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MORPHOLOGICAL CHANGE IN RESPONSE TO MASS EXTINCTION: A CASE STUDY OF STROPHOMENIDA (BRACHIOPODA) AT THE LATE ORDOVICIAN

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by

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ABSTRACT

There have been five mass extinctions throughout the Phanerozoic, all of which were caused by catastrophic disruptions to the earth system and resulted in significant biotic upheaval. Anthropogenic climate change, combined with other human activities, is pushing Earth towards a possible sixth mass extinction. The fossil record of extinctions contains clues about what might happen to Earth's biota in the near future.

I focus on the Late Ordovician mass extinction, which is the first of the "big 5" mass extinctions and the second largest. It was caused by a rapid climate event that resulted in the growth of continental glaciers and a drop in sea level. The ecological effect of this extinction is less than might be expected given the amount of taxonomic loss. Studying the nuances of this pattern from an evolutionary and ecological perspective might yield insight into some of the more complex metrics of quantifying changing biodiversity.

To achieve this, I quantify morphology of the brachiopod order Strophomenida. Morphology is a product of evolution and ecology, allowing for the analysis of both. Results indicate a morphologic bottleneck at the Late Ordovician mass extinction event. This observed restriction in morphologic variability occurs within one clade that originates during the Silurian recovery interval. Further exploration of the data indicates no clear ecological signature to the bottleneck. The complex relationship between ecology and evolutionary history highlights the need to employ both approaches to develop a more complete understanding of intervals of biotic change.

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Introduction

There have been five mass extinctions throughout the Phanerozoic. That is, five times during which greater than 75% of all species on the planet rapidly went extinct (Raup and Sepkoski 1982). These events were caused by catastrophic disruptions to the Earth system and resulted in significant biotic upheaval. Anthropogenic climate change, combined with other human activities, is pushing Earth towards a possible sixth mass extinction (Barnosky et al. 2011, Payne et al. 2016). Predicting how these rapid and elevated extinction rates will alter ecosystems is difficult, but insights can be gleaned from the fossil record, which preserves the rebound in biodiversity in the aftermath of previous mass extinction events.

Although the importance of mass extinctions for resetting evolutionary trends has been well established (Simpson 1953, Jablonski 1986, 2000, 2005, Raup 1987, 1994, Benton 1987, 1996, Westrop 1989, Sepkoski 1996, Foote 1997, 2000, Erwin 2000, Brusatte et al. 2008), questions still remain, especially when there is a disconnect between the magnitude of taxonomic loss and the magnitude of loss of other measures of biodiversity (i.e., phylogenetic, ecological, morphological). This disconnect between the loss of species richness and the evolutionary and ecological impact of removing those species is common but complicates the interpretation of biotic recovery (Erwin 2001).

Because the current extinction event, whether a true mass extinction or not, has surpassed the point of inevitability and because, even after the most extreme extinction events, life has rebounded, this dissertation focus is on understanding the complexities of mass extinction, in terms of both survival and diversification. The focus is on the Late Ordovician mass extinction because it was caused by a changing climate and because it has the largest suggested disconnect between taxonomic loss and ecological impact (Droser et al. 2000, McGhee et al. 2004, McGhee et al. 2012).

The Late Ordovician Mass Extinction

The Late Ordovician extinction was the first of the big five Phanerozoic mass extinction events (Raup and Sepkoski 1982) and the second largest, with about 60% of genera eliminated (Sepkoski 1996). Nearly all marine groups experienced taxonomic turnover (e.g., Copeland 1981, Ausich 1987, Eckert 1988, Harper and Rong 1995, Barnes and Zhang 1999).

At many localities, there are two clusters of last occurrences, one at the Katian-Hirnatian boundary, the other at the end of the Hirnantian, suggesting a double-pulsed extinction event. The first pulse resulted from the expansion of glaciers across Northern Africa and a drop in sea level (Sheehan 1973, Berry and Boucot 1973, Finnegan et al. 2011, Finnegan et al. 2012). The second pulse was caused by anoxic marine water flooding the continent during deglaciation (Brenchley et al. 2003, Zhou et al. 2015). A recent sequence stratigraphic model suggests that the two pulses are controlled by the stratigraphic architecture (Holland and Patzkowsky 2015). Although these two interpretations suggest slightly different extinction regimes, both unequivocally demonstrate that extinction rates were rapid and taxonomic loss was high during the Late Ordovician. Many studies have identified substantial differences in the nature of selectivity at the two clusters of last occurrences. During the first cluster, at the Katian-Hirnantian boundary (Sheehan 2001), the build-up in ice drained the epicontinental seas. This loss of habitat drove incumbent epicontinental sea taxa to extinction (Sheehan 1973, Berry and Boucot 1973, Finnegan et al. 2011, Finnegan et al. 2012) and cosmopolitan continentalmargin taxa replaced the shallow-water taxa (Sheehan 2001). During the second cluster, at the end of the Hirnantian, the rapid rise in sea level due to deglaciation flooded the continent with anoxic waters and eliminated the Hirnantian faunas (Brenchley et al. 2003, Zhou et al. 2015, Finnegan et al. 2016).

The Early Silurian recovery has been described as rapid, with diversity returning to pre-extinction levels by the mid-Silurian (Sheehan 2001). Patterns of recovery varied between paleocontinents, largely because of differences in immigration rates (Krug and Patzkowsky 2004, 2007). Rates also differed between groups, especially at higher taxonomic levels (Sheehan 2001), with some orders increasing in diversity and others declining (Harper and Rong 1995). This coincides with a shift in phylogenetic clumping of extinction and origination patterns from slightly dispersed among families in the Ordovician to clumped in the Silurian (Krug and Patzkowsky 2015). Phylogenetic clumping is a measure of how dispersed speciation and extinction is across the branches of the trees. The shift from dispersed to clumped at the Ordovician-Silurian boundary means that the removal and addition of taxa occurred randomly throughout phylogenetic trees in the Late Ordovician and preferentially within certain families in the Early Silurian. This suggests that recovery potential is dependent on family membership.

Despite well-documented selectivity and taxonomic turnover, some have argued that the Late Ordovician extinction had little effect on ecological structure (Droser et al. 2000, McGhee et al. 2004, McGhee et al. 2012). These studies are qualitative assessments of taxonomic and ecological functional group membership of dominant taxa. At this coarse assessment, these authors conclude that change in the dominant components of ecological communities was minor. That is, taxa that were abundant in the Ordovician (i.e., brachiopods, rugose and tabulate corals, stromatoporoid sponges, graptolites, conodonts, nautiloids, bryozoan, crinoids) returned to dominance shortly after the start of the Silurian. These results are inconsistent with the selectivity observed by many other studies, many of which focus on a single marine group (e.g., brachiopods, crinoids, etc.). It is possible that within group, or even within clade, examinations of ecological change need to be conducted. Selectivity might change depending on taxonomic scale of study (Hadley et al. 2009).

Summary of major findings

Chapter 1

In Chapter 1, I asked whether changes in taxonomic diversity across the Late Ordovician mass extinction reflect changes in morphological diversity, which might indicate changes in ecological diversity. I focused on Strophomenida, an order of brachiopods, which has a recently revised phylogenetic tree (Congreve et al. 2015), and used a morphospace analysis to quantify discrete characters for each member of the clade. I then tracked changes in morphology across the Late Ordovician mass extinction and recovery to examine how the overall morphology of this order evolved over time. Results indicate that the extinction was random with respect to morphology, but origination was non-random. Non-random origination reduced morphological disparity for this order until the Late Devonian. These results suggest that selectivity during the recovery from the Late Ordovician mass extinction might be more important to Paleozoic benthic communities than previously thought. Ultimately, examining both an extinction and its subsequent recovery interval is important to a complete understanding of the evolutionary impact of the event.

Chapter 2

In this Chapter, I used the data set from Chapter 1 to explore possible ecological explanations for the observed morphological change. Essentially, I tested the phylogenetic distance, ecological difference hypothesis (PDED), or the idea that closely related taxa should be ecologically similar (Cadotte et al. 2017). To do this, I conducted a preliminary study of the relationship between morphology, ecology, and evolutionary history by calculating pairwise distances in morphospace, along an ecological gradient, and between tips on the tree. I compared the pairwise distances and found that morphology and phylogeny are not well correlated with ecology for Strophomenida. I explored this relationship for three environmental gradients (depth, substrate, and latitude), four phylogenetically defined groups within the order-level tree (from Congreve et al. 2015), and a single clade with a more detailed phylogeny (from Congreve et al. 2019). None of these comparisons resulted in a relationship.

I use these results to emphasize the differences between the fossil record and modern ecology, where the PDED was developed. Specifically, the increase in temporal and spatial scale from the modern to the fossil record reflects macroecological and macroevolutionary processes. Although the strophomenide phylogenies do not support the PDED, they do provide evidence that ecology evolved via an early burst model, where most of the variability occurred during the initial clade diversification. The fundamental difference in spatial and temporal scale between modern and fossil data highlights the importance of both disciplines to understanding evolution and ecology. Understanding the complexity involved in scaling ecological and evolutionary processes up is an important avenue for further research.

Chapter 3

In Chapter 3, I aim to better understand how the morphology of strophomenide brachiopods changes over time and whether this change corresponds to ecological change. One explanation for the lack of relationship found in chapter 2 is that the characters used for phylogenetic analyses are not the most ecologically meaningful. For example, a phylogeny does not include continuous change in characters such as ribbing and globosity, which are commonly thought to vary along a gradient of water depth (e.g., Lee et al. 2018, Haney et al. 2001). To better quantify this continuous variation, I developed a workflow using the photogrammetry method Structure-from-Motion (SfM, Westoby et al. 2012). With SfM, I can visualize brachiopod shells in three dimensions and measure the external morphology of Strophomenida. I employed this method to quantify the 3D external morphology of specimens of genera within Strophomenida.

Results indicate that these external characters, which are continuous measurements, better reflect ecological preference than the discrete characters used for phylogenetics. However, the continuous characters do not demonstrate as strong of a response to the Late Ordovician mass extinction as the discrete characters used in Chapter 1. These results highlight the importance of collaboration between phylogeneticists and paleoecologists and utilizing multiple types of data to more comprehensively assess mass extinction events.

Chapter 1

Effects of mass extinction and recovery dynamics on long-term evolutionary trends: a morphological study of Strophomenida (Brachiopoda) across the Late Ordovician mass extinction

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Abstract

Mass extinctions affect the history of life by decimating existing diversity and ecological structure and creating new evolutionary and ecological pathways. Both the loss of diversity during these events and the rebound in diversity following extinction had a profound effect on Phanerozoic evolutionary trends. Phylogenetic trees can be used to robustly assess the evolutionary implications of extinction and origination.

We examine both extinction and origination during the Late Ordovician mass extinction. This mass extinction was the second largest in terms of taxonomic loss but did not appear to radically alter Paleozoic marine assemblages. We focus on the brachiopod order Strophomenida, whose evolutionary relationships have been recently revised, to explore the disconnect between the processes that drive taxonomic loss and those that restructure ecological communities.

A possible explanation for this disconnect is if extinction and origination were random with respect to morphology. We define morphospace using principal coordinate analysis (PCO) of character data from 61 Ordovician-Devonian taxa and their 45 ancestral nodes, defined by a most parsimonius reconstruction in Mesquite. A bootstrap of the centroid of PCO values indicates that genera were randomly removed from morphospace by the Late Ordovician mass extinction, and new Silurian genera were clustered within a smaller previously unoccupied region of morphospace. Diversification remained morphologically constrained throughout the Silurian and into the Devonian. This suggests that the recovery from the Late Ordovician mass extinction resulted in a long-term shift in strophomenide evolution. More broadly, recovery intervals may hold clues to understanding the evolutionary impact of mass extinctions.

Introduction

Mass extinctions are important mechanisms for resetting evolutionary trends and creating new ecological opportunities (Simpson 1953; Jablonski 1986, 2000, 2005; Raup 1987, 1994; Benton 1987, 1996; Westrop 1989; Sepkoski 1996; Foote 1997, 2000; Erwin 2000; Brusatte et al. 2008; Congreve et al. 2017 and references therein). This is a general pattern that is well-studied, and has been described taxonomically (e.g., Jablonski and Raup 1995; Foote 2000), morphologically (e.g., Foote 1994, 1997, 1999; Ciampaglio et al. 2001; Ciampaglio 2004; Lockwood 2004; Erwin 2007), ecologically (e.g., Jablonski 1986; Benton 1987, 1996; Brusatte et al. 2008), and phylogenetically (e.g., Carlson 1991; Congreve and Lieberman 2010, 2011; Congreve 2013; Wright and Stigall 2013; Lamsdell 2016; Lamsdell and Selden 2017, Wright and Toom 2017). However, the focus has often been on the loss of diversity during the extinction, with origination of diversity during the recovery has receiving much less attention.

Erwin (2001) argued that because there is often a disconnect between the magnitude of taxonomic loss and the loss of unique evolutionary history (and potentially the subsequent restructuring of ecological communities afterwards), the dynamics of origination during recovery intervals might have a more significant effect on long-term evolutionary trends than the dynamics of extinction. Central to this argument is a simulation of extinction patterns at the clade-level that demonstrated that a loss of 95% of species diversity within a clade can still preserve up to 80% of the structure of a phylogenetic tree (Nee and May 1997). This discrepancy in our understanding of extinction intensity has been further supported by multiple analyses of the disconnect

between ecological severity and taxonomic loss (McGhee et al. 2004, 2012, 2013; Christie et al. 2013)

One mechanism through which high extinction intensity can result in little evolutionary and ecological change is when extinction and recovery are random. This means that the features driving organisms to extinction are not taxon-specific, that is, any single species is equally likely to become extinct, regardless of morphological or ecological characteristics. Raup (1991) termed this the "field of bullets" scenario. Random extinction tends to preserve more evolutionary history (phylogenetic diversity *sensu* Faith 1992) than selective extinction, increasing the probability of at least one member of a clade surviving (Nee and May 1997). For an extinction event to cause minimal ecological and evolutionary changes on the biosphere, a similar scenario of random origination must also operate during the recovery interval. Under this scenario, features driving post-extinction radiation would, likewise, not be selective, and all surviving clades would be equally likely to evolve new species.

Here, we use the Late Ordovician mass extinction as a case study to explore the effect of post-extinction origination on long-term evolution of clade morphology. We combine phylogenetic trees (hypotheses of evolutionary relationship) with morphometric analyses (studies of phenetic similarity) to assess the degree to which the extinction event and recovery interval follows the random expectation (Raup 1991). Previous studies have demonstrated that morphological disparity and taxonomic diversity are often not linked (Foote 1991, 1993, 1994), therefore, any assessment of the selectivity of an extinction or radiation that does not look at both diversity and disparity is potentially only looking at half of the pattern. By including the recovery interval in our assessment of this extinction

event, we can determine if origination occurred preferentially in certain clades or if it was randomly distributed throughout the tree. If taxa that evolve after an extinction are phylogenetically, morphologically, or ecologically distinct from those that evolved before, we can interpret the extinction event as having a meaningful impact on the evolution of that group. Conversely, if post-extinction taxa are broadly similar to pre-extinction taxa, the extinction event can be interpreted as having little evolutionary impact (*sensu* McGhee et al. 2004, 2012, 2013).

Background

Late Ordovician mass extinction and recovery

The Late Ordovician mass extinction is the first of the big five Phanerozoic mass extinction events (Raup and Sepkoski 1982) and the second largest, with about 60% of genera eliminated (Sepkoski 1996). Nearly all marine groups experience taxonomic turnover (e.g., Copeland 1981; Ausich 1987; Eckert 1988; Harper and Rong 1995; Barnes and Zhang 1999; Ausich and Deline 2012).

There are two clusters of last occurrences of species, one at the Katian-Hirnatian boundary and the other at the end of the Hirnantian, suggesting a double-pulsed extinction event. Under this interpretation, the first pulse resulted from the expansion of glaciers across Northern Africa and a drop in sea level (Sheehan 1973; Berry and Boucot 1973; Finnegan et al. 2011, 2012; but see also Ghienne et al. 2014 for another interpretation of causal mechanisms). The second pulse was caused by anoxic marine water flooding the continent during deglaciation (Sheehan 2001; Brenchley et al. 2003; Zhou et al. 2015). A recent sequence stratigraphic model provides an alternative explanation, suggesting that the two pulses are controlled by stratigraphic architecture, and instead interprets the event as a protracted interval of high extinction (Holland and Patzkowsky 2015). Despite the difference between these two interpretaions, both unequivocally demonstrate that extinction was high during the Late Ordovician.

Many studies have identified substantial differences in selectivity at the two clusters of last occurrences. During the first, at the Katian-Hirnantian boundary (Sheehan 2001), the drop in sea level drained the epicontinental seas. This loss of habitat drove incumbent epicontinental sea taxa to extinction (Sheehan 1973; Berry and Boucot 1973; Finnegan et al. 2011, 2012). Cosmopolitan continental-margin taxa that were adapted to the cooler waters of the Hirnantian replaced the shallow-, warm-water taxa (Sheehan 2001). During the second cluster, at the end of the Hirnantian, the rise in sea level due to deglaciation led to widespread anoxia (Sheehan 2001) which preferentially eliminated the faunas that had proliferated during the Hirnantian (Brenchley et al. 2003; Zhou et al. 2015). Furthermore, taxa with narrow latitudinal ranges during the Katian were particularly prone to extinction during the Hirnantian, suggesting a potential biogeographic selectivity across the extinction (Finnegan et al. 2016).

The Early Silurian recovery has been described as rapid, with diversity returning to pre-extinction levels by the mid-Silurian across all taxonomic groups (Sheehan 2001). Patterns of recovery from the Late Ordovician mass extinction varied between paleocontinents, largely because of differences in immigration rates (Krug and Patzkowsky 2004, 2007). Recovery rates differed between higher taxonomic levels (Sheehan 2001), with some orders increasing in diversity and others declining (Harper and Rong 1995). The Early Silurian also marked a shift in phylogenetic clumping of extinction and origination patterns from random to slightly dispersed among brachiopod families in the Ordovician to clumped (Krug and Patzkowsky 2015). This result suggests that the removal and addition of taxa occurred randomly across families in the Late Ordovician and preferentially within certain families in the Early Silurian. This is in contrast to the end-Cretaceous mass extinction, where bivalve extinction was phylogenetically clustered (Roy et al. 2009) and the recovery was random. These two studies used a taxonomic proxy for phylogeny, highlighting the need for examining phylogenetic trees to corroborate these patterns.

Despite well-documented selectivity and taxonomic turnover, some have used qualitative assessments of taxonomic and ecological functional group membership of dominant taxa to argue that the Late Ordovician mass extinction had little effect on ecological structure (Droser et al. 2000; McGhee et al. 2004, 2012). These authors conclude that change in the dominant components of ecological communities was minor. That is, taxa that were abundant in the Ordovician (brachiopods, rugose and tabulate corals, stromatoporoid sponges, graptolites, conodonts, nautiloids, bryozoan, crinoids) returned to dominance shortly after the start of the Silurian. These results are inconsistent with the selectivity observed by many other studies that focus on single taxonomic groups (e.g., brachiopods, Harper and Rong 1995; crinoids, Ausich and Deline 2012; trilobites, Chatterton and Speyer 1989). This suggests that within group, or even within clade, examinations of ecological change need to be conducted, as it is possible that selectivity is most important at this finer scale of study.

The Late Ordovician mass extinction is a clear example of a disconnect between the taxonomic and ecological impact of the extinction (*sensu* Erwin 2001). In this study, we investigated how a dramatic loss of taxonomic diversity resulted in little to no loss of ecological functional groups. We use a single order of brachiopods as a model to identify how morphological selectivity at lower taxonomic levels affects long-term clade evolution. While morphology has been often assumed to be a proxy for ecology given morphological adaptation (*sensu* Simpson 1944), morphological similarity can also be attributed to evolutionary relationship and therefore should also be correlated with phylogeny. In this way, it can bridge the gap between taxonomy and ecology and provide a better understanding of selectivity during the recovery (Lamsdell et al. 2017).

Strophomenida

The Strophomenida is an order of articulate brachiopods that originated in the early Ordovician and became extinct in the Carboniferous (Cocks and Rong 2000). Strophomenide brachiopods were a diverse and abundant component of the Paleozoic benthos. Individuals were morphologically complex and groups differed largely in terms of strategies for holding their valves together (Cocks and Rong 1989; Rong and Cocks 1994). The order as a whole was geographically widespread and survived two of the big five mass extinctions (Cocks and Rong 2000). Their long geologic duration and wide geographic distribution make them ideal for studying the long-term effects of a mass extinction. Because they were ecologically dominant, any change in this group is likely to be a meaningful reflection of change in the biosphere as a whole.

Congreve et al. (2015) revised the phylogenetic relationships of the Strophomenida (Fig. 1). This phylogeny is based on 69 discrete morphological characteristics of the shells and 61 exemplar species, representing all but 1 family within the order. The family not included in this phylogeny is the Foliomenidae because its phylogenetic placement was unable to be determined. The order can be divided into 4 main groups: a basal plectambonitoid grade, the chonetid clade, and two clades of strophomenoids, one that originates in the Ordovician and one that originates in the Silurian. This study uses this phylogenetic framework to examine the effect of extinction and origination on morphological evolution within the clade.

Models for morphological change in the extinction and recovery

There has been extensive research into how morphological disparity has changed through time (e.g., Foote 1994, 1999; Ciampaglio et al. 2001; Ciampaglio 2004; Lockwood 2004; Erwin 2007). Theoretical expectations for quantifying disparity (Ciampaglio et al. 2001; Korn et al. 2013) highlight two broad patterns, based largely on changes in the location of the centroid and extent of variation in ordination space. Korn et al. (2013) developed a model for the impact of extinction on morphospace. Depending on the selective nature of an extinction, the centroid of morphospace will either shift directionally or remain the same.

In this study, we examine morphological change across the Late Ordovician mass extinction and the Early Silurian recovery interval to assess the relative importance of selectivity during both extinction and origination. We apply both the Korn et al. (2013) model of extinction and our proposed model of origination (the two hypotheses described below) to examine morphological selectivity during the extinction and recovery. Additionally, we focus on a single order to explore the extent to which individual clades are able to morphologically innovate following a mass extinction. First, we use the Korn et al. (2013) model to determine if extinction was selective. If taxa that go extinct are preferentially removed from regions of morphospace, the centroid would shift directionally, indicating a selective extinction. In contrast, if taxa that go extinct are removed from throughout morphospace, the centroid would not change, indicating random extinction.

Second, we used the Korn et al. (2013) model as the basis for generating hypotheses of morphospace change during the recovery (Fig. 2). Taxa that originate during a recovery can fill morphospace in one of two ways: 1. new taxa can fill in existing space left by survivors, preserving the original centroid, or 2. new taxa can fill previously unoccupied space, resulting in a directional shift in the centroid. Under the first hypothesis, overall morphology and, presumably, ecology of the order will remain constant across the extinction boundary. In contrast, the second hypothesis would indicate the evolution of new morphologies and, possibly, new ecologies.

Methods

Ancestral state reconstruction

The study uses the Strophomenida phylogeny from Congreve et al. (2015). We created a time-scaled version of this phylogeny (Fig.1) using the "basic" model of age calibration, where each species in the phylogeny was assumed to be an exemplar for its assigned genus (Congreve et al. 2015). Studies focusing on numerical models (Bapst 2014) and fossil data (Bapst and Hopkins 2017) have suggested that the "basic" model tends to outperform minimum branch-scaling methods for origination times (e.g. Brusatte et al. 2008). It is worth noting that fossilized birth-death models such as cal3 tend to

outperform the basic model (Bapst 2014), but this sort of detailed modeling of stratigraphy was outside the scope of this study.

To time-scale the phylogeny, first and last occurrences of each taxon were determined from the geologic range of the taxon's genus in the Treatise of Invertebrate Paleontology (Cocks and Rong 2000). Ghost ranges were determined by extending the first occurrence of a taxon back to the youngest possible time of origination based on its evolutionary relationships (Norell 1993; Norell and Novacek 1992; Cavin and Forey 2007).

In addition to the 61 taxa in the tree, we reconstructed the character states for 45 ancestral nodes (Brusatte et al. 2011). The character states for these ancestral nodes were determined by calculating the most parsimonious character reconstruction in Mesquite (Maddison and Maddison 2015). This method determines the most parsimonious character state for each ancestral node, and in instances where it is equally parsimonious for a character to evolve earlier (ACCTRAN) or later (DELTRAN) on the tree, the method treats these nodes as being ambiguous (i.e. the node could be considered to have either morphological state) (Maddison and Maddison 2015). Since the Generalized Euclidean Distance method of Principal Coordinates Analysis cannot handle multiple or ambiguous states, all ambiguous ancestral character state reconstructions were treated as absent (NA) for the morphometric analysis. Stratigraphic ranges for these ancestral nodes were inferred from the ancestral branch lengths generated from the "basic" time calibration (Bapst 2014). We used these 106 taxa (61 taxa and 45 ancestors) to assess morphological change in the strophomenides from the time of the order's origination in the Ordovician through the Devonian.

Character data from the original phylogeny (Congreve et al. 2015) are available on Morphobank (http://morphobank.org/permalink/?P1037). Ancestral node reconstructions are in the supplemental. We also ran all analyses without including hypothetical ancestors and generated a morphospace that was broadly similar to the analysis that included ancestors. The results of these analyses without ancestors were similar to the analyses presented below, but they lack the statistical power to make strong conclusions about the radiation because of the low number of early Silurian taxa sampled (see Results for further discussion). These files are also included in the supplemental information.

Morphospace

Character state data from the phylogeny were ordinated using Principal Coordinates Analysis (PCO; Gower 1966) following the method of Hughes et al. (2013), which uses Generalized Euclidean Distance (a modification of a Euclidean Distance, see Wills 2001; Lloyd 2016) as a dissimilarity metric and corrects for negative eigenvalues using a Calliez correction (Lamsdell and Selden 2017; Cailliez 1983). The Hughes et al. (2013) method is a series of functions in R (R Core Team, 2014) that uses PCO to ordinate a dissimilarity matrix of character state data. Axes are drawn such that the distances between points are equal to their original dissimilarity (Gower 1966, 2005; McCune and Grace 2002; Anderson and Willis 2003). A major difference between PCO and other ordination methods is that the relationship between the axes and original variables is unknown but can be approximated. We identified differences in morphologies between species that separate along the major axes to explore explanations for variation.

After ordinating the data, the Hughes et al. (2013) method uses a matrix of stratigraphic ranges to calculate how morphospace occupation changes throughout the total stratigraphic duration of the dataset. Morphospace plots were made by plotting PCO axis 1 and 2 scores (all PCO scores are in supplemental). To further explore these patterns, we then coded morphospace by phylogenetic group membership. To determine morphological change of Strophomenida through time, separate morphospace plots were made for each of twenty stage-level time intervals from the early Ordovician through the Devonian (see supplemental).

The method of Hughes et al. (2013) also calculates a sum of ranges (SOR) and sum of variance (SOV) between all PCO axes. Both of these statistics measure morphological variation (disparity). SOR describes the total range of morphospace occupation, while the SOV measures the variation within morphospace, or how far apart points are spaced. Calculating these metrics for each stage-level plot allows us to quantify how the amount of morphological variation in Strophomenida changed through time.

Previous studies show that PCO used with cladistic data produce similar patterns as landmark data (Hethering et al. 2015) showing largely similar patterns in morphospace occupation and sum of ranges and sum of variances. Furthermore, studies that compare these PCO studies of discrete characters of entire organisms to detailed landmark analyses of single parts of organisms also obtain similar results (Hopkins 2017). These methods have been applied effectively to phylogenetic data similar to the data used in this study (Lamsdell 2016; Lamsdell and Selden 2017).

Potential sampling and biogeographic biases

For this analysis we used the established strophomenide phylogeny from Congreve et al. (2015) in order to investigate the broad-scale morphological shifts within the context of an established phylogenetic framework. This previous analysis focused on sampling a few exemplar species from families across the order. This resulted in a coarse sampling of the total generic diversity of the entire order, though one that attempted to sample common and widespread taxa from each family. However, some time periods and biogeographic areas were potentially under sampled in this analysis. Specifically, the earliest known strophomenoid taxa assigned to major families likely evolved in the Floian in equatorial Gondwanan regions around modern China, Australia, and Iran (e.g. Ghobadi Pour et al. 2011; Zhan et al. 2013; Popov and Cocks 2017). More importantly, these taxa appear to have unique suites of morphological characteristics that are not observed in later strophomenoids. The broad taxonomic sampling of this analysis may therefore not be a complete representation of the morphological variability of strophomenides throughout the Early to Middle Ordovician. Reconstruction of ancestral characteristics can alleviate this sampling issue to a point, but these methods still rely upon the already sampled taxa and therefore cannot incorporate morphological characteristics not present in the sampled species.

However, these Early to Middle Ordovician genera with complex suites of morphological characters ultimately do not persist to the mass extinction event, and, therefore, should not affect the patterns of morphological difference observed during and after the Late Ordovician mass extinction. In order to ensure that our ancestral state reconstructions did not negatively influence our observed patterns, we reran the analyses excluding ancestors (see supplemental). This suggested similar patterns of selectivity related to the extinction and radiation as the patterns observed in our complete dataset. As such, we are confident that our results for the Late Ordovician mass extinction are not biased by the exclusion of these earlier taxa. However, we refrain from commenting in detail on the changes in morphometric patterns that occurred in the early phases of the Ordovician radiation because our data may not fully represent this time interval.

Bootstrap analysis of extinction and recovery

PCO values were bootstrapped (Efron 1979; Kowalewski and Novack-Gottshall 2010) to determine if Late Ordovician mass extinction and Early Silurian origination were distributed randomly through strophomenide morphospace. Bootstrapping is a method of resampling with replacement and can be used to assess whether the observed pattern is consistent with what would be expected if the pattern were due to random chance.

To model random extinction in morphospace, we examined PCO scores for taxa that were extant in both the Katian and Hirnantian (44 taxa total). These data were combined for the two stages to capture the full temporal extent of the Late Ordovician mass extinction. The number of PCO axis 1 and axis 2 scores equal to the number of taxa that actually went extinct (32 taxa) were drawn randomly with replacement from the combined Katian/Hirnantian morphospace. This created a dataset of PCO scores for extinct taxa under a simulated random extinction. The centroid of this random sample was calculated. This process was repeated 1000 times to generate a data set of simulated centroids, for which a grand centroid and 95% confidence interval was calculated. This repeated random sampling generated an expected range of morphospace variation for random extinction.

To model random origination in morphospace, the same process was applied to the PCO values of taxa in the Rhuddanian (26 taxa total), the first stage of the recovery. Since the process of bootstrapping involves evaluating how the observed distribution compares to simulated randomness, as opposed to actually modeling the process of origination, it was applied to all of the Rhuddanian data, not just those that survived the extinction. Species PCO scores were drawn randomly with replacement from the entire distribution of taxa within Rhuddanian morphospace. The size of each random draw equaled the total number of taxa that originated during the Rhuddanian (14 total). This created a data set of PCO scores for new taxa under simulated random origination. The centroid of these scores was calculated, and this process was also repeated 1000 times. This generated a data set of simulated centroids for which a grand centroid and 95% confidence interval was calculated. This repeated random sampling generated an expected range of morphospace variation for new taxa under random origination.

Expected morphospace ranges for both random extinction and origination were compared to the actual PCO scores to assess whether extinction and origination during the Late Ordovician and Early Silurian were consistent with a random expectation.

Results

Morphospace occupation through time

The four phylogenetic groups (Fig. 1) clearly separate in morphospace (Fig. 3). The basal plectambonitoid grade occupies the right half of morphospace and the strophomenoids occupy the left. The chonetids fall in between these two groups along PCO axis 1, but have the highest values on PCO axis 2. Within the left half of morphospace, the Ordovician and Silurian/Devonian strophomenoids form distinct groups. The Silurian/Devonian strophomenoids have slightly lower PCO1 scores and slightly higher PCO2 scores than their Ordovician counterparts.

When total morphospace is divided into time slices, it is clear that morphospace occupation changes throughout clade duration (Fig. 4, see supplemental for more detail). The order originates in the lower right quadrant of morphospace, then expands to occupy the whole right half and bottom left half of morphospace during the Ordovician radiation (Darriwillian). Occupied morphospace remains consistent until the Late Ordovician mass extinction (Katian-Hirnantian). A significant number of taxa (32 total) go extinct at the end of the Ordovician. After the extinction (Rhuddanian), new taxa originate in a previously unoccupied region of morphospace (the upper left side). Throughout the Silurian and into the Devonian, taxa slowly go extinct within the old region of morphospace, new taxa primarily originate in the new region of morphospace, and old morphospace is never reoccupied to the extent it was in the Ordovician.

Comparing morphospace through time (Fig. 4) to the morphospace coded by phylogenetic group (Fig. 3) shows how each group changes through time. The basal plectambonitoid grade originated in the lower right quadrant of morphospace and expands to fill the right half of morphospace during the Ordovician radiation. Many members of this group went extinct at the Late Ordovician mass extinction, but a few survived into the Devonian. The ancestor to the chonetids originated during the Ordovician radiation and plots in the top middle of morphospace. This group expanded late in the Ordovician, survived the extinction and persisted until the Devonian. The Ordovician strophomenoids originated during the Ordovician radiation and quickly expanded to occupy the lower left quadrant of morphospace. This group was hit hard by the extinction, but a few taxa evolved in the Silurian and persisted through the Devonian. The ancestor to the Silurian/Devonian strophomenoids evolved during the Ordovician radiation, but the group as a whole did not diversify until the early Silurian. This group continued to expand its occupation of morphospace throughout the Silurian and into the Devonian. These groupings are also recovered in our analyses that exclude the inferred ancestral nodes (supplemental information).

The stability of morphospace throughout the Ordovician is also demonstrated by a constant sum of variance and sum of ranges (Fig. 5). This means that the total amount of morphospace occupied and the average variation between individual points in the morphospace are approximately the same over time. At the Late Ordovician mass extinction, the sum of variance drops, but the sum of ranges remains the same. This means that the extinction decreases variation in morphospace but does not change the total amount of morphospace occupied. During the recovery, sum of variance rebounds slightly but does not return to its pre-extinction level (Fig. 5A). It remains at this lower level into the Devonian. In contrast, the sum of ranges remains relatively constant throughout the history of the strophomenides (Fig. 5B). The disconnect between these two metrics means that extinction strongly affected the distribution of points in morphospace, but it did not change the overall shape of morphospace. These metrics in combination demonstrate that the Late Ordovician mass extinction and recovery had a significant and permanent effect on morphological disparity within strophomenides.
Are extinction and origination random?

Results from the bootstrap of PCO scores show that extinction during the Late Ordovician does not differ from a random expectation (Fig. 6a). This is because the centroid falls within the range of expected PCO scores if genera were randomly removed from morphospace. However, origination during the earliest Silurian does differ from a random expectation along PCO axis 1 (Fig. 6b, see supplemental for bootstrap values for other axes). The centroid falls outside of the range of expected PCO scores if genera were randomly added to morphospace. This implies that the extinction event did not target specific morphologies, and therefore may have been random with respect to morphological adaptations (in addition to being largely random with respect to taxonomic groups [Krug and Patzkowsky 2015; Congreve et al. 2015]). However, the recovery after the extinction was associated with a significant shift in morphospace. Extinct, surviving, and newly originating taxa in the early Silurian occupied different regions of morphospace (Fig. 6). The largest difference in morphospace occurred along PCO axis 1. Extinct taxa had the highest PCO 1 scores, surviving taxa fell in the middle, and new taxa had the lowest. Additionally, the centroid for taxa that originated in the Silurian was distinct from that of both those that survived and those that went extinct at the Late Ordovician mass extinction.

The patterns observed when our analyses include ancestral nodes (presented here) are largely consistent with our analyses that exclude ancestral nodes (in supplemental). Our dataset that excludes ancestral nodes also reconstructs the extinction as random with respect to morphology, but was unable to reject the null hypothesis that origination was random in the Silurian because only three taxa were sampled from the Rhuddanian. This limited sampling reflects both low diversity and low rock availability during this interval (Peters and Foote 2001). It also limits the statistical power of our bootstrap analyses such that almost any distribution of new taxa in morphospace would be considered random. However, it is clear that morphospace occupation did shift through time in the same way as in the analysis that included ancestors. Furthermore, based on the phylogenetic analysis, origination of these morphologies must have occurred earlier than their stratigraphic first occurrence, since the clade that radiated in the Silurian must have originated in the Ordovician. Our results provide further support for the importance of ancestral node reconstructions and time-calibrated phylogenies to understanding evolutionary transitions (Norell 1993; Lane et al. 2005; Brusatte et al. 2008), especially during periods of Earth's history when sample availability and diversity is generally low.

Overall the patterns of extinction and origination are consistent with the time scaled phylogeny (Fig. 1). Taxa that go extinct in the Late Ordovician are randomly removed from the basal plectambonitoid grade and the Ordovician strophomenoids, the two groups that occurred during that time. Much of the origination in the Early Silurian clustered within a new monophyletic group of strophomenoids. This rapid and clustered diversification is reflected in the location of these clades in morphospace (Fig. 3) and the pattern of morphospace evolution (Fig. 4).

The sum of variance and sum of ranges further support random extinction and non-random origination. The extinction did not change total morphospace occupied, but resulted in a persistent drop in morphological variation. Essentially, the total extent of morphospace is unchanged across this event, but the recovery favors a few areas within morphospace, as seen in the shifts in morphospace centroid and decrease in sum of variance. This is consistent with extinction removing morphologies randomly and origination selecting for certain morphologies.

Discussion

Impact of the Late Ordovician mass extinction

Our results demonstrate that the Late Ordovician mass extinction randomly affected strophomenides based on morphology and clade membership (Fig. 6). The centroid of extinct taxa was not distinguishable from a random expectation. However, the centroid of taxa that survive the extinction fell outside the random expectation, slightly shifting average morphology along principal coordinate axis 1. Although the sum of variance in the Silurian was less than it was during the Late Ordovician, the broad outline of morphospace was relatively unchanged.

For the Strophomenida, the probability of surviving the Late Ordovician mass extinction appears to have depended very little on morphology. In this respect, the Late Ordovician mass extinction differed substantially from other big five mass extinction events for which there was documented morphological (e.g., Ciampaglio 2004; Lockwood 2004) and phylogenetic (Roy et al. 2009) selectivity.

The Late Ordovician mass extinction did not appear to preferentially select for certain clades over others. Both the plectambonitoids and Ordovician strophomenoids survived the event with similarly low diversity (there were proportionally more chonetid survivors, but sample size for this group within this study was much lower). This means that, although the extinction reduced morphological variability within the strophomenides, it preserved a large amount of existing phylogenetic diversity, increasing

the potential for post-extinction diversification to occur within existing clades. The nonselective nature of the extinction is consistent with the suggestions of phylogenetic randomness (Krug and Patzkowsky 2015) and selectivity independent of taxonomy (Finnegan et al. 2016). This suggests that taxa were randomly removed from all evolutionary lineages during the Late Ordovician mass extinction, as opposed to preferentially removed from some evolutionary lineages. This randomness preserved a large amount of phylogenetic diversity, since most clades survived into the Silurian. Finnegan et al. (2016) also suggest that extinction selectivity was not taxon-specific because it was primarily based on bathymetric and biogeographic differences. That is, taxa that went extinct at the Late Ordovician mass extinction were those that lived in shallow water and higher latitudes. These authors argue that environmental gradients cross taxonomic groups, and thus, the impact of extinction was independent of group membership. This also supports the low familial clumping of extinction (Krug and Patzkowsky 2015) where taxa were removed from evolutionary lineages indiscriminately. However, its support of our findings of morphologically random extinction depends on how tightly morphology and environmental parameters are linked. Extinction that is selective based on environmental difference but random with respect to morphology implies that these environmental gradients might not be the primary driver of morphological diversity within this group. This could be an explanation for the disconnect between taxonomic loss and ecological restructuring. More importantly, it highlights the complexity of the relationship between morphology and ecology and the need for further research.

The importance of the Silurian recovery

Origination during the recovery from the Late Ordovician mass extinction had a directional impact on strophomenide morphospace. The centroid of originators was well outside both the original boundary of morphospace and the expectation of randomness. The sum of variance, although relatively constant throughout the recovery, was at lower levels than prior to the extinction. This reflects an overall decrease in the amount of variation within morphospace (a bottleneck). The reduction in morphological variability during the recovery is consistent with the change to phylogenetically clumped origination across the extinction boundary (Krug and Patzkowsky 2015), where new origination is concentrated within some families. This type of morphological bottleneck after an extinction event has been observed in multiple groups across multiple extinction events including ichthyosaurs (Thorne et al. 2011), horseshoe crabs (Lamsdell 2016), trilobites (Crônier 2013), and eurypterids (Lamsdell and Selden 2017), though our study is potentially unique given that the bottleneck appears to be caused by selective radiation as opposed to selective extinction.

The results of this study are consistent with our second hypothesis (Fig. 2) that diversification occurred in a new region of morphospace during the recovery, resulting in a directional shift in morphospace occupation. Recovery taxa (the Silurian/Devonian clade; Fig. 3) exploited a new, previously unoccupied region of morphospace, which meant that they were morphologically distinct from those that went extinct during the Late Ordovician. Our results also add support to previous studies from early Silurian brachiopod faunas, which suggested that ecological recovery after the extinction was rapid and dominated by the appearance of new, morphologically distinct taxonomic groups (Rong et al. 2006; Cocks and Rong 2008; Rong and Cocks 2014).

A major morphological difference between the Silurian-Devonian strophomenoids and the other strophomenide taxa was an increase in dentition at the hinge line and a change in muscle attachment structures (Congreve et al. 2015). It is unclear whether this trade-off conferred any evolutionary advantage or was non-adaptive (sensu Gould and Lewontin 1979). Initial exploration of the environmental affinities (sensu Simpson and Harnik 2009; Hopkins 2014) does not support water depth, substrate, or latitudinal affinities as an explanation for this pattern (Patzkowsky et al. in prep). As such, our interpretation of the impact of origination on ecology is complicated. While we acknowledge that morphological changes could be the result of non-adaptive processes, the shift in morphospace during the Silurian recovery may suggest that the current interpretation that the Late Ordovician mass extinction event had little ecological effect (e.g., McGhee et al. 2013) should be revisited. Further research is necessary to determine if the morphological bottleneck that occurred during the Silurian is due to functional constraints associated with shifts into new ecologies or if it is due to evolutionary changes associated with shared phylogenetic descent (Congreve et al. 2017).

The effect on long-term clade trajectory

Tracking morphospace change through clade history shows that, after the extinction, most diversification occurred in the region of morphospace that was not occupied throughout the Ordovician, at least at the level of the family. There are a few surviving taxa that persist in the Ordovician region of morphospace, but they slowly go

extinct throughout the Silurian and Devonian without being replaced. This suggests that morphological constraint during the recovery had a profound impact on overall strophomenide morphology. The selective nature of the recovery makes the amount of evolutionary history preserved by the random nature of the extinction unimportant to the long-term trajectory of the clade. While nearly all strophomenide groups survive the extinction, only a few families diversify in the recovery. Most of the strophomenide families that were dominant in the Ordovician experience a slow-decline until the Devonian and are essentially 'dead clades walking' (sensu Jablonski 2002). The origination of a new clade and the slow decline of the pre-extinction clades are consistent with the taxonomic patterns of turnover that have been identified during the recovery (Harper and Rong 1995; Rong et al. 2006; Cocks and Rong 2008; Rong and Cocks 2014).

This study adds to our existing understanding of the Late Ordovician mass extinction event by highlighting the significance of the recovery for long-term evolution. Focusing only on selectivity during the extinction itself would suggest that the extinction was not important to strophomenide evolution. However, we have demonstrated that this provides an incomplete picture of how the strophomenides responded. It is only by examining selectivity during the recovery that we are able to identify a shift in morphology and recognize that it persisted for the duration of this group. Similar patterns of selective origination after the Late Ordovician mass extinction has been demonstrated in crinoid phylogenies (Wright and Toom 2017) suggesting that this pattern where origination is concentrated within a single subclade may be a widespread phenomenon durign the Silurian recovery.

Conclusion

For the Strophomenida, the Late Ordovician mass extinction randomly removed taxa from morphospace. However, diversification during the recovery caused a change in morphospace that was decidedly non-random, and persisted for the remainder of the clade's duration. This indicates that diversification during the recovery had a greater impact on strophomenide evolution than the mass extinction. Furthermore, it implies that a better understanding of recovery dynamics at this time might lead to a re-evaluation of the importance of the Late Ordovician mass extinction in shaping the evolutionary history of the Paleozoic benthos.

The results of this study further emphasize that recovery intervals are at least as important in determining long-term evolutionary trajectories as extinctions themselves (Erwin 1998, 2001, 2008). We have demonstrated that understanding how mass extinctions create new evolutionary opportunities (Jablonski 1986) can only be tested by looking at the interval of time when these new opportunities allow for origination. Treating an extinction interval as separate from its subsequent recovery provides a fundamentally incomplete understanding of its evolutionary consequences. This becomes especially problematic when attempting to make generalizations about how life responds to catastrophic events. If we want to accurately understand how mass extinction affects the history of life, especially in regards to developing predictions for the future, we must expand our examination of recovery intervals.

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evolution produced four groups within this order: (1) a basal plectambonitoid grade, which originated in the Figure 1-1: Time scaled phylogeny of Strophomenida. The brachiopod order Strophomenida originated in strophomenoids, which originated in the Rhuddanian during the recovery from the Late Ordovician mass ranges for each genus are from the revised brachiopod Treatise on Invertebrate Paleontology (Cocks and extinction. This phylogeny is a time-scaled version of the one defined by Congreve et al. (2015), which Ordovician), and underwent a secondary radiation in the Rhuddanian (earliest Silurian). This pattern of contains exemplar genera within families. The tree contains 61 taxa and 45 ancestral nodes. Geological Tremadocian, (2) the chonetids, which have a ghost range that extends back to the Darriwillian, (3) the the Tremadocian (earliest Ordovician), underwent an initial radiation in the Darriwillian (middle Ordovician strophomenoids, which originated in the Darriwillian, and (4) the Silurian/Devonian Rong 2000).

Plectambonitoidea"	Chonetids	rstrialis - Strong - Strong - Strong - Strophomenoids - Douvilina dutertrei - Douvilina dutertrei - Stronghomenoids - Strophomenoids	Ordovician Strophomenoids	Famennian	370 360
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	etes tenui s comestu	- Maoristr - Leptostr - Leptostr - Dicoelos iata	chmonde	nsiləti∃ <u>A</u>	
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Figure 1-2: Hypothesized patterns for morphospace occupation during the recovery. When new taxa originate during a recovery, they can occupy morphospace in one of two broad ways. A, New taxa (black) can fill space within the existing boundary of surviving species (gray). This preserves the centroid (gray triangle) of morphospace and results in no directional shift in overall clade morphology. B, New taxa (black) can occupy a previously unexploited region of morphospace. This shifts the centroid of morphospace and results in a directional shift in overall clade morphology (gray triangle=surviving centroid; black triangle = new centroid). (Inspired by Korn et al. 2013)



Figure 1-3: Strophomenida morphospace coded by phylogenetic group membership. The four groups defined by the origination pattern in the time-scaled phylogeny separate in morphospace, indicating that these groups are morphologically distinct. Points are each of the 106 taxa. The 61 actual species are triangles, colored by group membership. The 45 ancestral nodes are the light gray circles. PCO 1 explains about 11% of the variance in the data and PCO2 explains about 6% of the variance.

Figure 1-4: Morphospace through time. The earliest members of Strophomenida occupy a small region of morphospace. Morphospace occupation expands during the radiation in the Darriwillian and remains constant until the Late Ordovician. The group is affected by the Late Ordovician mass extinction, during which no new taxa originate. After the mass extinction, new taxa that originate during the Silurian recovery occupy a smaller, previously unexploited region of morphospace. Throughout the Silurian and into the Devonian, taxa from the Ordovician region of morphospace slowly go extinct, while new taxa originate in the new constrained region of morphospace. Plots are for each stage from the Floian (Early Ordovician) to the Frasnian (Late Devonian). In each plot, points in black are taxa that originated during that stage, while points in gray are taxa that survived from the previous stage. Plots are spaced evenly, not scaled according to the length of time in each stage.





Figure 1-5: Sum of variance and sum of range. The sum of variance (A) increases with the radiation in the Darriwillian and remains constant throughout the Ordovician. It drops at the extinction and rebounds slightly in the Silurian, but never returns to pre-extinction levels. This reflects the constraint in morphospace during the recovery. The sum of range (B) is constant throughout this time interval. This reflects a consistent total amount of morphospace. In each plot, black line is the total variance or range for each stage with 95% confidence intervals. The region bounded by the gray lines is a confidence interval around randomness. Dotted line marks the Late Ordovician mass extinction boundary.



Figure **1-6**: Bootstrapped centroids of extinct and originating taxa. The centroid (dark gray triangle in A) of taxa that go extinct at the end of the Ordovician is distinct from that of both those that survive (light gray triangle) and those that originate in the Silurian (dark gray triangle in B). Bootstrapped values for extinct (gray ellipse in A) and new (gray ellipse in B) taxa identify a zone of random expectation. The centroid of taxa that go extinct at the end of the Ordovician falls within the random expectation (A), and the centroid of taxa that originate in the Silurian falls outside the random expectation (B).

Chapter 2

How similar are sisters? The relationship between morphology, ecology, and evolutionary history

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J.A. Sclafani did the data collection and analysis and wrote the manuscript. C.R. Congreve, and M.E. Patzkowsky advised the project and helped edit the manuscript.

Abstract

A fundamental question in paleobiology is whether morphology and ecology are correlated and reflect trends in evolutionary history. This question can be linked to the Phylogenetic Distance/Ecological Difference (PDED) hypothesis in ecology, which states that closely related taxa should be more ecologically similar. With phylogenetic trees, we can test this hypothesis in the fossil record to determine whether closely related evolutionary sisters are more ecologically similar to each other than to their distant relatives. By combining time-calibrated trees with genus occurrence data through time, we can understand how environmental preferences are distributed on a tree and evaluate support for the PDED and other evolutionary models such as early burst or Brownian motion. Exploring the parameters that lend support to each of these evolutionary models will help address questions that lie at the nexus of the evolutionary and ecological sciences.

We examined the relationship between morphologic distance, ecological distance, and phylogenetic distance between species pairs for 61 taxa used in a recent phylogenetic revision of the brachiopod order Strophomenida and for 50 taxa used in a recent phylogenetic revision of the superfamily Strophomenoidea. Morphological distance was calculated as the pairwise Euclidean distance in a principal coordinate ordination of character data. Ecological distance was calculated as the pairwise distance along gradients of water depth, carbonate, and latitudinal affinity. Phylogenetic distance was calculated as the pairwise branch length between tips of the tree. Our results show a strong positive correlation between morphological distance and phylogenetic distance and no relationship between ecological affinity and phylogeny. Since ecology does not show a strong correlation with phylogeny in the strophomenide brachiopods, the PDED is not supported. Instead, the evolution of ecologies within Strophomenida is more consistent with an early burst during the initial radiation of the clade. This difference results from the macroecological dynamics and macroevolutionary processes preserved in the fossil record, which reflect larger spatial and temporal scales than those available to modern ecology. The processes of scaling from micro- to macro-evolutionary and -ecological scales are complex. Teasing apart this complexity requires the collaboration of paleoecologists and modern ecologists and consideration of both evolutionary history and ecological function.

Introduction

The degree to which ecological preferences are constrained by evolutionary history underpins the subdiscipline of phylogenetic community ecology. The prevailing paradigm is that evolutionary similarity can serve as a proxy for ecological similarity (Webb et al. 2002), but recently studies suggest this relationship is more complicated (Gerhold et al. 2015; Cadotte et al. 2017). The mechanism to explain the expected linear correlation between phylogenetic distance and ecological difference is evolution via competitive exclusion (MacArthur 1958). Competitive exclusion operates in local communities, whereas ecospace-filling is more random at the larger scales that are more likely to be preserved in the fossil record (Cardillo 2011).

As a proxy, the relationship between phylogeny and ecology is used to understand community assembly, or the dynamics that promote the coexistence of species within an ecological community. However, the question of how communities assemble is still unanswered, and the dynamics involved contain complexities that might be inconsistent with a linear relationship between phylogeny and ecology. If phylogenetic distance and ecological difference do not co-vary linearly, it is possible that they can be related via other eco-evolutionary hypotheses (Figure 1). If closely related taxa exhibit a wide range of ecologies, they would reflect an early burst hypothesis, i.e., experimentation during times of radiation. Distantly related taxa with similar ecologies are examples of ecological convergence or niche conservatism. Finally, the region below the a 1:1 linear correlation represents evolution via Brownian motion or neutral community assembly, suggesting that at larger scales, support for the PDED might be obscured by random processes that generate noise in the data. The fossil record contains information that allows us to assess trait evolution over long time scales in order to understand how expected community-scale assembly processes might be reflected in a phylogenetic tree.

The aim of this work is to test the PDED hypothesis for brachiopods from the order Strophomenida. This hypothesis provides the opportunity to examine the role of niche vs. neutral regional assembly processes in driving diversification of a clade. We use recent evolutionary trees for this group for phylogenetic and morphologic character data (Congreve et al. 2015, 2019). This order experienced a morphological and phylogenetic bottleneck during the recovery from the Late Ordovician mass extinction (Sclafani et al. 2018). In exploring the PDED, we aim to investigate environmental variables that could explain this observed evolutionary bottleneck. Results will explain the assembly processes at play in the large spatial and temporal resolution of fossil data and inform

interpretations of ecological and evolutionary change in response to biotic crises throughout the Phanerozoic.

Background

The phylogenetic distance/ecological difference hypothesis

The phylogenetic distance/ecological difference (PDED; named in Cadotte et al. 2017) hypothesis originates from Darwin (1859) and was refined during the development of classical ecological theory (e.g., Mayr 1942; Brown and Wilson 1956; MacArthur 1958). It states that the distance between species on a phylogenetic tree can serve as an estimate for the degree to which their ecological preferences differ. The utility of the PDED is in understanding species co-occurrence and community assembly. However, this hypothesis rests on an assumption of purely niche-based assembly, a concept that has been recently called into question by neutral theory (e.g., Hubbell 2001, 2005; Alonso et al. 2006; Rosindell et al. 2010). Although the concept of neutral assembly has been strongly debated (e.g., Tilman 2004; Leibold and McPeek 2006; Adler et al. 2007; Purves and Turnbull 2010; Clark 2009, 2012), evidence suggests that communities are assembled via both competitive and stochastic processes (e.g., Adler et at. 2007; Cadotte 2007). Ultimately, the role that competitive exclusion plays in community assembly is poorly understood.

In addition, there are many examples in modern ecology where phylogenetic distance is a poor proxy for ecological dissimilarity. Perhaps the most well-known is the "paradox of the plankton" (Hutchinson 1961), or the idea that phylogenetically distant plankton species co-exist in pelagic environments despite limited resource availability,

implying that competitive exclusion does not control the distribution of plankton. Other organisms such as plants (Shmida and Ellner 1984), fish (Schlosser 1982), deep-sea deposit-feeders (Dayton and Hessler 1972), and benthic mollusks (Stanley 2008) have also been observed to coexist without much ecological differentiation and without one species driving others to extinction. Some explanations for a lack of competition are purely mathematical (Armstrong and McGehee 1980), but many invoke environments and species conditions that rapidly change over time and space (Hutchison 1961; Tilman et al. 1982; Chesson 1985; Huisman and Weissing 1999), often employing stochastic biological models (Chesson and Warner 1981; Cadotte et al. 2017 and references therein).

The PDED hypothesis has been less explored in the fossil record. A few studies that use both phylogenetics and geometric morphometrics draw upon the ideas behind the PDED to explain observed evolutionary patterns, using morphology as a proxy for ecology (e.g, Benton 2009; Hopkins 2014; Bapst et al. 2011; Lamsdell et al. 2017). However, none of these studies directly test whether morphology or phylogeny are actually correlated with ecology, as would be expected under the PDED. However, the pervasive nature of biofacies, or co-occurring groups of organisms with similar environmental affinities, throughout the geologic record (e.g., Zeigler 1965; Zeigler et al. 1968; Bretzky 1969; Ludvigsen and Westrop 1983; Boucot 1983; Kammer et al. 1986; Brett and Baird 1995; Patzkowsky and Holland 2016) suggest that the data for unraveling the PDED for fossil species are available.

Because of preservation processes that affect fossil assemblages, such as timeaveraging, the role of competitive exclusion in structuring the ecological communities remains difficult to test directly using the fossil record. Additionally, several studies have used neutral dynamics to successfully explain observed spatial and temporal turnover of fossil ecological communities (Olszewski and Erwin 2004; Tomasovych and Kidwell 2010; Sclafani and Holland 2013; Wang et al. 2013; Holland and Sclafani 2015; Holland 2018). A possible explanation for neutrality in fossil ecological communities is that at the long time scales preserved in the fossil record, competitive exclusion and other nicheprocesses might be obscured by more drift-based dynamics. Since the PDED hypothesis rests on an assumption of niche-based assembly rules, it might similarly be difficult to distinguish from (potentially) stochastically-assembled fossil communities.

Community Assembly

The manner by which ecological communities assemble has been the subject of much debate. The two main hypotheses are niche-based and neutral-based assembly. Niche-based assembly is based on the classical competitive exclusion principle where species that rely on the same resource will not co-exist in the same ecological community (Darwin 1859; Grinell 1922; Volterra 1926; Gause 1934; Lack 1947; MacArthur 1958; Hardin 1960; see Whittaker et al. 1973 for an overview of the evolution of the niche concept in classical ecology). Although the specifics vary, niche-based assembly is often treated as the default assumption in ecological studies (e.g., Segre et al. 2016). As such, competitive exclusion is supported by some evidence (e.g., Lack 1947; MacArthur 1958; Chesson and Huntley 1997; Violle et al. 2011), but there are many more examples of its effect on community structure being either more complicated than initially proposed (Dunson and Travis 1991; Goldberg and Barton 1992; Tilman 1997; Huisman and Weissing 1999; Mayfield and Levine 2010; De Léon et al. 2014) or mostly negligible (Hutchinson 1961; Dayton and Hessler 1972; Schlosser 1982). A recent response to this complication has been to increase the parameters or dimensionality of niche models (e.g., Soberon and Peterson 2005; Godsoe 2010; Wilson 2010) based on the n-dimensional hypervolume (Hutchinson 1958). While this resolves some of the problems, it is an overparameterized model, limiting its potential for broader theoretical application (Akaike 1973, see Johnson and Omland 2004; Warren and Seifert 2011 for discussions of model selection criteria and model complexity in ecology).

As opposed to adding parameters, neutral theory ignores competitive exclusion as an explanation for community assembly, instead treating trophically equivalent species as ecologically identical (Hubbell 2001). Neutral theory is based on the island biogeography models of MacArthur and Wilson (1967) and rests on the assumption that all species within a single trophic level of an ecological community are competitively equal. This assumption does not mean that all species have the same niches, rather, it is an extension of the concept of ecological functional groups (e.g, Grime 1973, Walker 1992, Wilson 1999, Bambach et al. 2002, Cadotte et al. 2011). Under neutral theory, any niche differences between members of a functional group are not important for assembling ecological communities.

Under neutral theory, the ability for any species to occupy space within a community is dependent on both its abundance within the community and dispersal ability. While many ecologists have criticized the simplicity of this model (e.g., Chesson and Huntley 1997; Purves and Turnbull 2010; Clark 2009; Clark 2012), others have demonstrated its utility in explaining some of the complexity observed with purely niche-

based models of community assembly (Tilman 2004; Leibold and McPeek 2006; Adler et al. 2007).

Although often presented as opposing ideologies, it is perhaps more accurate to think of these two hypotheses as end-members along a spectrum of possibilities (McPeek 2007). It might be that both niche and neutral processes are important to structuring ecological communities, but their effects play out at different temporal or spatial scales (Leibold and McPeek 2006; Chase and Myers 2011). We liken this debate to whether biotic (Red Queen hypothesis, Van Valen 1973) or abiotic (Court Jester, Barnosky 2001) factors are more important for driving species evolution. A resolution to this dichotomy proposed a hierarchy of spatial and temporal scale where biotic factors are more important at small scales and abiotic factors are more important at regional scales and over a taxon's geologic range (Benton 2009).

In community assembly, niche theory is a biotic perspective and neutral theory can be likened to an abiotic perspective. If we place assembly processes in the same hierarchy, we can begin to resolve the current debate in a way that encourages more exchange of information between ecologists and paleoecologists working at different spatial and temporal scales. From this we can develop a broader, more comprehensive understanding of how ecological processes have changed throughout Earth's history.

Expectations for the fossil record

The question of how assembly processes change with spatial and temporal scale is especially important when considering fossil ecological communities. Because of time averaging, or the accumulation of multiple ecological communities within a single lithologic bed, fossil assemblages generally represent the regional species pool (Kidwell 2002). This means that the most appropriate theories for fossil community ecology are likely to be those that center on regional or metacommunity dynamics (see Patzkowsky 2017 for a discussion of the role of regional dynamics in paleoecology).

Additionally, biofacies, or assemblages of co-occurring fossil taxa with similar environmental affinities, are prevalent throughout the fossil record (e.g., Zeigler 1965; Zeigler et al. 1968; Bretzky 1969; Ludvigsen and Westrop 1983; Boucot 1983; Kammer et al. 1986; Brett and Baird 1995; Patzkowsky and Holland 2016; for more complete reviews of ecological stability in the fossil record, see Morris 1996; Schopf 1996). Biofacies are consistent assemblages, tied to certain depositional environments, and persist over long intervals of geologic time. In an ecological context, biofacies can be considered to represent the regional species pool, such that general stability through time suggests that the niches of constituent species are conserved. However, their long-term stability does not mean that biofacies were assembled by competitive exclusion. Random processes also can create a stable system, as in the mathematical stable-roommate problem in which a system can be stably assembled in any configuration of pairs as long as no member prefers a different partner (Irving 1985). Ecologically, this suggests that if environmental affinity is weak, randomly assembled stable configurations exist because chances are low that a species would prefer something other than their random assignment.

Whether niches evolve on geological time scales is a pressing question in paleobiology (e.g., Holland and Zaffos 2011; Saupe et al. 2014; Qiao et al. 2016). The idea that niches might shift or be conserved over geologic time and that this pattern

should be detectable in the fossil record forms the basis of our exploration of how the ecology of strophomenide brachiopods evolved. Because of the resolution available in the fossil record, a substantial amount of data is at the genus or family level, including many biofacies. This is operationally acceptable (Patzkowsky 2017) and supports the idea that genera have niches determined by the niches of their constituent species (e.g., Smith et al. 2004; Hadly et al. 2009; Patzkowsky and Holland 2016). Note that although ecological data in this study is at the genus level, phylogenetic and morphological data are at the species level; each tip of the phylogeny represents a single species within a genus. Despite this limitation of resolution, the fossil record is ripe with ecological data that inform and are informed by long-term evolutionary patterns. Although assemblages of fossil organisms are rarely equivalent to modern ecological communities, they do contain vital information about the regional species pool and offer insight into how biodiversity changes on time scales that would be otherwise unknowable.

Expectations for Strophomenida

We examined phylogenetic, morphological, and ecological data from the same brachiopod genera within the order Strophomenida to look for correlations. To do this, we calculated pairwise distances along branches in the evolutionary tree (phylogenetic distance; data from Congreve et al. 2015), between taxa in morphospace (morphological disparity; data from Sclafani et al. 2018) and along a modeled environmental affinity gradient (ecological difference; methods described below).

If the PDED hypothesis holds true for these data, phylogenetic distance will be correlated with ecological difference. This would imply the assumption of competitive exclusion holds true as well, meaning that it was an important process in the post extinction rebound. If phylogenetic distance and ecological difference are not correlated, the PDED would not hold true. This might imply more neutral or stochastic processes were responsible for the post extinction rebound of strophomenide diversity.

Comparing morphological disparity to phylogenetic distance and ecological difference will indicate whether evolutionary history imposed constraints on strophomenide morphology and whether the post-extinction reduction in disparity seen in Sclafani et al. (2018) is related to environmental preference.

Methods

Phylogenetic data

Phylogenetic data were gathered from a recent revision to the brachiopod order Strophomenida, which ranges from the Early Ordovician to the Carboniferous (Congreve et al. 2015). This tree contains 61 exemplar genera from all but one family (Foliomenidae, which couldn't be placed within the order). This family-level phylogenetic analysis highlighted four groups within Strophomenida: a basal plectambonitoid grade, a clade of chonetids, a clade of strophomenoids that originated in the Ordovician, and a clade of strophomenoids that originated in the Silurian (figure 1 in Sclafani et al. 2018).

Pairwise phylogenetic distances between each taxon in the phylogeny were calculated using the 'cophenetic.phylo' function in the ape package (Paradis and Schliep 2018) of R (R Core Team 2018). This function calculates the distance between tips of the tree by measuring the branch length between them (see Figure 2A for a visual depiction
of how this works). Branch lengths were calculated using basic, minimum branch length (mbl), and equal time calibrations. The basic time calibration pulls the origin of groups back to the earliest possible time, whereas the mbl uses the latest possible time. The equal length method provides an estimate in the middle. To minimize biases introduced by the time calibration method selected, results from the equal calibration are reported here (see Appendix B for results from basic and mbl). Each distance was classified in terms of whether the measurements were within-group (pairs that are in the same evolutionary group) or between-group (pairs that are in different evolutionary groups).

Methods were repeated for a smaller tree of species in the superfamily Strophomenoidea that contains 50 exemplar taxa from 48 genera/subgenera (Congreve et al. 2019). Congreve et al. (2019) identified six groups within this superfamily: a Strophomeninae clade, a Glyptomenidae clade, a recovery clade containing species that originated after the Late Ordovician mass extinction, a Furcitellinae clade, a Rafinesquinidae clade, and a basal grade (figure 1 in Congreve et al. 2019). Since the PDED hypothesis assumes that a tree captures true speciation events, this finer scale tree can serve as a test of phylogenetic scale on the strength of this relationship. If the PDED is supported, the correlation between phylogenetic distance and ecological difference should be stronger for the tree that represents finer-scale evolutionary relationships.

Morphological data

Morphological data are from a morphospace of discrete phylogenetic character data (Congreve et al. 2015; Sclafani et al. 2018; Congreve et al. 2019). The morphospace was generated using Principal Coordinates Analysis (PCO) following the methods of Hughes et al. (2013). Each genus was thus assigned PCO scores, or coordinates that denote their position in morphospace. The pairwise distance in morphospace was calculated as the Euclidean distance between each point (Figure 2B) and served as a measurement of morphological difference between each genus. This analysis was performed on both trees.

Ecological data

Environmental affinities are used here as a metric for ecology. This assessment of ecology is based on lithologic and locality data that co-occur with fossils. Data available for fossil taxa include depositional environment relative to shoreline (a proxy for all of the variables that covary with water depth), substrate type, and latitude. Previous studies indicate that water depth and substrate are the most important for explaining regional genus distributions (Holland and Patzkowsky 2004, 2007, 2009), whereas environmental factors that vary with latitude such as, temperature, productivity, and ocean currents, control distribution at the global scale (Roy et al. 2000; Jablonski et al. 2006; Valentine et al. 2008; Powell 2009; Jablonski et al. 2013). These proxies can be evaluated in the geologic record and reflect a myriad of co-occurring physical and chemical factors that drive taxonomic distribution in the modern oceans. Combined, they are an approximation of the fundamental niche, essentially the abiotic factors that these organisms require for survival.

Affinity calculations use the following equation, which is based on previous studies (Simpson and Harnik 2009; Hopkins 2014) but modified to indicate the strength of environmental preference. This calculation relies on environmental data (water depth,

substrate, paleolatitude) that are associated with taxonomic occurrences from the Paleobiology Database.

$$A_x = \frac{\sum T_x}{\sum T_x + \sum T_y} - \frac{\sum O_x}{\sum O_x + \sum O_y}$$

Where x and y represent each side of an environmental binary (e.g., deep/shallow water environments, carbonate/siliciclastic substrate, tropical/extratropical latitudes). For example, if x is deep water, then this equation would calculate whether the proportion of deep-water occurrences of the taxon of interest (T) is greater than, equal to, or less than the proportion of deep-water occurrences of all taxa in the data set (O). Using the proportion of occurrences is necessary to control for variation in sampling between genera and environments.

The resulting value is the strength of the taxon of interest's preference for those environments, or its affinity. If A_x is greater than zero, the taxon has more deep-water occurrences than expected within the data set, or an affinity for deep water. If A_x is less than zero, the taxon has fewer deep-water occurrences than expected within the data set, or an affinity for shallow water. If A_x equals zero, the taxon has the same number of deep-water occurrences as expected within the data set, or no affinity for deep or shallow water. This affinity calculation generates an environmental affinity gradient for the phylogeny and provides a relative assessment of how each genus was distributed across benthic environments. Taxa at either end of the gradient have a strong preference, while taxa in the middle have a weak or no preference.

Environmental data from the Paleobiology Database were vetted before being included. Any genus without environmental data was necessarily excluded. Additionally,

any genus with fewer than 15 occurrences was removed. Environmental data were culled according to the methods in Foote (2014), which used only the primary lithology field and removed anything that could not be assigned to either a carbonate or clastic category. Criteria for classification into this carbonate/clastic binary are outlined in Table 1 (based on Hopkins 2014). Pairwise distances were calculated between the locations of each taxon along this modeled environmental affinity gradient (Figure 2C).

Results

Environmental affinities

Environmental affinity calculations demonstrate that genera within Strophomenida have only a weak affinity for deep water and siliciclastic substrates. However, for both trees, over 60% of occurrences for the genera included in the analysis occurred in rocks classified as deep or carbonate, compared to just over 55% of all Ordovician to Devonian brachiopod occurrences in the Paleobiology Database (Table 2). A few highly abundant genera such as *Strophomena* and *Rafinesquina* inflated the occurrence percentages, but overall, the ratio of strophomenide occurrences in deepwater, carbonate settings does not differ substantially from the ratio of available rock. In contrast, genera from both trees have a moderate preference for extraropical latitudes (greater than 25 degrees). This is consistent with the percent occurrence of strophomenides in tropical latitudes (just over 60%) compared to almost 97% of all brachiopod occurrences (Table 2).

In summary, the genera included in this study have weak to no preference for deep-water, siliciclastic environments, but a moderate to strong preference for

extratropical latitudes. It is important to keep in mind that these analyses are standardized to the data set, occurrences for genera that demonstrate no affinity are actually distributed across the binary environmental variables in the same proportion as all brachiopods in the Paleobiology Database, which do tend to occur more often in deep-water, carbonate substrates at tropical latitudes. The affinity scores do not mean that strophomenides aren't found in those settings, rather that they are found at a frequency that differs from the average for brachiopods.

For the order-level phylogeny (Congreve et al. 2015; Figure 3A), genus water depth affinities range from -0.57 to 0.43 with a median of 0.03, suggesting most genera have a very weak preference for deep water environments. For substrate, genera affinities range from -0.56 to 0.43 with a median of -0.07, suggesting a very weak preference for siliciclastic substrates. The range for latitude is -0.97 to 0.03 with a median of -0.31, suggesting a moderate to strong affinity for extratropical latitudes. Additionally, since the proportion of strophomenide genera occurrences from tropical paleolatitudes is much lower than for all brachiopods, this order is much less tropical than expected.

Genera in the more detailed phylogeny of the recovery clade (Congreve et al. 2019; Figure 3B) tend to prefer shallower environments slightly more than the order as a whole. Depth affinities for this tree range from -0.57 to 0.43 with a median of -0.05. There is a weak preference for carbonate substrates, with a range of -0.5 to 0.44 and a median of 0.10. Many genera are found almost exclusively in carbonate settings. Finally, the generic preference for extratropical latitudes is similar to that of the order, with a range of -0.97 to 0.03 and median of -0.32.

PDED in the order-scale phylogeny

Phylogenetic distance is not correlated with environmental affinity distance for the order-scale phylogeny, but morphological distance is weakly correlated with phylogenetic distance (Figure 4, Table 3). The correlation is equally poor for all three of the environmental variables and all three time-calibration methods. Although some plots in Figure 4 visually appear like there might be a trend, no correlation explains more than 15% of the variation. For the environmental variables, no correlation explains more than 3% of the variation in the data. Given the large sample size (over 1000 pairwise comparisons), there is not a correlation between phylogenetic distance and morphological or ecological difference for strophomenide brachiopods.

PDED in the recovery clade phylogeny

Phylogenetic distance is also not correlated with environmental affinity distance for the Strophomenoidae phylogeny (Figure 5, Table 3). In fact, in some cases, the correlation is slightly negative. However, like with the order-scale phylogeny, the percent variance explained is very low at less than 8% for phylogenetic distance and morphological difference and less than 3% for correlations with ecological difference. Thus, the expected relationship between evolutionary relatedness and ecological traits does not improve for the finer-resolution recovery clade phylogeny. Again, sample size is large for these data (either above or just under 1000), which means that there is no correlation between phylogenetic distance and ecological difference.

Discussion

Results indicate that this group of strophomenide brachiopods shows no clear relationship between phylogenetic distance and ecological difference. This is perhaps expected when evaluating what the PDED hypothesis means in terms of evolutionary and ecological processes and when considering the spatial and temporal scale of the fossil record. However, it is important to also address the methodological caveats with these results.

One potential explanation for the lack of relationship between strophomenide phylogeny and ecology is the quality of environmental data in the Paleobiology Database. Of those data used here, the depositional environment data that form the water depth proxy are the most potentially problematic because this interpretation was historically absent from fossil occurrences. In contrast, substrate and latitude are fairly robust because a carbonate or siliciclastic substrate designation is inherent in rock type identification and the Paleobiology Database automatically calculates latitude based on collection locality and paleogeographic reconstructions. For the order-level tree, there were 4612 useable depth occurrences, 8034 substrate, and 8398 latitude. For the Strophomenoidea tree, the distribution of occurrence data was similar with 3260 useable depth data points, 5732 substrate, and 6049 latitude.

If the lack of relationship between phylogeny and ecology was due simply to data quality, we might expect an improvement with the variables that are likely to be more accurate. Since there is no improvement in the relationship for variables with more useable data points, we conclude that the environmental variables available are not important for explaining evolution within the examined phylogenies. However, the differences in affinities that do exist between strophomenide genera suggest some environmentally-related niche differentiation occurred along the marine shelf. This apparent disconnect between what drives spatial distribution and what drives evolution for this order is an avenue of future research.

Another potential explanation for the lack of PDED within these brachiopods is the coarse phylogenetic resolution of the study. That is, for each phylogeny, species included are exemplars for genera. For the family-level phylogeny (Congreve et al. 2015), only one exemplar genus was included for each family. Because the PDED rests on an assumption of competitive exclusion, to truly see its effect, a phylogeny would need to include true sister species, that is, the two species that are the product of a single speciation event. However, it is extremely difficult to identify exact speciation events at macroevolutionary time scales. Additionally, in the fossil record, some sister species might not have been successful enough or abundant enough to be preserved.

We included a finer resolution tree to address this concern because a lower taxonomic level should improve the PDED relationship. However, the PDED for the genus-level phylogeny was less supported that it was for the family-level phylogeny. This could mean that the nature by which ecological preferences scale up with phylogenetic relatedness are more complicated that expected. Further testing of the assumptions of the PDED for modern groups is necessary to understand how it scales with evolutionary relatedness. However, if scaling does blur the PDED beyond what is recognizable, then we would never expect to see a correlation between phylogenetic distance and ecological difference for fossil taxa. Despite these caveats, we argue that the lack of PDED for Strophomenida highlights the need for further research into the conditions under which evolutionary history and ecological preference are correlated throughout geologic time. Additional studies quantifying the parameters of this model for other fossil groups are needed. Below we outline two possible explanations that we feel are particularly important for Strophomenida and which we hope will fuel larger research efforts to understand the relationship between evolution and ecology in the fossil record.

The evolution of ecologies during radiations

The order Strophomenida was affected by two radiations (during the Middle Ordovician and during the recovery from the Late Ordovician mass extinction). Lineage diversification is mostly restricted to these two time intervals. It is possible that morphological and ecological experimentation during times of rapid evolution results in more disparity that would be expected for closely related species under the PDED. This is because once a new clade originates, rates of diversification are rapid as new species evolve to fill available adaptive space (Van Valen 1985; Sepkoski 1991; Patzkowsky 1995; Jablonski 2005). If a clade experiencing a radiation is more morphologically plastic, as some suggest, (Erwin 2007, 2015; Wood and Erwin 2017), members of the clade might demonstrate more convergence and/or a less clear connection between any type of selective pressures.

There remain numerous questions in both paleo and modern biology about how much of an organism's ecology is controlled by evolutionary history, i.e., constrained by evolution, and how much is the result of adaptation to changing environments, i.e., ecophenotypically plastic (Wood and Erwin 2017). Many of these questions are fundamental to understanding the adaptive potential of organisms during times of environmental crisis. The results of this study do not provide clear direction to answering this question for strophomenides. However, they do provide a more concrete picture of the complexity involved in untangling the effects of evolution and ecology on a radiating clade. More work is needed on potentially convergent and constrained strophomenide morphologies to evaluate how these characters vary across this radiation interval and how that compares to background morphological change. More broadly, we see the need for research on whether there are any emergent patterns that can explain convergence, i.e., is it more likely for certain clades, in certain environments, or under certain evolutionary rates.

Metacommunity theory and hierarchical scaling in paleoecology

Many ecologists (e.g. Darwin 1859) and some paleobiologists cite incomplete sampling as an explanation for a lack of support for modern ecological hypotheses in the fossil record. This has historically created a barrier to communication between these disciplines. There are certainly time intervals and geographic regions that are undersampled. While, targeted sampling efforts can help fill some of the gaps, they are unlikely to provide support for microecological theories. Because of time averaging, the fossil record preserves biological data at a fundamentally larger temporal and spatial scale than that which is observable in modern ecological communities (e.g., Kidwell 2002). Fossil assemblages represent the regional species pool quite well, but rarely preserve local associations. In many cases, it is not that the data have not been sampled, it is that the data, as expected in modern ecology, do not exist. This does not mean fossil data are not useful, but that they are best suited for different types of analyses.

The inherent difference in the scale of the fossil record means that evolutionary trees are pruned and that ecological communities do not include many short-lived and rare-taxa (Figure 6). If they were preserved and sampled, these taxa could follow hypotheses, such as the PDED, that are rooted in small spatial and short temporal scales. However, for much of the fossil record, macroevolutionary and macroecological scales are more appropriate. Essentially, instead of concluding that the PDED is not supported by this data set, we conclude that the PDED is not the best way to test for the evolution of ecological similarity in this data set.

Similarly, modern studies conducted at macroecological scales also tend to not support the PDED (Cadotte et al. 2017). Consistent with the compromise for the Red Queen and Court Jester hypotheses (Benton 2009), scale affects whether biotic or abiotic factors primarily drive evolution. It is thus necessary to consider how processes scale through the dual hierarchy theory (Congreve et al. 2018 and references therein).

This scale hierarchy highlights a fundamental difference between paleoecology and modern ecology and, yet, a need for both disciplines to inform each other. Understanding the processes driving biodiversity under these two very different regimes requires an understanding of the differences in the type of data available to each discipline and an acceptance of the importance of spatial and temporal scaling. Ultimately, assessments of ecological communities in the fossil record should center on macroecology and neutral theory, both of which are connected to metacommunity theory. And yet, none of this discounts the observations at small scales that support niche-based assembly. It simply lends support to arguments for the combined effect of both neutral and niche processes of community assembly and highlights the importance of spatial and temporal scale in averaging out ecological processes to only those of great enough magnitude to be preserved. Perhaps neutral dynamics dominate at the metacommunity scale, and niche dynamics can only be observed at much smaller spatial and temporal scales. This would explain why there is no detectible PDED relationship for strophomenide brachiopods. Moving forward, it is important to focus research efforts on understanding how ecological and evolutionary processes scale up so that we can better explain biodiversity patterns in the fossil record and make predictions for the present biodiversity crisis.

Conclusions

The results of this analysis do not support the PDED for strophomenide brachiopods. We think this is indicative of a fundamental difference in the ecological and evolutionary processes observable with fossil data as compared to that observable in the modern. The fossil record preserves organisms at the metacommunity scale, which is governed by assembly rules that are more neutral. Furthermore, our interpretation is not intended to throw support behind one side of the neutral-niche debate. Rather, we argue that both processes are important, albeit at different scales. We encourage an emphasis on untangling both the conditions under which each of these theories are supported and the nature by which communities scale from the local to the regional species pool.

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Figure **2-1**: Expected phylogenetic distance, ecological difference relationship. Under the predictions of the PDED, phylogenetic distance should be correlated with ecological difference. If species that are distantly related are ecologically similar, they would represent ecological convergence and/or niche conservatism. In contrast, if species that are closely related are ecologically different, they would represent high ecological plasticity such as what might be expected during an evolutionary radiation.



Figure **2-2**: Pairwise distance calculations. This is an artistic representation of the methods used to calculate pairwise distances. A) Phylogenetic distance was calculated as branch length between each pair of tips on the tree. B) Morphological distance was calculated as Euclidean distance between each pair of points in morphospace. C) Ecological distance was calculated as distance between each pair of points along the binary environmental variables.

Table 2-1: Scheme for categorizing environmental variables. This scheme was applied to brachiopod data downloaded from the Paleobiology Database. Substrate names are from the "lithology1" field. Water depth names are from the "environment" field. Latitude is from the "paleolat" field. Classification into these binary groups is based on the classification scheme used in Hopkins (2014).

Substrate	Carbonate	"limestone", "carbonate", "reef rocks", bafflestone, bindstone, dolomite, framestone, grainstone, lime mudstone, packstone, rudstone, floatstone, wackestone		
	Siliciclastic	"shale", "siliciclastic", claystone, conglomerate, mudstone, phyllite, quartzite, sandstone, siltstone, slate		
Water depth	Deep	basinal (carbonate), basinal (siliceous), basinal (siliciclastic), deep-water indet., deep subtidal indet., deep subtidal ramp, deep subtidal shelf, offshore, offshore indet., offshore shelf, slope, submarine fan, offshore ramp, basin reef, slope/ramp reef		
	Shallow	coastal indet., delta front, delta plain, deltaic indet., estuary/bay, foreshore, interdistributary bay, lagoonal, lagoonal/restricted, shallow subtidal, marginal marine indet., open shallow subtidal, fluvial-deltaic indet., paralic indet., peritidal, prodelta, sand shoal, shallow subtidal indet., shoreface, transition zone/lower shoreface, intrashelf/intraplatform reef, reef, buildup or bioherm, perireef or subreef, platform/shelf-margin reef		
Latitude	Tropical	Paleolatitude < 30		
	Extratropical	Paleolatitude > 30		

Table **2-2**: Strophomenida environmental preferences. For both trees, the majority of genus occurrences were in rocks that were classified as deep, carbonate, and tropical, indicating a strong preference for these environments.

	Total	Order-level tree	Strophomenoidea tree	
	brachiopod	(Congreve et al. 2015)	(Congreve et al. 2019)	
	occurrences			
Deep occurrences	57.1%	62.7 %	62.1 %	
Carbonate	56.3%	63.4 %	69.0 %	
occurrences				
Tropical	96.9 %	62.9 %	64.0 %	
occurrences				



Figure **2-3**: Environmental affinities. Results of the calculation of environmental affinity for each genus in the order-level tree (A) and in the Strophomenoidea tree (B). The line inside the box is the median, the edges are the first quartile, the whiskers mark the extremes. Vertical offset of points within each box plot is just to improve visualization of the data and has no scientific meaning.



Figure 2-4: Pairwise distances for order-level tree. Phylogenetic distance is plotted on a log₁₀ scale. The equal time calibration method is shown here. Points are color coded based on evolutionary group membership of taxa in the pairwise comparison. Purple = both taxa are in the Plectambonitoid grade. Teal = both taxa are in the Ordovician Strophomenoid clade. Yellow = both taxa are in the Silurian/Devonian Strophomenoid clade. Grey = taxa are in different groups.



Figure 2-5: Pairwise distances for Strophomenoidea tree. Phylogenetic distance is plotted on a log_{10} scale. The equal time calibration method is shown here. Points are color coded based on evolutionary group membership of taxa in the pairwise comparison. Yellow = both taxa are in the Furcitellidae clade. Green = both taxa are in the Strophomenidae clade, Glyptomenidae clade, or recovery clade; combined because groups are too small to represent individually. Purple = both taxa are in the Rafinesquinidae clade. Grey = taxa are in different groups.

Table 2-3: Pearson correlation statistics. Values are for a correlation between phylogenetic distance and each variable listed. Calculations were made for both trees and all time calibration methods. Although many values are technically significant (p value < 0.05), note: the percent variance explained is less than 15% for morphospace correlations and less than 3% for all environmental variables and degrees of freedom (reflects sample size) is very large.

		Pearson's product-moment correlation (r)	R ²	variance explained (%)	p value	Degrees of freedom (df)		
Order-level tree								
Basic	Morphospace	0.226	0.0511	5.11	1.25E-14	1037		
	Water depth	0.0847	7.17E-03	0.717	6.32E-03	1126		
	Substrate	0.124	0.0154	1.54	2.84E-05	1130		
	Latitude	-0.0117	1.37E-04	0.0137	0.693	1130		
		0.000	0.0400	(1273		
MBL	Morphospace	0.222	0.0499	4.93	1.01E-15	1174		
	Water depth	0.138	0.0190	1.90	2.07E-06	11/4		
	Substrate	0.141	0.0199	1.99	4.71E-07	1273		
	Latitude	-0.0274	7.51E-04	0.0751	0.329	1273		
Equal	Morphospace	0.35	0.123	12.3	2.20E-16	12/3		
	Water depth	0.0997	9.94E-03	0.994	6.19E-03	1174		
	Substrate	0.167	0.0279	2.79	1.80E-09	1273		
	Latitude	-0.0257	6.60E-04	0.0660	0.360	1273		
Strophomenoidea tree								
Basic	Morphospace	0.247	0.0610	6.10	1.91E-14	929		
	Water depth	-0.0667	4.45E-03	0.445	0.0528	842		
	Substrate	0.0335	1.12E-03	0.112	0.307	929		
	Latitude	-0.0927	8.59E-03	0.859	4.65E-03	929		
	· · · · · · · · · · · · · · · · · · ·							
MBL	Morphospace	0.277	0.0767	7.67	2.20E-16	988		
	Water depth	-0.0383	1.47E-03	0.147	0.25	901		
	Substrate	0.06	3.6E-03	0.36	0.059	988		
	Latitude	-0.0911	8.30E-03	0.830	4.13E-03	988		
Equal	Morphospace	0.162	0.0262	2.62	3.04E-07	988		
	Water depth	-0.0375	1.41E-03	0.141	0.26	901		
	Substrate	0.0377	1.42E-03	0.142	0.236	988		
	Latitude	-0.119	0.0142	1.42	1.68E-04	988		



Figure **2-6**: The effect of time averaging on fossil phylogenies. Taphonomic processes that time average the fossil record result in a phylogeny that does not preserve all of the evolutionary experimentation that might have occurred in local communities over short time scales. Instead, the phylogeny contains only those species that persisted long enough and at large enough abundance to be preserved. This fossil phylogeny reflects the larger species pool and allows for macroevolutionary and metacommunity analyses. However, species are more different than expected under competitive exclusion, which makes it unlikely to support the PDED.

Chapter 3

Ecological selectivity of Strophomenida (Brachiopoda) during and after the Late Ordovician mass extinction

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J.A. Sclafani did data collection and analysis and wrote the manuscript. B. Roselle, C. Gazze, and A. Bourne helped with method development and data collection for their senior theses. M. Christie contributed to development of the project. C.R. Congreve, and M.E. Patzkowsky advised the project and helped edit the manuscript.

Abstract

Quantifying three-dimensional shape is important to understanding the evolution and ecology of fossil organisms. Morphological characters serve as the basis for phylogenetic analyses and can provide clues to an organism's ecological preference. However, different suites of shape data are important for these related, but quite distinct questions. The characters used for phylogenetic analyses, where an effort is made to exclude any feature that might be convergent, are often not the most ecologically informative. In contrast, assessing whether morphology correlates with an environmental gradient relies on robust, field-identifiable features and is unlikely to capture any taxonomically important features that are only preserved on a handful of museum specimens.

The differences between ecologically- and phylogenetically- useful morphological data are especially stark for brachiopods. These benthic organisms sit closed on the sediment-water interface, only opening their valves occasionally to feed. This suggests that for the majority of a brachiopod individual's life, the exterior of the valve predominantly interacts with the abiotic environment. However, subtle changes of many external features (e.g., ribbing, convexity, valve shape) are difficult to include in phylogenetic analyses because they continuously grade into new states. As such, phylogenies tend to focus primarily on discrete structures such as muscle attachment structures and ridges on the valve interior.

In our previous work, we identified a morphological bottleneck of strophomenide brachiopods during the recovery from the Late Ordovician mass extinction. This bottleneck coincides with a reduction in phylogenetic diversity; only one clade of Strophomenida diversifies post extinction. To explore whether this pattern reflects a change in ecological preference, we used the photogrammetry method Structure-from-Motion to perform a morphometrics analysis of external shell features of five genera from the order Strophomenida. Unlike our previous phylogenetic-based study, these results do not demonstrate a bottleneck of morphology, but instead suggest only a slight constriction of morphospace. However, external shape-based characters do reflect an environmental gradient, which shortens after the extinction. These patterns highlight the complexities of the relationship between morphology, ecology, and phylogeny and emphasize the importance of addressing biotic change across mass extinctions from multiple perspectives.

Introduction

Morphology of the brachiopod order Strophomenida was non-randomly restricted during the recovery from the Late Ordovician mass extinction (Sclafani et al. 2018). Species that evolved in the Silurian occupied a significantly smaller region of morphospace and belonged to a single clade. Attempting to correlate this morphological bottleneck with environmental parameters yielded no relationship (Chapter 2 of this dissertation). In this previous work, we discussed how differences in temporal and spatial scale between modern ecology and the fossil record could lead to difficulty identifying clear environmental drivers of evolutionary change. However, it is also possible that there are differences between morphological patterns described by the most phylogenetically useful characters and morphological patterns described by the most ecologically meaningful characters (Heatherington et al. 2015). Here we use 3D morphometrics to produce a morphospace of Strophomenida from continuous shape characters and employ the principles of phylogenetic paleoecology to better understand the evolution of this order. Comparing results from this analysis to previous treatments of the same data will allow us to identify whether there are any differences in interpretable evolutionary and ecological patterns between continuous and discrete morphological characters. Any significant differences would signal a need to bridge the methodological gap between continuous and discrete data in order to best understand how evolution and ecology connect to an organism's morphology. By exploring the limits of these two methods, we can develop a more complete understanding of the recovery of morphological diversity after the Late Ordovician mass extinction. Although we focus on the Late Ordovician mass extinction, our hope is that this study will demonstrate the importance of employing both paleoecological and phylogenetic perspectives for understanding mass extinctions and other intervals of significant biotic change.

Background

Phylogenetic paleoecology at mass extinctions

Phylogenetic paleoecology draws from disparate disciplines and approaches to study macroevolution and macroecology in deep time (Lamsdell et al. 2017). In the context of mass extinctions, this perspective offers a more comprehensive assessment of how phylogenetic and ecological diversity reflects taxonomic loss by quantifying the amount of evolutionary history and ecological variability lost. The loss of phylogenetic and ecologic diversity is often disconnected from taxonomic loss (Nee and May 1997; Erwin 2001; McGhee et al. 2004, 2012, 2013; Christie et al. 2013), but it is the loss of phylogenetic and ecologic diversity, more so than species richness, that has the greatest effects on the recovery potential of clades and ecological communities.

In practice, one way in which a phylogenetic paleoecology study can be accomplished is through a detailed analysis of morphology as it pertains to both ecology and evolution. Because fossil species are defined by the morphological species concept, their fossil phylogenetic trees are based on discrete morphological characters. This morphological data can be combined with environmental occurrence data to identify whether morphology correlates with environmental preference. However, implicit to using phylogenetic data for this sort of paleoecological study is the assumption that the morphological characters that are most phylogenetically informative are also the most ecologically informative. This is problematic because convergent morphologies, which could be most closely tied to environmental preference, are considered evolutionary noise (Hennig 1966, Patterson 1982, Wiley 2008). As such, attempts are often made to exclude possibly convergent characters from phylogenetic analyses (Patterson 1982).

Additionally, phylogenetic methods use discrete characters. This means that subtle variations in shell morphology like ribbing, globosity, hinge length, etc., which are potentially important brachiopod ecological adaptations, might not be fully captured. For example, the amount of shell curvature can vary for resupinate brachiopods, where the pedicle valve is nestled inside the brachial valve, but in a phylogenetic analysis, this convexity pattern is coded as a single trait for all species that display it (Congreve et al. 2015). This categorical description of morphology can lump brachiopods with meaningful continuous variation as the same, ignoring potential ecologically important
nuances. This means that, especially for many groups of organisms, discrete character data might not always capture the complete ecological signal.

The question of whether the characters that are most important to ecological function are the same as those that are most acted upon by evolution is fundamental to evolutionary ecology but is difficult to assess and rarely explored in the fossil record. For evolutionary radiation after mass extinctions, understanding this question is important for explaining taxonomic origination and diversity partitioning. Ecological restructuring is expected following a mass extinction (Jablonski 2000), implying that recovery intervals should represent the clearest examples of ecological change in the fossil record. However, recovery intervals are also times of evolutionary experimentation, where clade morphology is more plastic (Erwin 2017). This means that distant taxonomic relations might be more morphologically or ecologically similar than their phylogenetic distance would predict (chapter 2). Additionally, closely related members of a clade might be more different than expected. These patterns can complicate the assessment of the impact of a mass extinction on ecology if only phylogenetic data are used.

We use the principles of "tree-thinking" inherent to phylogenetic paleoecology (Lamsdell et al. 2017) to frame our approach to quantifying morphology during the Late Ordovician mass extinction. This means that we are working within a previously established phylogenetic framework (Congreve et al. 2015), which has informed both the genera selected for this study and our approach to understanding morphological change at the extinction event. Additionally, the motivation for this study is a desire to explore how interpretations from phylogenetic approaches compare to interpretations from paleoecological approaches. That is, we aim to demonstrate that it is not enough to think only about trees or only about paleoecology, instead, we must incorporate both to understand changes in biodiversity at mass extinctions from multiple angles.

To better understand evolution within the order Strophomenida at the Late Ordovician mass extinction, we quantify external shell morphology and compare these continuous characters with the discrete phylogenetic characters to determine whether they show a random extinction and bottleneck during the recovery similar to that observed in Sclafani et al. (2018).

If there is selectivity during extinction and recovery, it can reflect two endmember explanations; change in diversity driven by either purely evolutionary or purely ecological processes. A purely evolutionary change in diversity might reflect contingent historical traits that appear ecologically random (e.g., Hunt 2007, Novack-Gottshall and Lanier 2008, Sookias et al. 2012). In contrast, a purely ecological change would reflect external selective pressures that drive an adaptive response (e.g., Simpson 1944, Wood and Erwin 2017). Like many end-member dichotomies, it is likely that both evolutionary constraints and ecological pressures are generally responsible for evolutionary radiations, but more research on this topic is needed to determine how both contribute (Gavrilets and Losos 2009).

Paleozoic articulate brachiopod diversity and functional morphology

As a group, articulate brachiopods were abundant, geographically ubiquitous, and dominant in benthic ecosystems throughout the post-Cambrian Paleozoic. At lower taxonomic levels, there is considerable spatial and temporal turnover in diversity (e.g., Harper and Rong 1995, Patzkowsky 1995, Carlson 2016, Congreve et al 2019) such that brachiopods were incredibly speciose. However, despite their abundance and diversity throughout the Paleozoic, the evolutionary and ecological mechanisms that drove articulate brachiopod diversification have been elusive. Aside from a handful of studies (e.g., Lee 1978, Alexander 2001, Butts 2005, Tyler and Leighton 2011, Forcino et al. 2017, He et al. 2017, Topper et al. 2017, Lee et al. 2018), there is limited quantified data about which environmental conditions were most favorable for which brachiopod morphologies.

Additionally, differences in the ecological function of brachiopod groups is difficult to infer because they have extremely low metabolic requirements (Thayer 1981) and contain an incredibly small amount of soft tissue (Carlson 2016 and references therein, Harper et al 2017). These bizarre aspects of their anatomy have spurred debates over whether predators in the Paleozoic oceans would have eaten them (Bruton 1966, Carriker and Yochelson 1968, Buehler 1969, Richards and Shabica 1969, Sheehan and Lespérance 1978, Thayer 1981, Alexander 1981, 1986, Bambach 1993). Brachiopods were globally distributed, although at lower taxonomic levels, there were regional constraints on geographic range. Spatial variability in species occurrences suggests some biological basis for difference in ecological preference. More work is necessary to understand the degree to which these patterns vary with taxonomic hierarchy and the degree to which this represents purely ecological adaptation or a more enigmatic nonselective evolutionary process (e.g., Gould and Lewontin 1979, Anderson and Allmon 2018).

Complicating the potential for generalizable trends is the disconnect between those characters that are used to classify brachiopods at higher taxonomic scales, those used in phylogenetic analyses, and those that have been observed to vary the most across environmental gradients. The lophophore, which allows the animal to feed and helps with respiration (Carlson 2016), and the pedicle, which relates to substrate attachment (Harper et al. 2017), are used to define class-level taxonomic groups (Williams et al. 2000). These anatomical features relate to shell characteristics such as hinge shape, hinge length, and globosity. Subordinal phylogenetic analyses tend to focus on mostly internal characters related to muscle and lophophore attachment (e.g., Williams et al. 2000, Congreve et al. 2015, Congreve et al. 2019). Field-based observations of occurrences highlight external shell features such as globosity, ribbing, and overall shape as characters that co-vary with environments of deposition (e.g., Cooper 1937, Patzkowsky 1995, Butts 2005, Topper et al. 2017, Lee et al. 2018). Many of these external features are related to phylogenetically meaningful anatomy, but quantifying the variation of these characters usually requires continuous characters, so they are, therefore, difficult to incorporate into phylogenetic analyses.

The degree to which brachiopod morphology varies with taxonomic scale, uncertainty about their role in the ecosystem, and the disconnect between phylogenetic specimen-based and paleoecological field-based observations highlight the complexity of working with a group that is almost completely extinct. These difficulties inherent to brachiopods also highlight the importance of employing a phylogenetic paleoecological approach to understand brachiopod spatial and temporal distribution. Phylogenetic trees can root ecological patterns in evolutionary history and facilitate more concrete interpretations about extinction and origination.

A model for brachiopod ecology

We focus on external shell morphology because it is the most easily preserved and it is the most clearly connected to sedimentologic variation. Because fossils are rarely transported outside of their original habitat (Kidwell and Bosence 1991), depositional environment interpretations of the strata where brachiopod fossils were found can serve as a proxy for the benthic environment where the animal lived. In particular, relative water depth, substrate type, and paleolatitude are well-preserved in sedimentological data and reflect co-varying physical, chemical and biological oceanic processes (e.g., light, salinity, temperature, bioturbation). Combined with taxonomic occurrence data, these paleoenvironmental parameters can be used to define the ecological preferences of extinct brachiopods (Holland and Patzkowsky 2004). The addition of a geometric assessment of shape to and occurrence-based ecological preference analysis allows us to quantify the degree of ecomorphology within this group. With this information, we can better understand if there was an ecological reason for why brachiopods within the order Strophomenida differed in their survival across the Late Ordovician mass extinction.

Geometric morphometrics

To quantify external brachiopod shape, we use 3D geometric morphometrics, or the statistical analysis of form based on Cartesian landmark coordinates (Mitteroecker and Gunz 2009). This numerical technique digitizes a shell into a series of landmarks, or homologous points that can be found on each specimen. By placing each specimen in the same coordinate plane, the change in position of each landmark between each specimen can be visualized and calculated. This results in a quantification of the amount of morphological change between specimens and the ability to identify the features that change the most.

This sort of landmark-based geometric morphometric analysis has been critical to building accurate, 3D models for biological shape analysis (Hassett and Lewis-Bale 2017). Over time, this method has become more widely accessible, inexpensive, and extremely user-friendly (Buser et al. 2017). Much of the improvement in morphometrics comes from biological anthropology and vertebrate paleontology, which require methods that can robustly quantify evolutionary and developmental morphologies (Slice 2007, Polly and MacLeod 2008). The study organisms of these fields are well suited to landmark-based approaches because vertebrate skeletons contain numerous homologous, easily identifiable features.

To apply geometric morphometrics to invertebrate shells, which contain far fewer homologous points, the method has been modified slightly such that semi-landmarks, or points that are identifiable but not necessarily homologous, can be used for analysis (Webster and Sheets 2010). For example, a recent study that used 3D semi-landmarks to understand evolution of the sulcus and shell outline in the brachiopod genus *Fasiculatia* demonstrated that variability was highly influenced by environmental factors (Lee et al. 2018). This study is one of only a handful to apply geometric morphometrics to brachiopod shells, but it demonstrates the utility of the technique.

3D imaging techniques

Before recent technological advances, 3D objects could only be translated into 1D or 2D representations (Buser et al. 2017). While 2D representations provide decent

models, there is a degree of distortion within the results; this approach focuses on a limited set of linear distances, ratios, and angles, which negatively impact the representation of shape data (Slice 2007, Cardini 2014, Buser et al. 2017). In order to avoid distortion, 3D imaging techniques must be employed so that specimens can be digitized as 3D models. The use of 3D models is particularly important when analyzing brachiopods, which vary considerably in terms of the convexity of their external shells (Lee et al. 2018).

Despite the benefits of 3-D models, their construction often requires costly imagery techniques, such as computed tomography (CT), magnet resonance imaging (MRI) scanners, optical surface laser scanners, or reflex microscopes (Mitteroecker and Gunz 2009, Lee et al. 2018). Although CT and MRI scanners produce high resolution images, the time and cost involved with producing a scan limits their use for morphometrics in paleobiology, especially for small abundant organisms like brachiopods. Lower-cost surface scanners and microscopes produce scans of slightly lower resolution but do so at a much lower cost and over much less time. Studies comparing surface scanners with CT scans demonstrate that they contain sufficient morphological detail for analysis (Sholts et al. 2010, Fourie et al. 2011, Marcy et al. 2018). However, these scanning devices have a high initial cost and are, thus, not widely accessible. A more accessible method, 3D photogrammetry requires only a standard digital camera and computer. Studies on small mammals (Muñoz-Muñoz et al. 2016) and hominids (Katz and Friess 2014) demonstrate that photogrammetry provides images that are comparable to 3D scanners.

We've used the photogrammetry method Structure-from-Motion (SfM) to image brachiopod shells. This method creates a 3D model from overlapping 2D photographs taken at intervals around an object of interest (Westoby et al. 2012). A computer program such as Agisoft Photoscan aligns the photographs based on pixel matching to create a 3D point cloud and mesh. SfM has the potential to pick up millimeter-scale features and has been recently applied to vertebrate morphometrics (e.g, Hassett and Lewis-Bale 2016), ichnofossils (e.g., Falkingham et al. 2018) and invertebrate fossils (Sclafani et al., in prep). Here we use it to digitize Paleozoic brachiopods in order to analyze differences in shell morphologies across the Late Ordovician mass extinction and recovery.

Methods

Data collection

Strophomenide brachiopod specimens were selected from the Yale Peabody Museum of Natural History's Invertebrate Paleontology collection and included representatives from the following genera: *Strophomena, Sowerbyella, Leptaena, Rafinesquina,* and *Strophodonta.* These genera were included in the recent phylogenetic revisions of Strophomenida (Congreve et al. 2015, 2019) and include taxa that went extinct at (*Strophomena, Sowerbyella, Rafinesquina*), crossed (*Leptaena*), and originated after (*Strophodonta*) the Late Ordovician mass extinction. These particular genera were selected because they were well-represented enough in the collections to generate a statistically significant sample size. Particular emphasis was placed on choosing wellpreserved brachiopods with intact valves that were not obscured by sediment. These criteria were important for accurately digitizing overall shell shape. Representatives from all available species, time periods, and geographic locations for each genus were included. This yielded nearly 300 specimens from Laurentia, Baltica, and Avalonia ranging from the Late Ordovician to Early Devonian (see supplemental for a list of all specimens included and their associated data).

Photogrammetry procedure

To digitize shells, specimens were placed one at a time on a circular rotating platform with a 1x1 cm grid for scaling. This allowed for the dorsal and ventral valves to be individually photographed from all angles, which is necessary for accurate photo alignment. A white background and lights surrounded the platform to provide a neutral, shadow-free setting. We used an iPhone camera for photography because early tests indicated that the autofocus and image stabilization features of this camera provided the best pictures for model alignment, although later tests suggested any high-resolution smart phone camera will work.

In order to be consistent during photo taking, the platform was divided into equal increments, designated by blue lines spaced approximately 21 degrees apart along the outer rim. Photos were taken from at least two horizontal angles at each blue line, resulting in 30-40 photographs of each valve of each specimen. Flash was always used when taking photos, as it produced sharper images. If a photo was not sharp (meaning features such as the growth lines and hinge were unclear or blurry) the photo was retaken. Subtly blurry photos were the most common cause of misaligned pixels and models with holes, and, as such, when evaluating photo quality, any photo that seemed suspect was removed from the set and re-photographed before generating the 3D model.

Models were generated using the standard Agiosoft Photoscan workflow of aligning photographs and creating a dense cloud and mesh. The shell was scaled using the grid and then extracted from the background. The model was then exported as a .csv file that contained x, y, and z coordinates for each point in the cloud.

Morphometric analysis

Files containing point cloud data were exported from Agiosoft Photoscan and read into R (R Core Development team). Geometric morphometric analysis was done using the Geomorph package (Adams and Otárola-Castillo 2013). This package allows the user to select points designating the outline of the object, which we treated as landmarks and sliding semi-landmarks. We selected four points for each shell (Figure 1): the beak (a true landmark), the spot directly across from the beak on the commissure, and two points that make a line perpendicular to the beak line at the cardinal extremities that mark the hinge line. The program then populates the surface of the shell with 200 points that can be treated as semi-landmarks with (x,y,z) coordinates. Point selection is standardized by the program so that points are in the same relative anatomical position for each specimen. Next, these points were Procrustes transformed to remove the influence of size so that a Principal Components Analysis (PCA) could analyze shape. PCA ordination was done using the FactoMineR package (Le et al. 2008). Plotting the first and second ordination axes of the Procrustes-transformed points generated a morphospace of the five brachiopod genera. The external collection data and genus occurrence data from the Paleobiology Database were used to interpret genus occupation of morphospace.

Environmental preference and geologic range

Environmental preference for each genus was determined using the affinity calculation defined in chapter 2. Geologic range for each genus was determined using the stratigraphically calibrated phylogeny in chapter 1. For the purposes of this study, genera were categorized based on whether the genus went extinct at, survived, or originated after, the Late Ordovician mass extinction.

Results

Morphologic change along an environmental gradient

Genera within the order separate along PCA axes 1 and 2 (Figure 2). Specimens with low axis 1 scores have more triangularly inflated valves, whereas those with higher axis 1 scores are flatter and less triangular. Axis 2 reflects a morphological shift from rectangular (low scores) to square (high scores). *Sowerbyella*, the genus with the flattest and most rectangular shells plots in the lower right of morphospace. In contrast, *Rafinesquina*, which has the most square and inflated shells, plots in the upper left. *Leptaena*, which contains a lot of variation, separates along axis 1 according to the degree of geniculation (inflation concentrated at the commisseure). Many highly geniculated shells are slightly triangular and have lower axis 1 scores. Additionally, *Leptaena* species vary in rectangularity, and more rectangular shells have lower axis 2 scores.

The environmental water depth gradient (as defined in Chapter 2) is oblique to both PCA axes but corresponds most to the rectangular to square morphological gradient along axis 2. The environmental affinity for each genus in this Chapter is the same as that calculated in Chapter 2 (see Appendix C). *Sowerbyella* has the deepest affinity, *Rafinesquina* and *Strophomena* have the shallowest affinities, and *Leptaena* and *Strophodonta* have intermediate affinities. Specimens from genera that prefer deeper water environments (*Sowerbyella*) fall on the lower right side of morphospace and are more rectangular. Moving diagonally up and to the left in morphospace, specimens are more square-shaped and from genera that prefer progressively shallower environments, with *Rafinesquina* at the upper left extreme.

Morphologic change across the Late Ordovician mass extinction

Genera that go extinct during the Late Ordovician mass extinction are on the edges of morphospace, removing the most extreme flat, triangular, rectangular, and square shell shapes. Extinction constricts overall morphospace, as only *Leptaena* survives (Figure 3). *Leptaena* species vary morphologically, but reflect an average of the shape and convexity extremes. Later in the Silurian and into the Devonian, *Leptaena* re-occupy some of the space occupied during the Ordovician, with more variation and a centroid that is largely consistent with the Ordovician centroid. *Strophodonta*, the genus that originated during the Silurian recovery, occupies a region of morphospace that is consistent with *Leptaena* morphospace and similarly, does not alter the position of the centroid.

Discussion

Ecological morphology

Although the total taxonomic coverage of Strophomenida in this study is less than in Chapter 1 (Sclafani et al. 2018), contrasting these two data sets, we find that environmental preference from the continuous characters produces a stronger signal than that from the discrete data. Because of constraints on specimen availability, including all genera in this study of external characteristics was not possible. However, even with this limited scope, the patterns of morphospace occupation of these genera as represented by multiple specimens are different than their representation as a single point. In Chapter 1, morphospace occupation was tightly controlled by clade membership. That is, each defined evolutionary group occupied a distinct region of morphospace. In contrast, the continuous data presented in this Chapter show considerable overlap between the genus from the plectambonitoid grade (*Sowerbyella*), the genera from the Ordovician strophomenoid clade (*Rafinesquina, Strophomena, Leptaena*), and the genus from the Silurian/Devonian strophomenoid clade (*Strophodonta*). Even if it were possible to add in more genera, it is not likely that they will contribute to tighter clade grouping in morphospace because many discrete characters that are important to defining those clades are not included in this study.

The difference between morphospace occupation for discrete phylogenetic characters and continuous geometric characters demonstrates that these two methodologies convey different interpretable patterns. The external continuous characters reflect brachiopod distribution along an environmental gradient much better than the discrete characters. All of the environmental groups have generic preferences that span the environmental gradient. If the primary control on morphospace occupation from the discrete characters is phylogenetic, it makes sense that the environmental signal is best represented in morphospace occupation from the continuous characters. However, since there is considerable morphological variability along the gradient, it is likely that these morphologies are not solely the result of ecological selectivity to a given environment. Instead, it is more likely that they reflect both ecomorphology and contingent historical constraints because of their shared evolutionary histories (Congreve et al., 2018).

Evolutionary morphology

The morphologic change across the Late Ordovician mass extinction depicted here is not as strong as that from phylogenetic characters (Sclafani et al. 2018). In the previous study, strophomenide morphological variation was statistically significantly reduced during the recovery. This study confirms the reduction in morphological disparity, but with the continuous characters used here, the loss is not a bottleneck. Rather, lost morphologies are those associated with the extreme ends of the environmental gradient such that these ecological parameters are not selected for or against. This is consistent with a reduction in variability but adds an ecological interpretation, albeit a weak one, to what was previously observed. It is possible that the pattern would be stronger if all of the genera in the phylogeny were able to be represented in this continuous character analysis. However, those specimens from the originating clade that are included fall morphologically within the space occupied by genera that went extinct. This pattern is fundamentally different from our previous work where new taxa occupied a previously unoccupied region of morphospace, changing the centroid (sensu Korn et al. 2013).

Phylogenetic paleoecology of mass extinctions

Combined, these results suggest that the Late Ordovician mass extinction might have had more of an evolutionary effect on strophomenide brachiopods (e.g, Hunt 2007, Sookias et al 2012) as opposed to an environmentally adaptive response. That is, instead of a clear identifiable environmental selective pressure, those members of this order that were able to rediversify in the aftermath of the extinction likely did so because of rapid diversification rates within a particular clade, rather than purely because of external selective pressure. This could be an indicator that a random model of evolution (Brownian motion) or an Ornstein-Uhleneck (OU) model, random with a directional pull (Hansen 1997) best explains diversification in this order. Preliminary investigation suggests that ecological traits evolve through this order under an OU model (Congreve et al. in prep).

In terms of what this means about how the Late Ordovician mass extinction affected strophomenide brachiopods, it seems that selection during this event primarily acted upon the building blocks determined by evolutionary history. That is, morphological novelties arose in a lineage, as the lineages were undergoing evolutionary experimentation. These novelties were able to persist and evolve within the lineage under a seemingly random process until something changed, triggering adaptive selection for certain traits over others (Erwin 2015, Erwin 2017). This means that the morphological bottleneck that we observed in Sclafani et al. (2018) was driven primarily by withinlineage evolutionary dynamics rather than an external ecological forcing mechanism. That is, this non-random recovery pattern was caused by random chance as stochastic extinction processes acted upon evolutionary innovation.

The bottleneck signal reflects ecological selection acting upon existing diversity at some time after it originated and promoting the radiation of one clade at the expense of the others. Essentially, any ancestor that survived the Late Ordovician mass extinction could have given rise to the recovery clade, as diversity for the entire order was low crossing the boundary, i.e., there is nothing about the clade that eventually diversified that makes it seem like it would have been the one to do so. It just stochastically happened to, and any ecological selection must have happened after the initial radiation. This idea of an evolutionary lag has recently been addressed (Erwin 2015, 2017), with the suggestion that the timing of selection might not clearly link to an environmental forcing mechanism. If an evolutionary lag is responsible for the apparent randomness to the recovery of Strophomenida, we might expect a more clearly selection-driven morphological change to occur later in the order's evolutionary history. Untangling these complexities would require detailed phylogenies for younger members of this order and is potentially important for understanding the true impact of enigmatic extinction events such as the Late Ordovician. It is possible that this event's impact on diversity extends much further into the later Paleozoic than is typically examined in extinction and recovery studies.

Ultimately, the results of this study produced more questions than they answered. This is a meaningful complication to an evolutionary question that should be rather straightforward, and further work beyond this dissertation is needed to determine how Strophomenida evolutionarily responded to the Late Ordovician mass extinction. It is our hope that the combined interpretations of how strophomenide morphology reflected distribution along an environmental gradient and how morphological and ecological traits evolved will provide a unified phylogenetic paleoecological understanding of strophomenide brachiopods across the Late Ordovician mass extinction and recovery.

Conclusions

The disconnect in the amount and nature of morphologic change between discrete phylogenetic characters and continuous ecological traits highlights the complex interplay between ecology and evolution. During mass extinctions and recovery intervals, it is the combined effect of both that drives extinction and origination of species. Evolution and ecological change during these intervals can be assessed using morphology, and they should be studied in tandem to avoid potential pitfalls of focusing on only one type of morphological characters. Continuous morphological characters provide more information about environmental preferences, while discrete characters provide more information about evolutionary history. With these datasets combined, a more nuanced interpretation of mass extinctions and recoveries is possible. As such, collaborations between phylogeneticists and paleoecologists are critical for understanding of intervals of extreme biotic change.

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Figure 3-1: Point cloud of a specimen with the four user-defined starting points in red.



Figure **3-2**: Morphospace coded by environmental preference. Colors from purple to yellow reflect a water depth gradient from deep to shallow and a general increase in squareness and triangularity.



Figure **3-3**: Morphospace coded by survivorship across the Late Ordovician mass extinction. Red points are specimens from genera that went extinct. Blue are specimens from genera that survived. Yellow are specimens from genera that originated in the Silurian.

Conclusions

This work focused on developing a deeper understanding of the impacts of the Late Ordovician mass extinction, with a focus on the morphology of brachiopods in the order Strophomenida.

Results from Chapter 1 demonstrate the first evidence of a morphological bottleneck at this event, suggesting that the long-term impact on clade diversity might be greater then previously thought.

In Chapter 2, our attempt to identify an ecological explanation for this bottleneck yield no positive correlation between any of the environmental variables available in a dataset of fossil occurrences and evolutionary history. However, results did highlight the importance of temporal and spatial scaling in paleobiology and the need for more research into how local ecological dynamics scale up.

By approaching the question of ecological selectivity from a different angle in Chapter 3, we were able to identify a weak correlation between brachiopod external shell morphology and occurrence along an environmental gradient. However, this approach did not yield an evolutionary pattern as significant as the one in chapter 1. These results suggest that ecological selectivity might not have been a driver of morphological change in strophomenides during the Late Ordovician mass extinction. Instead, stochastic intraclade diversification dynamics are likely what drove evolutionary patterns of this group. The overall conclusion of this dissertation is that the dynamics governing Strophomenida diversification after the Late Ordovician mass extinction are complicated. This work is only a small step towards understanding strophomenide response to what has been described as a complicated event. Moving the field of paleobiology towards a more concrete understanding of the Late Ordovician mass extinction requires work beyond the scope of what is capable in a single dissertation. However, throughout the process of finalizing this body of work, I have identified the following areas of further research:

- How do the patterns observed for Strophomenida compare with the evolutionary response of other brachiopod orders? Generic diversity of Orthida declines similarly at the Late Ordovician mass extinction. An assessment of morphological, ecological, and phylogenetic change of orthids would serve as a good comparison and help answer whether the strophomenide response was unique or reflected generalizable processes.
- How do ecological traits evolve within a phylogenetic tree? Since the phylogenetic distribution of ecologies was not as expected, it would be worthwhile to take a modeling approach to understand how environmental preferences might have evolved into their current distribution. This would aid in understanding how Strophomenida evolved during their radiation and could provide insight into how ecological experimentation might be reflected in a phylogeny.

How do external morphological characters evolve on the Strophomenida tree? A similar modeling approach to quantify external shape evolution of strophomenide genera could provide a better ordinal-wide understanding of the relationship between shape and environmental preference. Chapter 3 was limited by the available specimens. An extension of this framework that involves digitally evolving the point clouds would help build a framework that could fill in the specimen gap.

Appendix A: Supplemental file published with Chapter 1

Supplemental material

This supplemental file includes two parts: 1) the complete detailed image of morphospace change through time, and 2) a discussion of results of our analyses without ancestral nodes.

Part 1: Complete morphospace through time (with ancestral nodes)

The panels in the Supplemental figures 1.1-1.5, below, illustrate the details of morphospace occupation for Strophomenida from the Floian to the Frasnian. This analysis includes ancestral nodes. This figure contains the same information as Figure 4 in the manuscript, but is presented here in an expanded format so that the details are easier to read.



Supplemental figure 1.1



Supplemental figure 1.3



Caption for supplemental figures 1.1-1.5:

Morphospace through time (including ancestral nodes). Each frame is the morphospace (PCO axes 1 and 2) of species and ancestral nodes extant during a particular stage. Black dots are species that originate during that stage. Gray dots are species (or nodes) that survived from the previous stage.

Part 2: Results of running analyses without ancestral nodes

To test whether inclusion of ancestral nodes in our analysis affected the results, we re-ran analyses on the data without nodes. Overall results are similar since the nodes fill in regions of morphospace without altering the overall shape. Without ancestors, there is still a shift in morphospace through time, suggesting post-extinction morphological constraint.

Plots below are the morphospace (PCO axes 1 and 2) for each stage (supplemental figures 2.1-2.5). The occupation of morphospace through time changes in the same manner as the morphospace including nodes.

Note: The pattern is reversed, but the overall patterns are essentially the same. Reversal of points in ordination space is simply a result of ordinating a different data set. The absolute PCO values cannot be compared between the analysis with nodes and the analysis without nodes. However, the fact that the Late Ordovician mass extinction and recovery corresponds to a change in occupation of morphospace is consistent. This combined with the fact that Silurian and Devonian species in this analysis occupy a different region of morphospace than Ordovician species (the same trend we see when including nodes) gives us confidence in including ancestral nodes in our assessment of morphological change across the Late Ordovician mass extinction and recovery.

The only difference is in the ability to interpret the recovery interval. There are only 3 taxa that originate in the Rhuddanian. This makes it impossible to determine if origination is

random with respect to morphology because there is not enough statistical power (supplemental

figure 3).






Caption for supplemental figures 2.1-2.5:

Morphospace through time without ancestral nodes. Plots below are the morphospace (PCO axes 1 and 2) for each stage. Black dots are species that originate during that stage, while gray dots are species that survived from the previous stage.



Supplemental figure 3: Bootstrap of data without ancestral nodes. The overall pattern here is similar to that of the data with ancestral nodes. However, since only 3 taxa originate in the Rhuddanian, the bootstrap analysis does not have enough statistical power to distinguish the distribution in morphospace of new taxa from a random expectation.



Appendix B: Results of mbl and basic from Chapter 2

Figure **B-1**: Pairwise distances for order-level tree. Phylogenetic distance is plotted on a log_{10} scale. The mbl time calibration method is shown here. Points are color coded based on evolutionary group membership of taxa in the pairwise comparison. Purple = both taxa are in the Plectambonitoid grade. Teal = both taxa are in the Ordovician Strophomenoid clade. Yellow = both taxa are in the Silurian/Devonian Strophomenoid clade. Grey = taxa are in different groups.



Figure **B-2**: Pairwise distances for order-level tree. Phylogenetic distance is plotted on a log_{10} scale. The basic time calibration method is shown here. Points are color coded based on evolutionary group membership of taxa in the pairwise comparison. Purple = both taxa are in the Plectambonitoid grade. Teal = both taxa are in the Ordovician Strophomenoid clade. Yellow = both taxa are in the Silurian/Devonian Strophomenoid clade. Grey = taxa are in different groups.



Figure **B-3**: Pairwise distances for Strophomenoidea tree. Phylogenetic distance is plotted on a log_{10} scale. The mbl time calibration method is shown here. Points are color coded based on evolutionary group membership of taxa in the pairwise comparison. Yellow = both taxa are in the Furcitellidae clade. Green = both taxa are in the Strophomenidae clade, Glyptomenidae clade, or recovery clade; combined because groups are too small to represent individually. Purple = both taxa are in the Rafinesquinidae clade. Grey = taxa are in different groups.



Figure **B-4**: Pairwise distances for Strophomenoidea tree. Phylogenetic distance is plotted on a log_{10} scale. The basic time calibration method is shown here. Points are color coded based on evolutionary group membership of taxa in the pairwise comparison. Yellow = both taxa are in the Furcitellidae clade. Green = both taxa are in the Strophomenidae clade, Glyptomenidae clade, or recovery clade; combined because groups are too small to represent individually. Purple = both taxa are in the Rafinesquinidae clade. Grey = taxa are in different groups.

Appendix C: Occurrence and affinity data

	1		Occur	rrences			l	Affinities	
	Deep	Shallow	Carbonate	Clastic	Tropic	Extratropic	Deep	Carbonate	Tropical
Billingsella	35	12	69	7	48	25	0.174	0.345	-0.311
Strophomena	469	266	837	317	786	549	0.067	0.162	-0.380
Actinomena	2	5	2	9	3	17	-0.285	-0.381	-0.819
Oepikina	50	30	146	37	180	12	0.054	0.235	-0.031
Bekkerina	0	2	2	1	0	32	-0.571	0.103	-0.969
Furcitella	4	1	11	7	16	3	0.229	0.048	-0.126
Rafinesquina	810	413	1135	259	1180	274	0.092	0.251	-0.157
Kjaerina	6	29	19	31	11	43	-0.399	-0.183	-0.765
Kjerulfina	6	9	8	15	6	14	-0.171	-0.215	-0.669
Colaptomena	19	63	53	81	55	61	-0.339	-0.168	-0.494
Kiaeromena	15	14	30	33	8	62	-0.053	-0.087	-0.854
Leptaena	373	172	713	521	549	700	0.114	0.015	-0.529
Glyptomena	5	16	24	28	48	2	-0.333	-0.102	-0.009
Platymena	6	6	5	11	15	1	-0.071	-0.251	-0.031
Christiania	73	30	78	96	102	56	0.138	-0.115	-0.323
Leptaenoidea	1	1	14	0	8	0	-0.071	0.437	0.031
Leptaenisca	20	1	21	4	11	26	0.382	0.277	-0.671
Amphistrophia	33	7	54	54	48	68	0.254	-0.063	-0.555
Mesodouvillina	38	57	117	38	134	32	-0.171	0.192	-0.161
Maoristrophia	0	1	1	16	20	13	-0.571	-0.504	-0.363
Douvillina	38	66	55	141	74	223	-0.205	-0.283	-0.719
Douvillinaria	0	1	3	4	1	4	-0.571	-0.135	-0.769
Protodouvillina	25	16	18	9	4	49	0.039	0.103	-0.893
Douvillinella	1	0	10	3	3	0	0.429	-0.313	0.031
Dicoelostrophia	6	7	7	36	43	0	-0.109	-0.400	0.031
Leptodontella	2	0	3	50	43	6	0.429	-0.230	-0.569
Leptodomena	2 60	22	72	160	4	165	0.429	0.250	-0.509
Deptostrophia	24	22	250	109	88	105	0.101	-0.204	-0.621
Brachyprion	54	- 22	239	43	200	41	0.037	0.294	-0.105
Parapholidostrophia	22	0	3	20	52	14	0.429	-0.109	-0.135
Snaieria	22	3	49	30	52	14	0.244	0.057	-0.181
Eostrophonella	0	2	8	19	9	16	-0.5/1	-0.267	-0.609
Plectambonites	4	1	33	10	37	11	0.229	0.204	-0.198
Isophragma	4	8	10	11	18	0	-0.237	-0.087	0.031
Ahtiella	0	7	15	13	3	12	-0.571	-0.028	-0.769
Leptella	19	19	39	17	44	11	-0.071	0.133	-0.169
Bimuria	17	12	21	33	41	9	0.016	-0.174	-0.149
Sowerbyites	8	18	36	6	42	1	-0.263	0.294	0.008
Leptellina	43	44	70	72	116	26	-0.076	-0.070	-0.152
Leptelloidea	6	6	15	10	8	14	-0.071	0.037	-0.605
Palaeostrophomena	10	4	7	16	13	10	0.144	-0.259	-0.403
Alwynella	1	0	5	1	0	3	0.429	0.270	-0.969
Leptestia	1	4	5	2	1	5	-0.371	0.151	-0.802
Sampo	26	3	30	35	4	51	0.326	-0.102	-0.896
Xenambonites	2	2	3	4	4	1	-0.071	-0.135	-0.169
Metambonites	1	0	0	1	1	0	0.429	-0.563	0.031
Aegiromena	24	17	4	60	18	37	0.015	-0.501	-0.641
Epelidoaegiria	0	0	1	6	7	0	NA	-0.420	0.031
Hesperomena	1	0	3	0	3	0	0.429	0.437	0.031
Anoptambonites	13	27	56	30	72	10	-0.246	0.088	-0.091
Sowerbyella	402	244	606	347	686	280	0.052	0.073	-0.258
Eochonetes	66	9	197	61	188	31	0.309	0.200	-0.110
Plectodonta	43	5	37	98	98	50	0.325	-0.289	-0.306
Ptychoglyptus	16	6	34	17	37	10	0.157	0.103	-0.181
Strophochonetes	26	9	27	52	43	33	0.172	-0.221	-0.403
Ctenochonetes	0	0	18	10	27	1	NA	0.080	-0.004

Table C-1. Occurrence and affinity data for order-level tree

	Occurrences					Affinities			
	Deep	Shallow	Carbonate	Clastic	Tropic	Extratropic	Deep	Carbonate	Tropical
Strophomena	469	266	837	317	786	549	0.067	0.162	-0.380
Actinomena	2	5	2	9	3	17	-0.285	-0.381	-0.819
Holtedahlina	22	34	84	10	55	42	-0.178	0.330	-0.402
Longvillia	1	8	6	9	5	19	-0.459	-0.163	-0.760
Leigerina	0	0	1	0	0	3	NA	0.437	-0.969
Pseudostrophomena	2	0	3	0	0	11	0.429	0.437	-0.969
Furcitella	4	1	11	7	16	3	0.229	0.048	-0.126
Bekkerina	0	2	2	1	0	32	-0.571	0.103	-0.969
Bellimurina	9	6	32	16	35	12	0.029	0.103	-0.224
Biparetis	1	0	2	7	4	5	0.429	-0.341	-0.524
Dactylogonia	12	14	76	24	87	7	-0.109	0.197	-0.043
Geniculina	2	1	11	0	12	18	0.096	0.437	-0.569
Katastrophomena	34	8	67	101	61	77	0.239	-0.164	-0.527
Chunanomena	0	0	0	0	2	0	NA	NA	0.031
Luhaia	5	1	11	7	6	17	0.263	0.048	-0.708
Molongcola	6	2	8	0	8	0	0.179	0.437	0.031
Murinella	3	9	7	8	9	3	-0.321	-0.097	-0.219
Pentlandina	26	5	50	14	44	11	0.268	0.218	-0.169
Oepikina	50	30	146	37	180	12	0.054	0.235	-0.031
Quondongia	3	4	7	0	6	0	-0.142	0.437	0.031
Crassoseptaria	0	0	1	0	0	3	NA	0.437	-0.969
Haljalanites	0	5	7	0	0	17	-0.571	0.437	-0.969
Colaptomena	19	63	53	81	55	61	-0.339	-0.168	-0.494
Kjerulfina	6	9	8	15	6	14	-0.171	-0.215	-0.669
Rafinesquina	810	413	1135	259	1180	274	0.092	0.251	-0.157
Megamyonia	16	1	69	47	115	2	0.371	0.032	0.014
Rhipidomena	9	3	44	1	44	1	0.179	0.415	0.009
Kjaerina	6	29	19	31	11	43	-0.399	-0.183	-0.765
Leptaena	373	172	713	521	549	700	0.114	0.015	-0.529
Hollardina	0	0	13	7	20	0	NA	0.087	0.031
Kiaeromena	15	14	30	33	8	62	-0.053	-0.087	-0.854
Leptaenopyxis	2	7	10	26	22	12	-0.348	-0.285	-0.322
Leptagonia	6	5	28	28	26	30	-0.025	-0.063	-0.504
Notoleptaena	0	0	1	14	4	10	NA	-0.497	-0.683
Glyptomena	5	16	24	28	48	2	-0.333	-0.102	-0.009
Paromalomena	8	12	14	21	33	9	-0.171	-0.163	-0.183
Platymena	6	6	5	11	15	1	-0.071	-0.251	-0.031
Leptaenoidea	1	1	14	0	8	0	-0.071	0.437	0.031
Qianomena	0	0	6	0	1	0	NA	0.437	0.031
Resupinsculpta	1	2	3	0	3	0	-0.237	0.437	0.031
Leptaenisca	20	1	21	4	11	26	0.382	0.277	-0.671
Mesodouvillina	38	57	117	38	134	32	-0.171	0.192	-0.161
Brachyprion	34	22	259	43	260	41	0.037	0.294	-0.105

Table C-2. Occurrence and affinity data for Strophomenoidea tree

Appendix D: Catalogue numbers of specimens used

Catalogue			
number	Species	Location	Age
221148	Stropheodonta inflexa	USA	Late Devonian
334030	Rafinesquina alternata ponderosa	USA	Late Ordovician
539605	Strophodonta sp.	USA	Middle Devonian
539606	Strophodonta sp.	USA	Middle Devonian
539607	Strophodonta sp.	USA	Middle Devonian
551061	Strophomena planoconvexa	USA	Late Ordovician
575932	Strophomena planumbona	USA	Late Ordovician
588668	Strophomena filitexta	USA	Late Ordovician
588672	Strophomena filitexta	USA	Late Ordovician
605466	Sowerbyella sp.	USA	Ordovician
7536	Rafinesquina alternata ponderosa	USA	Late Ordovician
S-2261	Leptaena rhomboidalis	USA	Late Ordovician
334031	Rafinesquina alternata ponderosa	USA	Late Ordovician
S-2265	Leptaena concinna	Sweden	Silurian
334037	Rafinesquina alternata	USA	Late Ordovician
334422	Sowerbyella sp.	USA	Middle Ordovician
38541	Rafinesquina alternata	USA	Ordovician
404340	Strophodonta sp.	USA	Early Devonian
505999	Strophomena sp.	USA	Late Ordovician
506003	Strophomena septata	USA	Middle Ordovician
524626	Sowerbyella sericea recedens	USA	Late Ordovician
524630	Sowerbyella sericea recedens	USA	Late Ordovician
221154	Stropheodonta navalis	USA	Late Devonian
524631	Sowerbyella sericea recedens	USA	Late Ordovician
524636	Sowerbyella sericea recedens	USA	Late Ordovician
524646	Sowerbyella clarksvillensis	USA	Late Ordovician
524653	Sowerbyella clarksvillensis	USA	Late Ordovician
524660	Sowerbyella clarksvillensis	USA	Late Ordovician
524663	Sowerbyella clarksvillensis	USA	Late Ordovician
525454	Sowerbyella sp.	USA	Late Ordovician
533470	Rafinesquina fracta	USA	Late Ordovician
539143	Strophomena planumbona		Late Ordovician
539146	Strophomena planumbona	USA	Late Ordovician

Table **D-1**. Yale Peabody Museum specimens included in Chapter 3 analysis.

300567	Strophomena rugosa	USA	Late Ordovician
539149	Strophomena planumbona	USA	Late Ordovician
539150	Strophomena incurvata	USA	Middle Ordovician
539151	Strophomena incurvata	USA	Middle Ordovician
539164	Strophomena planoconvexa	USA	Late Ordovician
539165	Strophomena planoconvexa	USA	Late Ordovician
539166	Strophomena planoconvexa	USA	Late Ordovician
539174	Strophomena incurvata	USA	Middle Ordovician
539214	Strophomena elongata	USA	Late Ordovician
539222	Strophomena elongata	USA	Late Ordovician
539224	Strophomena elongata	USA	Late Ordovician
300607	Strophomena rugosa	USA	Late Ordovician
539235	Strophomena incurvata	USA	Middle Ordovician
539244	Strophomena planumbona	USA	Late Ordovician
	subtenta?		
539256	Leptaena sp.	Sweden	Late Silurian
539257	Leptaena sp.	Sweden	Late Silurian
539258	Leptaena rhomboidalis	USA	Late Ordovician
539259	Leptaena rhomboidalis tenuistriata	USA	Late Ordovician
539263	Leptaena rhomboidalis tenuistriata	USA	Late Ordovician
539264	Leptaena rhomboidalis tenuistriata	USA	Late Ordovician
539265	Leptaena rhomboidalis tenuistriata	USA	Late Ordovician
539286	Leptaena rhomboidalis	USA	Early Devonian
300609	Strophomena rugosa	USA	Late Ordovician
539288	Leptaena rhomboidalis	USA	Early Devonian
539289	Leptaena rhomboidalis	USA	Early Devonian
539290	Leptaena rhomboidalis	USA	Early Devonian
539291	Leptaena rhomboidalis	Sweden	Late Silurian
539293	Leptaena sp.	USA	Early Devonian
539294	Leptaena sp.	USA	Early Devonian
539316	Leptaena rhomboidalis	Sweden	Early Silurian
539319	Leptaena rhomboidalis	Sweden	Middle Silurian
539321	Leptaena rhomboidalis	Sweden	Middle Silurian
300611	Strophomena rugosa	USA	Late Ordovician
539322	Leptaena rhomboidalis	Sweden	Middle Silurian
539325	Leptaena rhomboidalis	USA	Middle Silurian
539341	Leptaena rhomboidalis	Sweden	Silurian
539342	Leptaena rhomboidalis	Sweden	Silurian
539343	Leptaena rhomboidalis	Sweden	Silurian

539354	Leptaena rhomboidalis	USA	Early Devonian
539355	Leptaena rhomboidalis	USA	Early Devonian
539356	Leptaena rhomboidalis	USA	Early Devonian
539373	Leptaena sp.	USA	Late Ordovician
539374	Leptaena sp.	USA	Late Ordovician
300614	Strophomena rugosa	USA	Late Ordovician
539401	Leptaena rhomboidalis tenuistriata	USA	Late Ordovician
539410	Leptaena sp.	Sweden	Silurian
539411	Leptaena rhomboidalis	USA	Early Silurian
539412	Leptaena rhomboidalis	USA	Early Silurian
539426	Leptaena rhomboidalis	USA	Silurian
539427	Leptaena rhomboidalis	USA	Silurian
539428	Rafinesquina alternata	USA	Late Ordovician
539431	Rafinesquina alternata	USA	Late Ordovician
539432	Rafinesquina alternata	USA	Late Ordovician
539436	Rafinesquina alternata	USA	Late Ordovician
329576	Stropheodonta demissa	USA	Middle Devonian
539445	Rafinesquina alternata	USA	Ordovician
539446	Rafinesquina alternata	USA	Ordovician
539464	Leptaena rhomboidalis	UK	Late Silurian
539478	Sowerbyella sp.	USA	Late Ordovician
539486	Sowerbyella sp.	USA	Ordovician
539487	Sowerbyella sp.	USA	Ordovician
539488	Sowerbyella sericea	USA	Late Ordovician
539489	Sowerbyella sericea	USA	Late Ordovician
539490	Sowerbyella sericea	USA	Late Ordovician
539518	Sowerbyella sp.	USA	Late Ordovician
334023	Rafinesquina alternata ponderosa	USA	Late Ordovician
539519	Sowerbyella sp.	USA	Late Ordovician
539520	Sowerbyella sp.	USA	Late Ordovician
539540	Sowerbyella sp.	USA	Middle Ordovician
539541	Sowerbyella sp.	USA	Middle Ordovician
539542	Sowerbyella sp.	USA	Middle Ordovician
539562	Sowerbyella sericea	USA	Middle Ordovician
539563	Sowerbyella sericea	USA	Middle Ordovician
539564	Sowerbyella sericea	USA	Middle Ordovician
539565	Sowerbyella sericea	USA	Middle Ordovician
539604	Strophodonta sp.	USA	Middle Devonian

Vita Judith A. Sclafani

Education

Ph.D. Candidate, Geosciences, Pennsylvania State University - Fall 2019 (expected) Dissertation: Morphological diversity and disparity of Strophomenida (Brachiopoda) during the Late Ordovician mass extinction and recovery Advisor: Mark E. Patzkowsky

M.S., Geology, University of Georgia - 2013

Thesis: Using Hubbell's neutral theory to test the species-area relationship in the Late Ordovician of Laurentia

Advisor: Steven M. Holland

B.S., Cum Laude, Primary major: Geology with honors, Second major: Environmental Science, College of William and Mary - 2011

Honors thesis: A morphological and phylogenetic examination of the Miocene and Pliocene bivalve genus *Chesapecten*

Advisor: Rowan Lockwood

Teaching Experience

Visiting Instructor, Geology Department, Pomona College (2019-2020)

Courses: Sedimentology with Laboratory, Mass Extinctions Seminar

Online Instructor, Department of Geosciences, Pennsylvania State University (Summer 2017) Courses: Geology of the National Parks

Teaching assistant, Department of Geosciences, Pennsylvania State University (2015-2019)

Courses: The Sea Around Us, Dinosaur Extinctions and Other Controversies, Geobiology Laboratory, Earth History Laboratory, Field Stratigraphy

Teaching assistant, Geology Department, The University of Georgia (2011-2012)

Courses: The History of Global Change Laboratory

Publications (*Undergraduate student collaborator)

Articles

- Sclafani, J.A., M. Christie, B. Roselle*, A. Bourne*, M. Cone*, C. Gazze*, M. O'Brien*. *in prep.* Morphology in time and space: a method for adding morphometrics to the stratigraphic paleobiology toolkit. Paleontological Electronica.
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- Holland, S.M. and **J.A. Sclafani**. 2015. Phanerozoic diversity and neutral theory. Paleobiology, 41(3): 369-376.
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