sepDCA <- distCent/mean(c(sd(int1DCARotated[,1]),
sd(int2DCARotated[,1])))
     }

     if (nIntervals > 2) {
          cent <- myCentroids[ ,2:3]
          distCent <- dist(cent)
          sepDCA12 <-
distCent[1]/(mean(c(sd(int1DCARotated[,1]),
sd(int2DCARotated[,1]))))
          sepDCA13 <-
distCent[2]/(mean(c(sd(int1DCARotated[,1]),
sd(int3DCARotated[,1]))))
          sepDCA23 <-
distCent[3]/(mean(c(sd(int2DCARotated[,1]),
sd(int3DCARotated[,1]))))
          sepDCA <- c(sepDCA12, sepDCA13, sepDCA23)
     }

     sepDCA

}
     int2DCA <-
data.frame(as.vector(dca1[(rows1+1):(rows1+rows2),]),as.vec
tor(dca2[(rows1+1):(rows1+rows2),]))
     if(nIntervals > 2) int3DCA <-
data.frame(as.vector(dca1[(rows1+rows2+1):(rows1+rows2+rows
3),]),
as.vector(dca2[(rows1+rows2+1):(rows1+rows2+rows3),]))

     int1DCARotated <- rotateMatrix(as.matrix(int1DCA),
atan(slope))
     int2DCARotated <- rotateMatrix(as.matrix(int2DCA),
atan(slope))
     if(nIntervals > 2) int3DCARotated <-
rotateMatrix(as.matrix(int3DCA), atan(slope))

     # DCA Separation Index

     if (nIntervals == 2) {
          cent <- myCentroids[ ,2:3]
          distCent <- dist(cent)
          sepDCA <- distCent/mean(c(sd(int1DCARotated[,1]),
sd(int2DCARotated[,1])))
     }
```

```
     if (nIntervals > 2) {
          cent <- myCentroids[ ,2:3]
          distCent <- dist(cent)
          sepDCA12 <-
distCent[1]/(mean(c(sd(int1DCARotated[,1]),
sd(int2DCARotated[,1]))))
          sepDCA13 <-
distCent[2]/(mean(c(sd(int1DCARotated[,1]),
sd(int3DCARotated[,1]))))
          sepDCA23 <-
distCent[3]/(mean(c(sd(int2DCARotated[,1]),
sd(int3DCARotated[,1]))))
          sepDCA <- c(sepDCA12, sepDCA13, sepDCA23)
     }

     sepDCA

}
```