Selectivity of the Lower Kellwasser Mass Extinction Event (Late Devonian) in the Appalachian Basin

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Selectivity of the Lower Kellwasser Mass Extinction Event
(Late Devonian) in the Appalachian Basin

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Selectivity of the Lower Kellwasser Mass Extinction Event (Late Devonian) in the Appalachian Basin

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Acknowledgements

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Abstract

Mass extinctions are often associated with multiple environmental perturbations. For example, the Upper and Lower Kellwasser Events (the two pulses of the Frasnian-Famennian mass extinction in the Late Devonian) coincide with both global cooling and ocean anoxia/dysoxia. Assessing the selectivity of extinction—which types of organisms survived versus died—can help constrain which environmental changes were most important as kill mechanisms. Here, selectivity is examined with respect to several factors during the Lower Kellwasser Event. A thick package of siliciclastic sediments was deposited in the Appalachian Foreland Basin during the Late Devonian. Thanks to recent stratigraphic revisions, the Kellwasser Events can be traced along a paleoenvironmental gradient that shallows from west to east in New York and northern Pennsylvania. Previous studies have shown that brachiopod species composition varies significantly along this gradient, and that the Lower Kellwasser Event was the more severe of the two extinctions. The Wiscoy Formation was targeted for this study as it immediately predates the first extinction pulse. We collected bulk samples from numerous localities along the paleoenvironmental gradient and identified 7,933 brachiopod fossils from 21 genera and 26 species. Non-metric multidimensional scaling was used to quantify variation among species in environmental preference; variation in extinction intensity among habitats could indicate that anoxia was a kill mechanism, because oxygen levels likely varied with depth. Brachiopod orders varied in latitudinal distribution in the Devonian, so variation in extinction intensity among orders could implicate cooling as a kill mechanism. We also tested the effects of abundance and body size on probability of extinction. Multiple logistic regression strongly supported global cooling as a major kill mechanism—species belonging to orders prevalent at low latitudes had higher probability of extinction than those belonging to orders common at high latitudes. In contrast, paleoenvironmental preference was not a major predictor of extinction in these data.
I. Introduction

The Late Devonian Extinction, one of Raup and Sepkoski’s (1982) ‘Big Five’ mass extinctions, occurred near the Frasnian-Famennian boundary (F-F, 372.2 ± 1.6 Ma) and consisted of two extinction pulses, the Lower and Upper Kellwasser Events (LKW and UKW). The UKW occurred at the F-F boundary and the LKW occurred approximately 800,000 years earlier (De Vleeschouwer et al., 2013, 2017). The Kellwasser Events have been globally correlated and are associated with major environmental perturbations that include global cooling, sea level change, and widespread anoxia in marine environments (Joachimski and Buggisch, 1993, 2002; Carmichael et al., 2014; Bush et al., 2015, 2017; Lash, 2017). Previous studies have observed that tropical, warm-water marine taxa especially suffered during the Kellwasser Events (House, 1985; Joachimski and Buggisch, 1993; Copper, 1994, 2002, 1998). Numerous clades were affected, including brachiopods, ammonoids, placoderm fishes, rugose corals, tabulate corals, and stromatoporoids (House, 1985; Copper, 1998, 2002).

More than two-thirds of species and as many as 21% of marine families died out during the Frasnian-Famennian extinction, coupled with low species origination rates which exacerbated the decline in diversity (McGhee, 1996; Bambach et al., 2004; Stigall, 2012; Lash, 2017). However, the specific mechanisms that contributed to this biodiversity crisis remain controversial (House, 1985; Joachimski and Buggisch, 1993). Several kill mechanisms and triggers have been proposed, including widespread ocean anoxia, global cooling, ocean acidification, volcanism, and bolide impacts (Johnson et al., 1985; McGhee, 1988; Buggisch, 1991; Joachimski and Buggisch, 2002; Sandberg et al., 2002; Bond et al., 2004).
During mass extinction events, certain traits correlate with survival, whereas other traits appear to have increased susceptibility to climatic and environmental changes (Finnegan and Droser, 2008; Clapham and Payne, 2011; Finnegan et al., 2012). Selectivity refers to how certain traits promote species survival or extinction, given a particular perturbation to environmental conditions such as productivity, temperature, pH, or oxygenation (Orzechowski et al., 2015).

Assessing mass extinction selectivity can help constrain which environmental changes were the most effective kill mechanisms. Here, we test selectivity with respect to several traits for brachiopod species during the Lower Kellwasser Event, the first pulse of the Frasnian-Famennian extinction in the Appalachian Basin. The two most commonly cited kill mechanisms for this event are widespread ocean anoxia and global cooling, and extinction selectivity may help constrain which was most important during the Lower Kellwasser Event (Johnson et al., 1985; Joachimski and Buggisch, 1993). Variables related to species abundance and body size are also evaluated.
II. Background

Anoxia

Anoxia refers to a lack of oxygen, and any organisms that require oxygen cannot persist under such conditions. Euxinic environments lack oxygen, but also contain hydrogen sulfide, which is toxic to most animals. Dyoxia refers to low-oxygen conditions. These various environmental conditions can be interpreted through geologic, isotopic, and fossil evidence (Boyer and Droser, 2009; Boyer et al., 2014; Formolo et al., 2014; Lash, 2017). Widespread anoxia has repeatedly been proposed as a significant kill mechanism for the Kellwasser Events, which coincide in many locations with dark, organic-rich shale or limestone beds. Dark, organic-rich rocks are typically deposited under anoxic or dysoxic settings, which could result from a range of conditions including enhanced primary productivity, eutrophication, stratification, sea level rise, and recycling of limiting nutrients such as nitrogen or phosphorus (Hallam and Wignall, 1999; Sandberg et al., 2002; Bond and Wignall, 2008a; Bond et al., 2004; Carmichael et al., 2014). Shallow marine shelves and epicontinental seaways were common in the Late Devonian, and mixing in these settings may have been less effective, contributing to intermittent dysoxic conditions and black shale formation (Joachimski and Buggisch, 1993; John et al., 2010; Carmichael et al., 2014; Hull, 2015).

Geochemical evidence supports the presence of anoxic and euxinic conditions during the Kellwasser Events. Positive $\delta^{13}$C excursions across both intervals suggest burial of organic matter, which could result from anoxic or euxinic conditions (Joachimski, 1997; Murphy et al., 2000; Lash, 2017). Abundance of trace metals can sometimes indicate oxygen level variation of bottom waters. Elements such as molybdenum and iron become enriched under anoxic to euxinic
conditions, which also seem to correspond with sulfide accumulation (Boyer and Droser, 2009; Boyer et al., 2011; Boyer et al., 2014). Other elements may become depleted under oxygen limited conditions, which can also be an indicator of dysoxic to anoxic pulses on a seasonal basis (John et al., 2010; Formolo et al., 2014). Trace metal levels within the Kellwasser Events in offshore paleoenvironments of the Appalachian Basin suggest intermittent periods of anoxia that interrupt a predominantly dysoxic setting (Murphy et al., 2000; Boyer and Droser, 2009; Boyer et al., 2011, 2014).

Pyrite framboid size has been used as a proxy for paleo-redox conditions during periods of marine sediment deposition (Boyer and Droser, 2009; Formolo et al., 2014; Lash, 2017). Anoxic conditions are optimal for framboid growth along a sulfidic chemocline, making pyrite framboids one possible indicator of anoxic conditions (Hallam and Wignall, 1999; Bond and Wignall, 2008b; Formolo et al., 2014). According to pyrite abundance through the Kellwasser interval in offshore settings in the Appalachian Basin, waters must have cycled through intermittently anoxic or euxinic periods, likely due to seasonal changes (Boyer and Droser, 2009; Lash, 2017).

Organism abundance, diversity, and size can also provide clues about oxygen levels because all three parameters generally decrease as oxygen levels decrease. For brachiopod faunal assemblages, low species richness and dominance of certain tolerant species indicate very low oxygen levels (Boyer and Droser, 2009). Bioturbation intensity and burrow size can be used to gauge oxygen levels as well, since they record the abundance and size of soft-bodied animals. Studies of the Kellwasser Horizons in western New York have observed limited bioturbation and reduced burrow sizes alternating with more active bioturbation and more abundant fossils, indicating fluctuating oxygen levels (Boyer et al., 2011, 2014). The brevity of these oxygen-
limited pulses might suggest seasonal inputs of excess nutrients into the marine system, resulting in eutrophic blooms (Boyer and Droser, 2009; Boyer et al., 2011). Oxygen levels in offshore settings were certainly unstable throughout the Kellwasser Events, ranging from well-oxygenated to anoxic conditions.

For modern oceans, stagnant waters or those limited in circulation are most susceptible to dysoxia and anoxia (Gray et al., 2002). Environments that have suffered from eutrophic conditions can take decades to fully recover, making eutrophication and anoxia a plausible kill mechanism for the Late Devonian.

The LKW and UKW also correlate with well-documented fluctuating sea levels that exacerbated the spread of oxygen-limited bottom waters (Johnson et al., 1985; Joachimski and Buggisch, 1993; Copper, 2002; Bond et al., 2004; Bond and Wignall, 2008a; Lash, 2017). Rising sea level would have caused the spread of warm saline waters over epicontinental seaways, further promoting anoxic conditions when in concert with possible high primary production (Joachimski and Buggisch, 1993). However, it is more difficult to generate anoxic conditions in shallow waters that mix with the atmosphere, and the spread of anoxic conditions during sea-level rise could simply coincide with many species tracking oxygenated habitats upslope.

**Climate Change**

The Late Devonian was a time of changing climate, a common characteristic of mass extinction events. The Devonian was a warm, humid greenhouse climate where sea surface temperatures averaged 30°C (Joachimski and Buggisch, 2002). Conodont δ¹⁸O records indicate cooling of low latitude surface waters by 5-7°C around the LKW and UKW (Buggisch, 1991; Joachimski and Buggisch, 1993; Joachimski and Buggisch, 2002). The spread of anoxic
conditions likely led to massive organic carbon burial associated with black shale deposition, which in turn may have reduced atmospheric CO$_2$ concentrations and initiated cooling (Joachimski and Buggisch, 1993). If temperature decrease was a major kill mechanism in the Late Devonian extinction, one can predict that warm water taxa should especially suffer—tropical, low latitude species should be less able to migrate to favorable conditions (Copper, 1998, 1994, 2002; Averbuch et al., 2005; Royer, 2006; Lash, 2017). The Pliocene-Pleistocene and Ordovician extinctions exhibited this pattern, with high-latitude, cold-water species faring better during cooling conditions (Stanley, 1984; Finnegan et al., 2012).

**Volcanism**

Volcanism has been rarely considered a substantial cause of the Frasnian-Famennian biodiversity crisis. However, recent dating of the Viluy Traps of Eastern Siberia place a potentially significant volcanic event close to the F-F boundary, as do mercury enrichments in sedimentary rocks (Courtillot et al., 2010; Racki et al., 2018). This volcanism seems to have occurred in several pulses, which corresponds with the extended timescale of the Kellwasser Events (Racki et al., 2018). The eruption of Large Igneous Provinces coincided with the other four of the ‘Big Five’ mass extinction events, as well as with numerous smaller events (Courtillot et al., 2010; Jones et al., 2017).
III. Hypotheses

A hypothetical sequence of events for the F-F extinction begins with a volcanic trigger, weathering of fresh rock, and increased nutrient input to the oceans. This would lead to eutrophication and widespread anoxia, further exacerbated by sea level rise. Anoxia would lead to increased carbon burial, CO$_2$ drawdown, and ultimately cooling climate. CO$_2$ drawdown could also be driven by increased weathering reactions. Many authors have argued for either anoxia or global cooling as the primary kill mechanism for the Late Devonian, although there has yet to be a quantitative study of extinction selectivity that addresses this debate (Johnson et al., 1985; Buggisch, 1991; Joachimski and Buggisch, 2002; Sandberg et al., 2002; Bond et al., 2004). Here, I will test for extinction selectivity with respect to several factors using brachiopod fossils from the northern Appalachian Basin. These factors, and their relationship to potential kill mechanisms, are discussed below.

Anoxia may be the leading kill mechanism proposed for the Kellwasser Events, having been suggested from initial studies of the Late Devonian Extinction (Johnson et al., 1985; Bond et al., 2004; Bond and Wignall, 2008b; Boyer et al., 2014). In modern marine environments, shallow, near-shore waters mix more efficiently with the atmosphere and therefore are typically well oxygenated. In contrast, deeper environments that experience less mixing are more prone to anoxia (Gray et al., 2002; Gobler et al., 2014). Given these observations, I predict species that prefer deeper-water environments should be more susceptible to extinction driven by an anoxic event (Finnegan et al., 2016).

Oxygen isotope data indicates a significant cooling trend during the Kellwasser Events, and cooling should preferentially affect tropically adapted species with limited options for
migrating to more hospitable environments (Joachimski and Buggisch, 1993). The tropics are generally more uniform in temperature and precipitation, resulting in taxa with particularly narrow environmental ranges that largely diminish the likelihood of successful migration (Janzen, 1967).

For example, during the Ordovician extinction, species with narrow thermal tolerances could not keep up with climate shifts, ultimately leading to their disappearance (Finnegan et al., 2016). This was also the case for the late Paleozoic ice age, during which tropical species suffered, while high latitude species continued to diversify during the cooling phase (Powell, 2005). These studies have shown that the paleolatitude at which a taxon lives can be used as a proxy for temperature tolerance. Taxa inhabiting high latitudes should be less susceptible to cooling due to broader habitat ranges and their ability to track changes equatorward. Low latitude, tropical species are more susceptible to climate changes due to their narrow environmental ranges, limited temperature tolerance, and inability to move to more hospitable habitats (McGhee, 1996; Murphy et al., 2000; Finnegan et al., 2012).

Organismal body size can be affected by several environmental factors including oxygen availability, nutrient accessibility, and predation stress these (Zhang et al., 2015; Shi et al., 2016). Physiological constraints often determine body size for marine animals, where it is often beneficial to be large, especially in colder climates (Heim et al., 2015). In areas of limited oxygen availability, organisms tend to be smaller so that larger surface area to volume ratios permit the more efficient transfer of oxygen (Shi et al., 2016). Given its connection to many biological and environmental parameters, body size is often considered in studies of extinction selectivity (Payne and Finnegan, 2007; Harnik et al., 2012; Hull, 2015; Orzechowski et al., 2015; Payne, Bush, Heim, et al., 2016).
Selectivity has also been studied in terms of species abundance, where abundant, widespread taxa with broad environmental ranges exhibit a lesser extinction risk than rare, endemic taxa with narrow ranges (Finnegan et al., 2012). Extinction risk for species has historically been heavily weighted by geographic range and abundance, where highly abundant taxa that encompass a larger range are more likely to survive perturbations in a specific environment. Their range across habitats also promotes survivorship where in marine species latitudinal distribution, water depth, and substrate preference determine their extinction risk over long timescales (Clapham and Payne, 2011; Harnik et al., 2012). For the Devonian, due to environmental confines of epicontinental seaways, abundance may have been a selective factor for shallow marine taxa (Copper, 1994). However, being abundant and widespread may not confer as significant an advantage during mass extinctions (Jablonski, 1986; Payne and Finnegan, 2007).
IV. Geologic Setting

During the Late Devonian, a thick fossiliferous package of siliciclastic sediments was deposited in the Appalachian Foreland Basin, including present-day New York and Pennsylvania. A paleoenvironmental gradient spans this region from offshore shales in western NY southeastward to onshore marine facies and ultimately terrestrial strata in northern Pennsylvania. Recent stratigraphic revisions have correlated the Upper and Lower Kellwasser events throughout the marine paleoenvironments (Bush et al., 2015; Beard et al., 2017), and it appears that the LKW extinction is much more severe than the UKW in this basin (Bush et al., 2015; Beard et al., 2017; Bush et al., 2017).

The Pipe Creek Formation is temporally equivalent to the Lower Kellwasser Event and consists of dark, organic-rich shale or silty shale deposited in a calm, offshore marine environment that was probably dysoxic or anoxic (Over, 1997; Boyer and Droser, 2009; Bush et al., 2015; Beard et al., 2017; Bush et al., 2017).

Figure 1. Map of study area and sample locations. Modified from Bush et al. (2015). Large symbols represent measured sections from which numerous samples were collected; small symbols represent additional sampling localities.
al., 2015; Beard et al., 2017). The Pipe Creek Formation is immediately preceded by the upper portion of the Angola Formation in the west and the Wiscoy Formation in the east. The upper Angola Formation consists of gray shales with some black shales interbedded, indicative of a calm, offshore depositional environment (Pepper et al., 1956).

The Wiscoy Formation represents shallower marine environments (McGhee and Sutton, 1981). Through the upper portion of the Wiscoy, sediments fine upward leading into the Pipe Creek. We refer to the uppermost Wiscoy just preceding the Pipe Creek as the “Muddy Member” and the lower Wiscoy as the “Sandy Member” (Beard et al., 2017).

![Figure 2. Generalized stratigraphic section of the upper Wiscoy and Pipe Creek formations. Within the Wiscoy, sediments fine upward from the “Sandy Member” to “Muddy Member”. The Pipe Creek is correlative with the Lower Kellwasser extinction interval. Near the DAN and BCP sections (Fig. 1), the “Sandy Member” represents a lower shoreface environment, probably just above mean storm weather wave base, where mudstones, siltstones, and very fine to fine grained sandstones are interbedded, sometimes with hummocky or swaley crossbedding indicative of storm reworking (facies S3 of Beard et al., 2017). Farther to
the southeast at CAM and TGB, the “Sandy Member” transitions to mid-lower shoreface; fine grained sands dominate over muds, and swaley cross-bedding is common (Fig. 1). The environment is interpreted to be above storm-weather wave base but still below fair-weather wave base (facies S2 of Beard et al., 2017). Farthest into Pennsylvania (location TF), grain size increases into coarser sandy sediments, plant material becomes more abundant, and sedimentary structures indicate tidal influence. The “Muddy Member” consists mostly of muddy sediments with interbeds of silt or fine sand; Beard et al. (2017) described it as facies M1, deposited at or below storm-weather wave base.

![Figure 3](image-url)

**Figure 3.** (A) Extinction interval at section TGB in Tioga, Pennsylvania. Staff in picture represents 2 meters for scale. (B) Exposed fossils in upper Wiscoy ‘Muddy Member’ at location HNS. PC: Andy Bush

The Wiscoy Formation contains plentiful crinoid fragments, rugose corals, mollusks, and bryozoans. Brachiopod fossils are abundant and generally well preserved, although they become sparse to the west of Dansville and are virtually absent at Wiscoy Creek. Previous studies have shown that brachiopod species in these strata vary in depth preference (McGhee, 1977; McGhee and Sutton, 1981, 1983; Bush and Brame, 2010).
V. Methods

Data Collection

Bulk samples were collected from the Wiscocoy Formation from 17 localities along the paleoenvironmental gradient. A large number of samples were collected from measured stratigraphic sections through the upper Wiscocoy (Figure 1), while other samples were taken from smaller outcrops (Bush et al., 2015). Some samples were previously used by Christie et al. (2013), although the fossils in these samples were here re-identified and recounted for consistency. We identified 7,933 brachiopod fossils from 21 genera and 26 species, as well as 107 rugose coral specimens. Identifications were based on several sources that have illustrated the brachiopod fauna (Hall 1867; Cooper and Dutro 1982; Linsley 1994; Bush et al. 2017). Species can be distinguished, although some genus-level placements require revision. Species difficult to classify at the species level due to small size, extremely poor preservation, and very low abundance (<10) were grouped at the genus level which included chonetids, generic lingulids, and athyrid species. To avoid double-counting of individuals, parts and counterparts of fragmented rock samples were compared, and only brachiopods with at least half a valve visible were counted. In total, abundance data were assembled for 94 samples, each consisting of at least 30 identifiable brachiopod individuals. All samples either represent a single bed or a few adjacent beds of similar facies lumped together to increase sample size. Sample grain sizes were classified as mudstone, siltstone, very fine-grained sandstone, fine-grained sandstone, or medium-grained sandstone.

Due to the nature of sampling, the volume of individual samples varied depending on outcrop characteristics, and fossil density varied due to sedimentological factors. To control for
varying sample size, brachiopod abundances were normalized by calculating the proportional abundance of each species per sample.

Previous collecting trips also sampled material from the Canaseraga Formation, which overlies the Pipe Creek. Through comparison of species content for both formations, the victims and survivors of the Lower Kellwasser Event were identified (Bush et al., 2015; Beard et al., 2017; Bush et al., 2017).

Regression

To determine which parameters best predict extinction risk, we ran a multivariate logistic regression with four predictor variables: 1) environmental preference, which may relate to anoxia susceptibility, 2) paleolatitude, which is a proxy for temperature tolerance, and might be significant if climate change was a major kill mechanism, 3) body size, and 4) abundance (Clapham and Payne, 2011; Orzechowski et al., 2015; Payne et al., 2016). Certain brachiopod species and groups were removed for regression analyses including those unidentifiable to species level, those only present in one total sample, and those with less than ten total individuals across samples. This included chonetids, lingulids, athyrids, Pseudoatrypa devoniana, Camarotoechia mesacostalis and Devonoproductis walcotti. Analyses were conducted using R Statistical Software version 3.4.1 and the AICcmodavg Package.

Environmental Preference. Non-metric multidimensional scaling (NMDS) was used to quantify variation in species composition. Ecological ordination techniques, such as NMDS, are applied to species abundance or occurrence data to expose major gradients in composition among samples of fossil assemblages that may correlate with paleoenvironmental gradients (Scarponi and Kowalewski, 2004; Bush and Brame, 2010). NMDS has become a popular
ordination method for its ability to counteract distortions introduced by other methods (Fasham, 1977; Tomašových, 2006; Bush and Brame, 2010). NMDS places samples within a pre-determined low-dimensional space based on rank-order dissimilarity, such that samples that are more similar in composition plot closer than those that are dissimilar.

Following Holland et al. (2001), samples including only one species were removed to minimize effects of extremely abundant taxa on analyses. Species counts were normalized by calculating the proportional abundance per sample for each species. Our NMDS analysis was run in three dimensions because two dimensions produced no convergence and limited dimensions are most useful for interpreting patterns or gradients within the data. General paleoenvironments were interpreted following Beard et al. (2017) based on sample lithology, sedimentary structures, and plant material abundance.

For the regression, species environmental preferences were calculated as weighted averages of species NMDS Axis 1 scores (“mean depth”). To visualize species’ distributions in NMDS space, we plotted the proportional abundance of each species per sample against the NMDS Axis 1 scores and applied Loess (Lowess) regression. Loess fits a weighted regression curve to smooth variation (Cleveland, 1979; Bambach et al., 2004). The loess curves visually summarize the preferred habitat, environmental range, and abundance for each species. All NMDS analyses were run using the Vegan Package.

**Temperature Tolerance.** To test whether temperature tolerance impacts extinction selectivity, paleolatitudinal preferences were calculated for each taxonomic order based on fossil data occurrences downloaded from the Paleobiology Database (PBDB; paleobiodb.org). The PBDB has few records for Frasnian high latitude species, which are needed to assess latitudinal range, so Early and Middle Devonian data were used. Working at the order level permitted a
general assessment of thermal tolerance even when detailed information on specific genera was lacking. Data from the northern and southern hemispheres were combined, and the proportional abundance of each brachiopod order was calculated in ten degree latitudinal bins. For each order, the “preferred paleolatitude” was calculated as the weighted average based on these proportional abundances. Each species within the same taxonomic order was given the same latitudinal value.

**Body Size.** Body size measurements were obtained for at least twenty individuals of each species, or for all available specimens if fewer than twenty were present, and the geometric mean of length and width was calculated. The third potential body size measurement was excluded since most fossils were molds and could not accurately be measured for ‘height’ or ‘depth’.

**Mean Abundance.** Mean proportional abundance for each species was calculated using the R Package Vegan. Values were then logged to mitigate large differences in abundance among species.
VI. Results

Single Variables

*Environmental Preference.* NMDS produced an ordination with a stress of 0.1216. On NMDS Axis 1, muddy samples tend to plot at the most negative end, silty to fine-grained sandy samples plot in the middle, and the coarser sandy samples from location TF plot towards the most positive end (Figure 4). Going from the negative to the positive end, there are clusters of samples from the ‘Muddy Member’ at the westernmost sections (DAN and BCP), the “Muddy Member” at a more eastern section (CAM), the ‘Sandy Member’, and, finally, the easternmost section (TF), which displayed evidence of deposition under tidal influence (Fig. 4B). Thus, NMDS Axis 1 matches the expectations of an onshore-offshore gradient. Samples that plot at the negative end of NMDS Axis 2 contain a high abundance of *Ambocoelia gregaria*, which has been described as an opportunistic species that does not fall cleanly along onshore-offshore gradients in ordinations (Bush and Brame, 2010). To separate the effects of ‘depth’ from the effects of opportunistic species blooms for purposes of the regression analysis, the NMDS results were rotated slightly (Fig. 5), which can be justified since the orientation of the point cloud in the original NMDS was based on statistical properties of the data instead of biological properties (Bush and Brame, 2010).
Figure 4. NMDS Axes 1 and 2 showing sample scores labeled by (A) sample lithology, (B) site, with symbols matching those in Figure 1, and (C) species scores, where red text = extinct.
Figure 5. Rotated NMDS showing sample scores labeled by (A) sample lithology, (B) site, with symbols matching those in Figure 1, and (C) species scores, where red text = extinct.
For samples from measured sections (DAN, BCP, CAM, TGB), NMDS ‘depth’ scores can be compared to stratigraphy (Figure 6). Scores shift to more negative values from the sandy to the muddy member of the Wiscoy Formation along NMDS Axis 1. Loess curves exhibit a variety of environmental depth ranges for both extinct and surviving species (Figures 7 and 8). A Mann-Whitney test indicated that for mean depth the difference between the species that went extinct and those that survived was not statistically significant ($W=31, p=0.175$).

Figure 6. NMDS Axis 1 scores (‘Depth’) compared with stratigraphy from measured sections DAN, BCP, CAM, and TGB. For sample locations refer to Fig. 1.
Figure 7. Loess curves depicting distribution of species along NMDS Axis 1 ('Depth'). (A-L) species that succumb to extinction. (M-Y) surviving species. Each point represents a species’ abundance in one sample. Note that the vertical scale varies among panels.
Figure 8. Loess curves depicting distribution of (A) extinct and (B) surviving species on NMDS Axis 1 (‘Depth’). For individual species distributions, refer to Figure 7. Note that the vertical scale varies among panels.
**Temperature Tolerance.** Paleolatitudinal distribution can be used as a proxy for relative temperature tolerance to test if global cooling was a primary kill mechanism (Finnegan et al., 2012, 2016). As discussed above, the paleolatitudinal distribution of brachiopod orders was used as a proxy for the temperature tolerance of constituent species, given limited high-latitude sampling in the Late Devonian. For each order, a value was calculated indicating the average paleolatitude at which it occurs. All species within the same order were assigned the same paleolatitude value (Figure 9). A Mann-Whitney test indicated that the probability of a species going extinct was greater if it belonged to an order that occurs in high relative frequency at low latitudes relative to high latitudes ($W=13$, $p=0.004$).

![Latitudes of Taxonomic Orders](image)

*Figure 9. Inferred temperature tolerance for species that go extinct in the LKW (top, red) and for those that survive (bottom, green) based on paleolatitudinal distribution of orders.*
**Body Size.** Figure 10 illustrates the average body size for brachiopod species that survived (green) or went extinct (red) during the LKW. A Mann-Whitney test indicated that there was no statistically significant difference between the species that went extinct and those that survived ($W=47, p=0.882$).

Figure 10. Species body sizes for extinct species (top, red) and survivors (bottom, green).
**Mean Abundance.** A Mann-Whitney test indicates that there is not a statistically significant difference in log mean proportional abundance between species that go extinct and those that survive ($W=46$, $p=0.824$) (Fig. 11).

![Species Proportional Mean Abundance](image)

Figure 11. Species mean proportional abundance per sample for both extinct (top, red) and surviving (bottom, green) species. Axes are on a logarithmic scale.

**Regression**

All possible model combinations of predictor variables (including a null model) were run and AICc values and weights calculated (Table 1). AICc values were selected to correct for small sample size (Hurvich et al., 1995; Payne, Bush, Chang, et al., 2016; Zhang et al., 2015; Clapham and Payne, 2011).
Table 1: All possible model combinations of predictor values for species extinction (L=Latitude, BS=Body Size, MD=Mean Depth, SM=Mean Proportional Abundance Per Sample, $K=\#$ parameters, LL=log-likelihood of each model, AICc=Akaike values, Delta_AICc=DeltA AIC, ModelLik=Relative likelihood of the model, AICc Wt=Akaike weights, Cum.Wt=Cumulative Akaike weights).

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>LL</th>
<th>AICc</th>
<th>Delta_AICc</th>
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To better determine which factors were most reliable in predicting extinction, model AICc weights were summed for all models containing each variable to determine the relative importance of each parameter to include within the model set (Burnham and Anderson, 2002). There was very strong support for the inclusion of latitude in the model set (wt=0.99) and some support for the inclusion of body size (wt=0.38) (Table 2).

Table 2: Summary results for each parameter determining likelihood of each for species extinction. Results were calculated from averaging top five models from Table 1.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Unconditional Standard Error</th>
<th>Confidence Interval</th>
<th>Relative Importance</th>
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<td>1.38</td>
<td>(-3.22, 2.19)</td>
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The top five models from Table 1 were selected for model averaging since they were within 4 ΔAICc values of the ‘best’ model. With the AICcmodavg Package in R, model weights were recalculated based on these models. The results of model averaging are summarized in Table 2, where parameter estimates have standardized effect sizes and are therefore on a comparable scale (Grueber et al., 2011). According to Table 2, latitude is the only statistically significant parameter for predicting extinction at the 0.05 level (i.e., 95% confidence interval for latitude does not include zero; Figure 12), which is consistent with the univariate analyses. Since body size was the second most supported predictor, we ran an interaction model between latitude and body size but did not find evidence of interaction.
VII. Discussion

NMDS Ordination

From our NMDS results we can distinguish a clear paleoenvironmental depth gradient along NMDS axis one that matches the general deepening trend from Pennsylvania to New York (Figures 4 and 5). This gradient is also consistent with sediment grain size and interpreted depositional environments (Beard et al. 2017). Finer mudstones and siltstones are common on the negative end of axis one, whereas sandstones are abundant on the positive end, with a mixture in between (Figure 4A and 5A). Although grain size is not a perfect paleoenvironmental indicator, it does help orient which end of the gradient is which for further interpretation of depositional environments (Bush and Brame, 2010). Samples from the “Muddy Member”, which represent the most offshore settings sampled from the Wiscoy Formation, plot farthest to the left (Figure 4B and 5B) (Beard et al., 2017). Furthermore, samples from the “Muddy Member” from the two sections located farthest west (DAN and BCP) plot farther to the left than those from CAM. Samples from the “Sandy Member” plot farther to the right. Finally, samples from the TF section in Bradford County, Pennsylvania have the highest NMDS axis one scores, and these samples derive from nearshore, tidally influenced environments in which large plant debris is common.

Individual species prefer specific paleoenvironments (Figs. 7 and 8), which may not solely depend on ‘depth’, but may include a series of other factors such as food availability, temperature, oxygenation, storm frequency, ocean chemistry, and habitat structure (Holland et al., 2001). For example, *Cupularostrum eximium* preferred nearshore, tidally influenced environments and has the highest axis one values, and *Cyrtospirifer inermis* also preferred relatively shallow environments. Species that prefer shallow subtidal, primarily sandy habitats
plot in the middle of NMDS Axis 1, while species like *Stainbrookia infera* that preferred deeper offshore muddy environments have the most negative values. Species that succumbed to extinction span the entire ‘depth’ range.

A number of samples cluster towards the bottom of Figure 4A-C due to an overwhelming abundance of *Ambocoelia gregaria*, known for its opportunistic blooming behavior in areas most brachiopod species find unsuitable, presumably following disturbance events like storms (Goldman and Mitchell, 1990; Bush and Brame, 2010). Its extreme abundance pulls sample and species scores into the bottom left corner of the NMDS results, somewhat complicating the interpretation of Axis 1. Likewise, blooms of *A. gregaria* complicated attempts to recognize paleoenvironmental gradients in Upper Devonian assemblages from Virginia, which supports the rotation of our data (Bush and Brame, 2010). In the rotated results, *Cupularostrum eximium* is dominant in samples at positive values of Axis 2, which were interpreted as representing tidally influenced environments (Figure 5). We interpret NMDS Axis 2 in the rotated results as reflecting environmental stability; samples from stable environments plot in the middle of the axis and those from unstable or stressful environments plot at either extreme.

Four measured stratigraphic sections in the field area record the transition from the “Sandy Member” of the Wiscoy to the “Muddy Member” (Figure 6), which marks a shift from onshore to offshore paleoenvironments and a basin-wide deepening event leading into the Pipe Creek Formation (Beard et al., 2017). NMDS Axis 1 values shift from high to low across this transition (Figure 6), indicating a strong faunal response to the fining-upward transition. Within each member, scores increase from west to east, consistent with the west-to-east shallowing trend. Within the “Sandy Member”, the average score is -0.096 at DAN, 0.08 at BCP, 0.43 at CAM, and 0.61 at TGB. Within the “Muddy Member”, the average score is -1.06 at DAN, -1.17
at BCP, and -0.48 at CAM. These patterns all support interpretation of NMDS Axis 1 as an onshore-offshore ‘depth’ gradient.

**Extinction Selectivity**

Temperature tolerance, as assessed using paleolatitude, was the only statistically significant predictor for extinction in both the univariate tests and the logistic regression. Species belonging to orders common in tropical, warm waters were preferentially selected for extinction, whereas species belonging to orders common at high latitudes survived preferentially. This supports climatic cooling during the LKW as an important kill mechanism. All strophomenid and atrypid brachiopods present in the Wiscoy went extinct during the LKW, and these two orders had strongest affinity for low latitudes. On a global scale, these orders disappear entirely or almost entirely through the Kellwasser Events (Rong and Cocks, 1994; Copper, 1998). Given that they never successfully inhabited high latitudes, they likely did not possess physiological adaptations to colder climates. Within the subphylum Rhynchonelliformea, to which the regression analysis was confined, the strophomenids and atrypids are not closely related (Carlson and Leighton, 2001). This separation indicates that their similar reaction to the Kellwasser events was unlikely to result from other shared physiological similarities or constraints resulting from phylogenetic proximity (Carlson and Leighton, 2001).

Depth preference did not predict extinction, and the NMDS results show that species across the entire ‘depth’ gradient were victims of extinction (Figures 4C and 5C). Thus, there is no evidence that anoxia was a primary kill mechanism in this fauna, which is consistent with other results that show anoxia was not persistent within the Appalachian Basin (Boyer et al., 2011, 2014). Likewise, low abundance and body size did not correlate with extinction. However,
with more data, one might detect additional significant relationships (Finnegan et al., 2012; Harnik et al., 2012).
VIII. Conclusions

We have examined Late Devonian brachiopod assemblages from the Wiscoy Formation along a depth transect from Pennsylvania to New York to test for selectivity associated with the Lower Kellwasser Extinction Event. Inferred temperature tolerance, based on latitudinal distribution of brachiopod orders, was the only significant predictor of extinction, suggesting that global cooling may have been the most important kill mechanism in this region. Global disappearances of tropical species, particularly strophomenids and atrypids, are consistent with this pattern of selectivity. Species extinction does not correlate significantly with inferred depth preference, providing no evidence that anoxia associated with depth was a primary driver of extinction. Body size and abundance were not significantly correlated with species extinction. Collection of more data may help constrain other significant predictors associated with extinction selectivity during the Lower Kellwasser Event.

Climatic changes have been associated with all mass extinction events, and cooling has been closely connected with the Ordovician and Devonian mass extinctions and a number of smaller events (Raup and Sepkoski, 1982; Stanley, 1984; Finnegan et al., 2012). Tropical, warm-water taxa seem to be repeatedly hit hard by these cooling events. Our results indicate that cooling was the most important kill mechanism for the Lower Kellwasser Event during the Late Devonian, when the Earth was warmer, and the tropics reached a much larger geographic area than they do today.
IX. References


# Appendix 1: Location Coordinates

Appendix 1. Sample location latitude and longitude coordinates.

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<tr>
<td>BCP</td>
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Appendix 2: Species Taxonomic Order

Appendix 2. List of species and the order level used for each for PBDB analysis.

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Appendix 3. Table of sample and species count data included for analyses. For Lithology (Lith.), MS=Medium Sand, FS=Fine Sand, VFS=Very Fine Sand, S=Siltstone, M=Mudstone. For Formation (Fm.), Sandy refers to the “Sandy Member”, Muddy refers to the “Muddy Member”, and Unass. refers to unassigned samples from the Wiscoy Formation. Correlated stratigraphic heights (Corr. Strat. Height) were calculated to normalize stratigraphic heights across sample locations of measured sections.

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### Appendix 4: Regression Data Table

Appendix 4. Values for each species incorporated into regression analysis.

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<th>Per Sample Mean Proportion</th>
<th>Log of Per Sample Mean</th>
<th>Latitude</th>
<th>Mean Depth</th>
<th>Body Size</th>
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library(vegan)

FNMDSS <- read.csv('Pier GLMM Final.csv', header=TRUE)
FNMDSS$Correlated.Stratigraphic.Heights[is.na(FNMDSS$Correlated.Stratigraphic.Heights)] <- 0
FNMDSS$Height[is.na(FNMDSS$Height)] <- 0
FData2 <- as.data.frame.matrix(FNMDSS)
FData2 <- as.data.frame(FData2)
FNORMData <- decostand(FData2, method='total')
NMDS.1 <- metaMDS(FNORMData, k=3, dist='bray', autotransform=FALSE, trymax=100)
NMDS.L <- with(FNMDSS, MDSrotate(NMDS.1, Correlated.Stratigraphic.Heights))
NMDS.L.P <- as.data.frame(NMDS.L$points)
NMDS.L.sp <- as.data.frame(NMDS.L$species)
NMDS.L.sp$species <- rownames(NMDS.L.sp)

#Rotate Function:
rotate.F <- function(x, y, angle) {
  new.pts <- x*cos(angle) - y*sin(angle)
  new.pts2 <- y*cos(angle) + x*sin(angle)
  results <- cbind(new.pts, new.pts2)
  results}
#Lithology Plot:
results.F <- rotate.F(NMDS.L.P$MDS2, NMDS.L.P$MDS1, -90)
results.F <- as.data.frame(results.F)
col.lith <- c("gold", "goldenrod", "goldenrod4", "seashell4", "darkslategray")
col.lith.p <- c("goldenrod4", "gold", "darkslategray", "seashell4", "goldenrod")
sed.shape <- c(19,10,15,15,21)
plot(results.F$new.pts2, results.F$new.pts, type='n', main="NMDS with Lithology",
     xlab="Axis 1 'Depth'", ylab="Axis 2 'Ecological Disturbance'")
points(results.F$new.pts2, results.F$new.pts, col=col.lith.p[FNMDSS$Lithology],
        bg=col.lith.p[FNMDSS$Lithology], pch=sed.shape[FNMDSS$Lithology], cex=1.25)
legend('bottomright', legend=lith, levels(FNMDSS$Lithology), bty=1,
       col=col.lith, pch=c(10,19,21,15,15),
       pt.bg=col.lith)
#For Species Plot:
results.sp <- rotate.F(NMDS.L.sp$MDS2, NMDS.L.sp$MDS1, -90)
results.sp <- as.data.frame(results.sp)
library(calibrate)
plot(results.sp$new.pts2, results.sp$new.pts, type='n', xlab="Axis 1 'Depth'",
     ylab="Axis 2 'Ecological Disturbance'", main="NMDS of Species Distribution")
textxy(results.sp$new.pts2, results.sp$new.pts, Species, offset=0, col='black',
        cex=0.8)
identify(results.sp$new.pts2)
#Site Plot Onshore/Offshore:
col.ross <- c("blue", "blue", "turquoise2", "green3", "green3", "red", "purple",
             "orange", "black")
size.ross <- c(15, 0, 7, 17, 2, 18, 8, 1, 4)
plot(results.sp$new.pts2, results.sp$new.pts, type='n', main="NMDS by Site",xlab="Axis 1 'Depth'",
     ylab="Axis 2 'Ecological Disturbance'")
points(results.sp$new.pts2, results.sp$new.pts, col=col.ross[results.sp$Ross],
       pch=size.ross[results.sp$Ross], cex=1, bg=col.ross[results.sp$Ross])
legend("bottomright", legend=levels(results.P$Ross), col=col.ross, pch=size.ross, pt.bg=col.ross)

#Measured Section Stratigraphy Plot:
results.P$Correlated.Stratigraphic.Heights <- Strat
results.P$Location <- Location
results.P$Height <- Height
results.P$Ross <- Ross
View(results.P)

BCP <- subset(results.P, Location=="BCP")
CAM <- subset(results.P, Location=="CAM")
DAN <- subset(results.P, Location=="DAN")
TGB <- subset(results.P, Location=="TGB")

plot(TGB$new.pts2, TGB$Height, type='o', xlim=c(-1.75, 1.25), ylim=c(0, 25), col="orange", pch=19, xlab="NMDS Axis 1 'Depth'", ylab="Stratigraphic Height", main="TGB Depth")
plot(DAN$new.pts2, DAN$Height, type='o', xlim=c(-1.75, 1.25), ylim=c(0, 25), col="red", pch=19, xlab="NMDS Axis 1 'Depth'", ylab="Stratigraphic Height", main="DAN Depth")
plot(CAM$new.pts2, CAM$Height, type='o', xlim=c(-1.75, 1.25), ylim=c(0, 25), col="green3", pch=19, xlab="NMDS Axis 1 'Depth'", ylab="Stratigraphic Height", main="CAM Depth")
plot(BCP$new.pts2, BCP$Height, type='o', xlim=c(-1.75, 1.25), ylim=c(0, 25), col="blue", pch=19, xlab="NMDS Axis 1 'Depth'", ylab="Stratigraphic Height", main="BCP Depth")

#Loess Curves:
NMDS_env <- data.frame(NMDS.L$points)
Depth.sp <- results.sp
Depth.sp$Species <- NMDS.L.sp$species

Lingula <- (FNormData$Lingula)
NMDS_env$Lingula <- Lingula
R.grandis <- (FNormData$R.grandis)
NMDS_env$R.grandis <- R.grandis
D.arcuata <- (FNormData$D.arcuata)
NMDS_env$D.arcuata <- D.arcuata
D.cayuta <- (FNormData$D.cayuta)
NMDS_env$D.cayuta <- D.cayuta
S.coelata <- (FNormData$S.coelata)
NMDS_env$S.coelata <- S.coelata
N.nervosa <- (FNormData$N.nervosa)
NMDS_env$N.nervosa <- N.nervosa
D.walcotti <- (FNormData$D.walcotti)
NMDS_env$D.walcotti <- D.walcotti
W.hirsuta <- (FNormData$W.hirsuta)
NMDS_env$W.hirsuta <- W.hirsuta
F.chemungensis <- (FNormData$F.chemungensis)
NMDS_env$F.chemungensis <- F.chemungensis
S.infera <- (FNormData$S.infera)
NMDS_env$S.infera <- S.infera
S.impressa <- (FNormData$S.impressa)
NMDS_env$S.impressa <- S.impressa
S.amanaensis <- (FNormData$S.amanaensis)
NMDS_env$S.amanaensis <- S.amanaensis
Orthid.sp.A <- (FNormData$Orthid.sp.A)
NMDS_env$Orthid.sp.A <- Orthid.sp.A
C.contractum <- (FNormData$C.contractum)
NMDS_env$C.contractum <- C.contractum
C.mesacostalis <- (FNormData$C.mesacostalis)
NMDS_env$C.mesacostalis <- C.mesacostalis

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```r
C.eximium <- (FNormData$C.eximium)
NMDS_env$C.eximium <- C.eximium
S.hystrix <- (FNormData$S.hystrix)
NMDS_env$S.hystrix <- S.hystrix
S.trulla <- (FNormData$S.trulla)
NMDS_env$S.trulla <- S.trulla
P.devoniana <- (FNormData$P.devoniana)
NMDS_env$P.devoniana <- P.devoniana
Athyrid.sp <- (FNormData$Athyrid.sp)
NMDS_env$Athyrid.sp <- Athyrid.sp
C.inermis <- (FNormData$C.inermis)
NMDS_env$C.inermis <- C.inermis
C.chemungensis <- (FNormData$C.chemungensis)
NMDS_env$C.chemungensis <- C.chemungensis
S.williamsi <- (FNormData$S.williamsi)
NMDS_env$S.williamsi <- S.williamsi
T.mesacostalis <- (FNormData$T.mesacostalis)
NMDS_env$T.mesacostalis <- T.mesacostalis
A.gregaria <- (FNormData$A.gregaria)
NMDS_env$A.gregaria <- A.gregaria
C.hamiltonensis <- (FNormData$C.hamiltonensis)
NMDS_env$C.hamiltonensis <- C.hamiltonensis

Depth <- results.P$new.pts2
NMDS_env$Depth <- Depth

# Stacked Survivor Loess:
survive.col <- c("black", "darkgreen","royalblue1", "darkolivegreen4", "dodgerblue", 
"blue", "darkolivegreen", "darkolivegreen2", "darkorchid", 
"aquamarine", "darkslategrey", "slategray2", "purple")
survivors <- c("Lingula", "R.grandis", "F.chemungensis", "C.contractum", 
"C.mesacostalis", 
"D.walcotti", "W.hirsuta", "C.chemungensis", "C.inermis", 
"T.mesacostalis", 
"A.gregaria", "S.impressa", "C.eximium")
lo <- loess.smooth(NMDS_env$Depth, NMDS_env$Lingula, span = 2/3, degree = 1, 
parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$Lingula,bty='n', ylim=c(0,0.325),type="n",xlab='Depth 
Gradient', ylab='% Abundance', main="Surviving Species Environmental Ranges")
lines(lo, col='black', lwd=3)
legend('topleft', legend=survivors,bty='n', lty=1, lwd=4,pch=NA, col=survive.col)
par(new=TRUE)
lo <- loess.smooth(NMDS_env$Depth, NMDS_env$R.grandis, span = 2/3, degree = 1, 
parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$R.grandis, bty='n',ann=F,ylim=c(0,0.325),type="n",axes=F,yaxt="n",xaxt="n")
lines(lo, col="darkgreen", lwd=3)
par(new=TRUE)
lo <- loess.smooth(NMDS_env$Depth, NMDS_env$F.chemungensis, span = 2/3, degree = 1, 
parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$F.chemungensis, bty='n',ann=F,ylim=c(0,0.325),axes=F,type="n",yaxt="n",xaxt="n", las=1)
lines(lo, col="royalblue1", lwd=3)
par(new=TRUE)
lo <- loess.smooth(NMDS_env$Depth, NMDS_env$C.contractum, span = 2/3, degree = 1, 
parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$C.contractum, bty='n',ann=F,ylim=c(0,0.325),type="n",axes=F,xaxt="n", las=1)
lines(lo, col="darkolivegreen4", lwd=3)
```

par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$C.mesacostalis, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$C.mesacostalis, bty='n', ann=F,ylim=c(0,0.325),xaxt="n",yaxt="n", axes=F,las=1)
lines(lo, col="dodgerblue", lwd=3)
par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$D.walcotti, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$D.walcotti, bty='n', ann=F,ylim=c(0,0.325),xaxt="n",yaxt="n", type="n",axes=F,las=1)
lines(lo, col="blue", lwd=3)
par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$W.hirsuta, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$W.hirsuta, bty='n', ann=F,ylim=c(0,0.325),xaxt="n",yaxt="n",axes=F,type="n",las=1)
lines(lo, col='darkolivegreen', lwd=3)
par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$C.chemungensis, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$C.chemungensis, bty='n', ann=F,ylim=c(0,0.325),xaxt="n",yaxt="n", axes=F)
lines(lo, col="darkolivegreen2", lwd=3)
par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$C.inermis, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$C.inermis, bty='n', ann=F,ylim=c(0,0.325),type="n",axes=F,yaxt="n",xaxt="n", las=1)
lines(lo, col="darkorchid", lwd=3)
par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$T.mesacostalis, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$T.mesacostalis, ann=F,ylim=c(0,0.325),bty='n', type="n",yaxt="n",axes=F)
lines(lo, col='aquamarine', lwd=3)
par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$A.gregaria, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$A.gregaria, bty='n', ann=F,ylim=c(0,0.325),type="n",xaxt="n",yaxt="n")
lines(lo, col='dark slate grey', lwd=3)
par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$S.impressa, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$S.impressa, bty='n', ann=F,ylim=c(0,0.325),type="n",yaxt="n",axes=F,xaxt="n")
lines(lo, col="slategray2", lwd=3)
par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$C.eximium, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$C.eximium, bty='n', type="n",axes=F,ann=F)
lines(lo, col='purple', lwd=2)
par(new=TRUE)
#Stacked Extinct Loess:

extinct.col <- c("coral4", "indianred4", "darkorange4", "darkgoldenrod2", "red", "violetred", "tomato", "yellow2", "plum2", "sienna1", "deeppink")

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$C.hamiltonensis, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$C.hamiltonensis, bty="n", type="n", xlab='Depth Gradient', ylab='% Abundance', main="Extinct Species Environmental Ranges")
lines(lo, col="coral4", lwd=2)
legend('top', legend=extinct,bty='n', lty=1, lwd=4,pch=NA, col=extinct.col)

par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$P.devoniana, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$P.devoniana, type="n",bty='n', axes=F,ann=F)
lines(lo, col="indianred4", lwd=2)

par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$S.hystrix, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$S.hystrix, bty='n', type="n", axes=F,ann=F)
lines(lo, col="darkorange4", lwd=2)

par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$S.trulla, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$S.trulla, bty='n', type="n", axes=F,ann=F)
lines(lo, col="darkgoldenrod2", lwd=2)

par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$N.nervosa, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$N.nervosa, bty='n', type="n", axes=F,ann=F)
lines(lo, col="red", lwd=2)

par(new=TRUE)

lo <- loess.smooth(NMDS Env$Depth, NMDS_env$S.coelata, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$S.coelata, bty='n', type="n", axes=F,ann=F)
lines(lo, col="violetred", lwd=2)

par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$D.arcuata, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$D.arcuata, bty='n', type="n",axes=F, ann=F)
lines(lo, col='tomato', lwd=2)

par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$D.cayuta, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$D.cayuta, bty='n', type="n", axes=F,ann=F)
lines(lo, col="yellow2", lwd=2)

par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$S.infera, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$S.infera, bty='n', type="n", axes=F,ann=F)
lines(lo, col="plum2", lwd=2)
par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$Orthid.sp.A, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$Orthid.sp.A, bty='n', type="n",axes=F,ann=F)
lines(lo, col="sienna1", lwd=2)

par(new=TRUE)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$S.amanaensis, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$S.amanaensis, bty='n', ann=F,ylim=c(0,0.325),axes=F,yaxt="n",type="n")
lines(lo, col="deeppink", lwd=3)

par(new=TRUE)

#Individual Species Loess:
lo <- loess.smooth(NMDS_env$Depth, NMDS_env$Lingula, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$Lingula, bty='n', ylim=c(0,0.01), xlab='NMDS Axis 1 Depth', ylab='Mean prop. Abund.', main="Lingula", las=1)
lines(lo, col='black', lwd=3)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$S.impressa, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$S.impressa, bty='n', main="S.impressa", ylim=c(0,0.25), las=1)
lines(lo, col="slategray2", lwd=3)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$C.mesacostalis, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$C.mesacostalis, xlab='NMDS Axis 1 Depth', ylab='Mean prop. Abund.', main="C.mesacostalis", bty='n', ylim=c(0,0.02))
lines(lo, col="dodgerblue", lwd=3)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$R.grandis, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$R.grandis, xlab='NMDS Axis 1 Depth', ylab='Mean prop. Abund.', main="R.grandis", bty='n', ylim=c(0,.025), las=1)
lines(lo, col="darkgreen", lwd=3)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$D.walcotti, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$D.walcotti, xlab='NMDS Axis 1 Depth', ylab='Mean prop. Abund.', main="D.walcotti", bty='n', ylim=c(0,.001),las=1)
lines(lo, col="blue", lwd=3)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$W.hirsuta, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$W.hirsuta, xlab='NMDS Axis 1 Depth', ylab='Mean prop. Abund.', main="W.hirsuta", bty='n', ylim=c(0,1), las=1)
lines(lo, col='darkolivegreen', lwd=3)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$A.gregaria, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$A.gregaria, xlab='NMDS Axis 1 Depth', ylab='Mean prop. Abund.', main="A.gregaria", ylim=c(0,1), las=1)
lines(lo, col="darkslategrey", lwd=3)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$C.contractum, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$C.contractum, xlab='NMDS Axis 1 Depth', ylab='Mean prop. Abund.', main="C.contractum", bty='n', ylim=c(0,.25), las=1)
lines(lo, col='darkolivegreen4', lwd=3)
lo <- loess.smooth(NMDS_env$Depth, NMDS_env$T.mesacostalis, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$T.mesacostalis, xlab="NMDS Axis 1 Depth", ylab="Mean prop. Abund.", bty='n', main="T.mesacostalis", ylim=c(0,0.08), las=1)
lines(lo, col="aquamarine", lwd=3)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$C.chemungensis, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$C.chemungensis, xlab="NMDS Axis 1 Depth", ylab="Mean prop. Abund.", bty='n', main="C.chemungensis", ylim=c(0, .3), las=1)
lines(lo, col="darkolivegreen2", lwd=3)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$C.inermis, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$C.inermis, xlab="NMDS Axis 1 Depth", ylab="Mean prop. Abund.", main="C.inermis", bty='n', ylim=c(0,0.5), las=1)
lines(lo, col="darkorchid", lwd=3)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$F.chemungensis, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$F.chemungensis, xlab="NMDS Axis 1 Depth", ylab="Mean prop. Abund.", main= "F.chemungensis", bty='n'

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$C.eximium, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$C.eximium, xlab="NMDS Axis 1 Depth", ylab="Mean prop. Abund.", main="C.eximium", bty='n', las=1)
lines(lo, col='purple', lwd=2)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$S.infera, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$S.infera, ylab="Mean Prop. Abund.", xlab="NMDS Axis 1 Depth", bty='n', las=1, main="S.infera")
lines(lo, col="plum2", lwd=2)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$S.amanaensis, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$S.amanaensis, ylab="Mean Prop. Abund.", xlab="NMDS Axis 1 Depth", bty='n', ylim=c(0,.5), las=1, main="S.amanaensis")
lines(lo, col="deeppink", lwd=2)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$S.trulla, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$S.trulla, ylab="Mean Prop. Abund.", xlab="NMDS Axis 1 Depth", bty='n', ylim=c(0,.2), las=1, main="S.trulla")
lines(lo, col='darkgoldenrod2', lwd=2)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$D.arcuata, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$D.arcuata, ylab="Mean Prop. Abund.", xlab="NMDS Axis 1 Depth", bty='n', las=1, main="D.arcuata")
lines(lo, col='tomato', lwd=2)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$Orthid.sp.A, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$Orthid.sp.A, bty='n', ylab="Mean Prop. Abund.", xlab="NMDS Axis 1 Depth", ylim=c(0,0.15), las=1, main="Orthid.sp.A")
lines(lo, col="sienna1", lwd=2)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$D.cayuta, span = 2/3, degree = 1, parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$D.cayuta, ylim=c(0, 0.3), ylab="Mean Prop. Abund.",
xlab="NMDS Axis 1 Depth", bty='n', las=1, main="D.cayuta")
lines(lo, col="yellow2", lwd=2)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$N.nervosa, span = 2/3, degree = 1,
parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$N.nervosa, ylim=c(0,0.45), ylab="Mean Prop. Abund.",
xlab="NMDS Axis 1 Depth", bty='n', las=1, main="N.nervosa")
lines(lo, col="red", lwd=2)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$P.devoniana, span = 2/3, degree = 1,
parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$P.devoniana, ylim=c(0,0.0015), ylab="Mean Prop. Abund.",
xlab="NMDS Axis 1 Depth", bty='n', las=1, main="P.devoniana")
lines(lo, col="indianred4", lwd=2)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$S.williamsi, span = 2/3, degree = 1,
parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$S.williamsi, xlab='NMDS Axis 1 Depth', ylab='Mean Prop.
Abund.', bty='n', main="S.williamsi", ylim=c(0,.15), las=1)
lines(lo, col='darkslategrey',lwd=3)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$C.hamiltonensis, span = 2/3, degree = 1,
parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$C.hamiltonensis, ylim=c(0, 0.2), ylab="Mean Prop. Abund.",
xlab="NMDS Axis 1 Depth", bty='n', las=1, main="C.hamiltonensis")
lines(lo, col="coral4", lwd=2)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$S.hystrix, span = 2/3, degree = 1,
parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$S.hystrix, ylim=c(0,1), ylab="Mean Prop. Abund.",
xlab="NMDS Axis 1 Depth", bty='n', las=1, main="S.hystrix")
lines(lo, col="darkorange4", lwd=2)

lo <- loess.smooth(NMDS_env$Depth, NMDS_env$S.coelata, span = 2/3, degree = 1,
parametric=F, family = "gaussian")
plot(NMDS_env$Depth, NMDS_env$S.coelata, ylim=c(0, 0.4), ylab="Mean Prop. Abund.",
xlab="NMDS Axis 1 Depth", bty='n', las=1, main="S.coelata")
lines(lo, col="violetred", lwd=2)

#Regression:
Brach.reg <- read.csv('Pier Regression.csv', header=TRUE)
Brach.reg2 <- Brach.reg[,2:(ncol(Brach.reg))]
Brach.reg2 <- subset(Brach.reg2, select=-c(Total.Proportion...., Order,
 Per.Sample.Mean.Proportion, Endemism, Range))
model.null = glm(Extinct ~ 1,
data=Brach.reg2,
family = binomial())

model.full = glm(Extinct ~ Log.Sample.Mean + Latitude + Mean.Depth + Body.Size,
data=Brach.reg2,
family = binomial())

model.L = glm(Extinct ~ Latitude, data=Brach.reg2, family = binomial())
model.L.BS = glm(Extinct ~ Latitude + Body.Size, data=Brach.reg2, family = binomial())
model.L.MD = glm(Extinct ~ Latitude + Mean.Depth, data=Brach.reg2, family = binomial())
model.L.SM = glm(Extinct ~ Latitude + Log.Sample.Mean, data=Brach.reg2, family = binomial())
model.L.BS.MD = glm(Extinct ~ Latitude + Body.Size + Mean.Depth, data=Brach.reg2,
family = binomial())
```r
model.L.BS.SM = glm(Extinct ~ Latitude + Body.Size + Log.Sample.Mean, data=Brach.reg2, family = binomial())
model.L.BS.MD.SM = glm(Extinct ~ Latitude + Body.Size + Mean.Depth + Log.Sample.Mean, data=Brach.reg2, family = binomial())
model.BS = glm(Extinct ~ Body.Size, data=Brach.reg2, family = binomial())
model.BS.MD = glm(Extinct ~ Body.Size + Mean.Depth, data=Brach.reg2, family = binomial())
model.BS.SM = glm(Extinct ~ Body.Size + Log.Sample.Mean, data=Brach.reg2, family = binomial())
model.BS.MD.SM = glm(Extinct ~ Body.Size + Mean.Depth + Log.Sample.Mean, data=Brach.reg2, family = binomial())
model.MD = glm(Extinct ~ Mean.Depth, data=Brach.reg2, family = binomial())
model.MD.SM = glm(Extinct ~ Mean.Depth + Log.Sample.Mean, data=Brach.reg2, family = binomial())
model.SM = glm(Extinct ~ Log.Sample.Mean, data=Brach.reg2, family = binomial())

library(AICcmodavg)
all_model_list <- list(model.null,  
model.L, model.L.BS, model.L.MD, model.L.SM, model.L.BS.MD, model.L.BS.SM,  
model.L.BS.MD.SM, model.BS, model.BS.MD, model.BS.SM, model.BS.MD.SM,  
model.MD, model.MD.SM, model.SM)
all_model_names <- c("model.null",  
"model.L.BS.MD.SM", "model.BS", "model.BS.MD", "model.BS.SM", "model.BS.MD.SM",  
"model.MD", "model.MD.SM", "model.SM")
allmodelsel<-aictab(all_model_list, all_model_names, second.ord=T)

# Model Averaging:
top_5 <- list(model.L, model.L.BS, model.L.MD, model.L.SM, model.L.BS.SM)
top_5_names <- c("model.L", "model.L.BS", "model.L.MD", "model.L.SM", "model.L.BS.SM")
top_5_BS <- list(model.L.BS, model.L.BS.SM)
names_BS <- c("model.L.BS", "model.L.BS.SM")
top_5_MD <- list(model.L.MD)
names_MD <- c("model.L.MD")
top_5_SM <- list(model.L.BS.SM, model.L.SM)
names_SM <- c("model.L.BS.SM", "model.L.SM")

Parameter.Latitude <- modavg(top_5, 'Latitude', modnames=top_5_names, conf.level=0.95)
Parameter.Latitude
Parameter.BodySize <- modavg(top_5_BS, 'Body.Size', modnames=names_BS,  
conf.level=0.95)
Parameter.BodySize
Parameter.MeanDepth <- modavg(top_5_MD, 'Mean.Depth', modnames=names_MD,  
conf.level=0.95)
Parameter.MeanDepth
Parameter.SampleMean <- modavg(top_5_SM, 'Log.Sample.Mean', modnames=names_SM,  
conf.level=0.95)
Parameter.SampleMean

# Histograms:
Extinct.R <- subset(Brach.reg2, Extinct==1, select=-Extinct)
Survive.R <- subset(Brach.reg2, Extinct==0, select=-Extinct)
par(mfrow=c(2,1))

BS.E.log <- log10(Extinct.R$Body.Size)
BS.E.log
BS.S.log <- log10(Survive.R$Body.Size)
L.E.log <- log10(Extinct.R$Latitude)
```
L.S.log <- log10(Survive.R$Latitude)

hist(L.E.log, col="red", xlab="", xlim=c(1.3,1.8), main="Latitudes of Taxonomic Orders")
hist(L.S.log, col="green2", ylim=c(0,8), xlim=c(1.3,1.8), xlab="Latitude", main="")
hist(Extinct.R$Latitude, col="red", xlim=c(20, 55),main="Latitudes of Taxonomic Orders", ylab="", yaxt="n", xlab="")
axis(4, ylim=c(0,8))
hist(Survive.R$Latitude, col="green", xlim=c(20, 55), ylim=c(0,8), main="", xlab="Paleolatitude")

hist(Extinct.R$Body.Size, col="red", xlim=c(5, 35), main="Species Body Size", xlab="", ylab="")
axis(4, ylim=c(0,3))
hist(Survive.R$Body.Size, col="green", xlim=c(5,35), main="", xlab="Geometric Mean (mm)")

hist(BS.E.log, col="red", xlim=c(0.6,1.6),xlab="",main="Species Body Size")
hist(BS.S.log, col="green2", ylim=c(0,4), xlab="Geometric Mean (mm)", main="")

hist(Extinct.R$Mean.Depth, col="red", xlim=c(-1.5, 2), main="Species Preferred Depth", xlab="")
hist(Survive.R$Mean.Depth, col="green", xlim=c(-1.5, 2), main="", xlab="NMDS Axis 1 'Depth'")

hist(Extinct.R$Log.Sample.Mean, col="red", xlim=c(-3, -0), main="Species Proportional Mean Abundance", yaxt="n", xlab="")
axis(4, xlim=c(0,5))
hist(Survive.R$Log.Sample.Mean, col="green", main="", ylim=c(0,5), xlab="Proportional Mean Abundance", xlim=c(-3,0))

t.test(BS.E.log, BS.S.log)
t.test(L.E.log, L.S.log)

#Mann-Whitney U Test:
wilcox.test(BS.E.log, BS.S.log)
wilcox.test(L.E.log, L.S.log)
wilcox.test(Extinct.R$Mean.Depth, Survive.R$Mean.Depth)

#Parameter CI Figure:
library(plotrix)

Mean <- c(-0.23, -0.16, -0.48, -0.52)
LCI <- c(-0.43, -0.44, -2.83, -3.22)
UCI <- c(-0.03, 0.11, 1.87, 2.19)
CI.mat <- cbind(Mean, LCI, UCI)
CI.mat
row.names(CI.mat) <- c("Latitude", "Body Size", "Mean Depth", "Abundance")
CI.mat <- data.frame(CI.mat)

plotCI(x=1, y=-0.23, ui=-0.03, li=-0.43, ylim=c(-3.5, 2.5), xlab="Coefficient", xlab="Parameter")
plotCI(x=2, y=-0.16, ui=0.11, li=-0.44, add=T)
plotCI(x=3, y=-0.48, ui=1.87, li=-2.83, add=T)
plotCI(x=4, y=-0.52, ui=2.19, li=-3.22, add=T)