ARE BIOGEOGRAPHIC PROVINCES DISCRETE OR GRADATIONAL: A TEST IN THE LATE ORDOVICIAN OF LAURENTIA

by

CHELSEA ELLEN JENKINS

(Under the Direction of Steven M. Holland)

ABSTRACT

Provinces are the standard method of characterizing the spatial distribution of communities in ecology and biogeography. Provinces do not always exhibit clear boundaries or homogenous and compellingly distinct compositions. Similar provinces with spatially meaningful compositional overlap may be divisions along a biogeographic gradient. Four provinces have been recognized in the Late Ordovician of Laurentia: Appalachian, Southern, Midcontinent, and Western. These provinces correspond to geochemically distinct water masses based on isotopic analysis, and have been documented for several taxonomic groups. Spatial trends in the Jaccard similarities and ordination scores of faunal communities in these provinces presented here suggest these provinces are divisions of a continent-scale gradient driven by siliciclastic input and associated environmental effects of the Taconic Orogeny. Gradients can be useful in considering faunal distribution in terms of influential environmental factors and vice versa.

Observation of a gradient where provinces have been inferred suggests gradients are insufficiently documented in paleobiogeography.

INDEX WORDS: province, gradient, biogeography, Laurentia, Ordovician

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CHELSEA ELLEN JENKINS

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CHELSEA ELLEN JENKINS

Major Professor: Steven M. Holland

Committee: Susan T. Goldstein
Arnold I. Miller

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
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CHAPTER 1

INTRODUCTION

This thesis is presented as one chapter, as it is composed in the format of a manuscript intended for submission to the journal *Paleobiology.* The second chapter includes the background, methods, results, discussion, and conclusions. The third chapter concludes this thesis.

Provinces are used to characterize the spatial distribution of communities in ecology and biogeography (Wallace 1876; Spalding et al. 2007). Criteria used for defining provinces varies by focus and by researcher (Ekman 1953; Briggs 1975; Knox 1980). Provincial boundaries are not always discrete. Furthermore, faunal compositions of adjacent provinces can be similar, and faunal composition is not homogenous across provinces (Adey and Steneck 2001). Adjacent provinces with similar faunal makeup may be divisions on a gradient.

Biogeographic provinces are often bounded by changes in environmental characteristics, and these environmental characteristics vary along gradients (Adey and Steneck 2001). For this reason, gradients may be useful in considering faunal distribution directly in terms of variation of important environmental factors.

The purpose of this study is to compare recognized biogeographic provinces in the Late Ordovician of Laurentia in terms of faunal similarity and spatial patterns in similarity to determine if distribution patterns are better described by distinct provinces or as a gradient.

CHAPTER 2

ARE BIOGEOGRAPHIC PROVINCES DISCRETE OR GRADATIONAL: A TEST IN THE LATE ORDOVICIAN OF LAURENTIA[1]

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[1] Jenkins, C.E., and Holland, S.M. To be submitted to Paleobiology.

"Provinces must, to be understood, be traced back, like species, to their history and origins in past time"

Forbes (1859)

Introduction

Biogeographic provinces are often used to describe the spatial organization of ecology. Provinces are the results of physical, chemical, and biological environmental factors that limit dispersion (Jablonski et al. 1985). As these factors change spatially and through time, provinces are dynamic, and because they describe how fauna are organized, they are considered a fundamental unit in biogeography. The size and number of provinces through time have implications for diversity, although it is unclear exactly how much provinciality, rather than community teiring and distance or habitat area, controls diversity (Valentine et al. 1978; Sepkoski 1988; Miller et al. 2009; Holland 2010). Provinces are used to guide biotic conservation efforts (Spalding et al. 2007), as ecological tools in paleobiogeographic studies (Sclafani and Holland 2013), and for reconstructing paleogeography (McKerrow and Cocks 1986).

Understanding the environmental factors that lead to provinciality promotes better characterization of faunal distributions. Applying the first tenant of biogeography suggests that closer locations will be more compositionally similar (Tobler 1970), but this alone does not describe ecological patterns. Physical boundaries, such as continents or large expanses of deep ocean often bound provinces, but other boundaries tend not to be so absolute, such as environmental bounding factors like temperature, salinity, or substrate (Spalding et al. 2007). There is no reason to expect that these environmental factors produce discrete boundaries in space. Environmental factors changing along a gradient are familiar (e.g., temperature, pressure, oxygen availability), and biogeographic provinces often do not have sharp or easily defined boundaries (Adey and Steneck 2001; Briggs and Bowen 2012). Biogeographic distributions known to be controlled, at least in part, by these factors could be expected to reflect the controlling gradients. Depending on the steepness of a gradient, divisions along the gradient, or provinces, may be discernible. However, if the factors that *control* the phenomena that provinces describe are of interest, gradients may be more useful.

Provinces are increasingly being utilized as units for conservation efforts as our own modern environment changes (Spalding et al. 2007). It is forecasted that the organization of provinces will become increasingly unstable as climate changes, with biogeographic provinces variably reacting to the rise or demise of certain key taxa as well as to the changes in boundary-defining conditions (Hiscock et al. 2004). Null models suggest climate change will disproportionately affect fauna near provincial boundaries, owing to the concentration of species occupying the extreme ends of their range (Roy 2001). The Late Ordovician is an ideal time to study the dynamics of provinces and potential gradients, as it is a time characterized by great and varied environmental change from Hirnantian glaciation and tropical cooling, as well as the effects of the Taconic orogeny (Holland and Patzkowsky 1996, 1997).

In the Late Ordovician of Laurentia, four provinces have been recognized: the Appalachian, Midcontinent (Missouri, upper Mississippi valley, Michigan, to western Pennsylvania and New York), Southern (Cincinnati Arch and Nashville Dome), and Western Provinces (New Mexico, Colorado, Wyoming, and most of Canada; Fig. 1).

These provinces correspond to geochemically distinct water masses based on isotopic analysis (Holmden et al. 1998). Faunal distribution patterns in some taxonomic groups support these provinces, including corals (Elias 1982; Elias 1983; Elias and Young 1998), conodonts (Sweet and Bergstrom 1974; Barnes and Fahraeus 1975; Bergstrom 1983), ostracods (Mohibullah et al. 2012), bryozoans (Antsey 1986), and other distinctive trace-fossil and community assemblages (Jin et al. 2012). These provinces also have distinct relative abundance distributions as indicated by analysis of Hubbell's theta (Sclafani and Holland 2013). Given that these provinces may have environmentally driven bounding factors that operate on a gradient, this study seeks to understand whether provinces adequately describe spatial patterns in faunal similarity at continental and regional scales in the Late Ordovician Laurentia, or if these patterns are better described as one or more gradients.

Background

Provinces.———Provinces have long been a cornerstone of biogeography (Wallace 1876; Jablonski et al. 1985; Spalding et al. 2007). In the hierarchical biogeographic area classification system, provinces are nested within realms, which tend to be continent to subcontinent-sized areas with coherent biotic assemblages at higher (generic to familial) taxonomic levels (Udvardy 1975). Provinces are a subdivision of these realms, and are generally delineated at the specific and generic taxonomic levels. Distinct, coherent suites of fauna at these levels arise from historical isolation and other abiotic controls, such as geomorphological features, hydrographic features (e.g., currents, upwelling, ice), and geochemical features (e.g., nutrient supply, salinity), where changes in these factors create boundaries to dispersal (Spalding et al. 2007). The concept of a province is theoretically straightforward, but the process of defining a province can be complicated.

Defining Provinces.———Provinces can be defined several ways, depending on available data. In modern environments, provinces can be delimited with detailed measurements of temperature, salinity, chemical characteristics, faunal characteristics, and productivity (Szekielda 2005). Such data may be unattainable in the distant past, so ancient provinces are usually defined with features observable in the rock record, such as faunal composition (Briggs 1995), and proxies for environmental characteristics, such as geochemical characteristics as a proxy for water mass mixing (Longhurst 1998).

Biogeographic provinces are based on faunal composition, and they are often characterized as regions with large numbers of shared endemic fauna (Albanesi and Bergstrom 2010). In marine systems, faunally defined provinces are generally nested within climate-based domains, which are in turn nested within water-depth based realms (Zhen and Percival 2003). While provinces have long been recognized in ecological studies (Wallace 1876), the criteria for defining provinces has been anything but standard. Early provinces tended to be more qualitative and corresponded largely to bathymetric divisions and climate zones (Wallace 1876; Forbes 1859). Early attempts to quantify provinces focused on degree of endemism (Woodward 1856) or on species spatial ranges (Schenck and Keen 1936). Problematically, thresholds of endemism to characterize provinces are highly variable and often author-dependent. Widely used classification systems cover a considerable range of endemic requirements: Woodward's provincial index (1856) requires at least 50% endemism to define a province, Ekman (1953) requires 20% endemism, Kauffman (1973) uses 25-50% endemism, Briggs (1974, 1995) requires 10% endemism, and Rosenzweig (1995) requires 60-80% endemism.

The use of endemism to define provinces, especially in the fossil record, is logistically problematic and perhaps even conceptually unsound (Adey and Steneck 2001). Endemic species tend to be less abundant than cosmopolitan species and so are less commonly preserved and likely to be underrepresented. When preserved, endemism can still be ambiguous. Even in the modern oceans, phylogenetic studies are reclassifying some known species that were previously unrecognized as endemic species (Bowen et al. 2006; Drew et al. 2010). Critics of the concept behind the endemism approach argue that regions with high endemism, which are often isolated, may not be representative of regional biogeography, and that using rare taxa is a poor way to characterize a biota (Adey and Steneck 2001). Defining provinces based on endemism alone yields a myriad of isolated island communities in the modern Pacific Ocean, but fails to distinguish separate communities in large areas of the Indo-Pacific over which faunal changes are gradual but drastic (Spalding et al. 2007). Steinbeck and Ricketts (1941) argue directly with the endemism approach, asserting that provinces should be defined based on the most populous and characteristic species of a region.

The endemism problem has been addressed in various ways, ranging from approaches rooted exclusively in faunal characteristics including species range (Schenck and Keen 1936; van den Hoek 1984) and community similarity (Campbell and Valentine

1977; Culver and Buzas 1980) to approaches that consider faunal characteristics in conjunction with physical or environmental factors (Knox 1980; Spalding et al. 2007), to approaches that nearly remove fauna from the process entirely, focusing instead on environmental characteristics to which faunal distributions respond (Adey and Steneck 2001). Schenck and Keen (1936) used collections of midpoints of species ranges under the assumption that these midpoints would converge at the center of provinces. This technique received some criticism (Newell 1948) for the use of midpoints and what were later considered faulty assumptions (Hedgpeth 1957). Van den Hoek (1984) improved on this method by defining provinces based on extensively overlapping ranges of groups of species. These provinces broadly agree with the endemism-based and widely agreed upon provinces of Briggs (1974). Campbell and Valentine (1977) considered provinces in terms of endemism as well as taxonomic similarity to adjacent regions by classifying the Virginia Province as a province despite insufficient endemism, because it contained less than 50% shared taxa with either neighboring province. Culver and Buzas (1980) did not consider endemism directly, and instead defined provinces in benthic foraminifera entirely on cluster analysis of taxonomic compositions. Knox (1980), in something of a synthesis of many of these approaches, used a combination of factors: characteristic groups of species, relict groups with long evolutionary history, absence of typical species or groups of species from adjacent areas, endemism, and characteristic habitat zonation.

Adey and Steneck (2001) focus on environmental and physical factors almost exclusively in their model to predict biogeographic provinces. Their provinces are constructed entirely based on temperature, coastal area, geographic isolation, and how these may change over the geologic time necessary to evolve distinct biotas (given in this study as less than 3-5 Myr). Provinces constructed using this physical/time model exhibited 90% spatial and taxonomic agreement with the recognized taxonomically defined hard-substrate algae provinces of Briggs (1974).

With the benefit of increased phylogenetic work, Spalding et al. (2007) expanded on all of the aforementioned techniques by combining faunal and environmental characteristics. They considered: endemism, shared evolutionary history, patterns of dispersal, isolation, distinct bathymetry, hydrography, climate, and geochemistry in defining provinces. Increased integration of spatial patterns in physical environmental characteristics to modern biogeographic classifications provides a compelling case for understanding how environmental characteristics preserved in the fossil record, such as substrate composition, might have controlled ancient biogeography.

Defining ancient provinces raises additional complications owing to the challenges of observing ecosystems through the lens of the rock record. Environmental factors that may serve as boundary conditions for a province are not directly measurable in the distant past. Some of these factors may be addressed through proxies, such as isotopic signatures that may relate to temperature or indicate the degree of water mixing. There is precedent for using geochemical criteria to delineate provinces in the modern ocean (Longhurst 1998). Preservational biases may also complicate biogeographic classification. Nonetheless, analyses of distributional ranges and faunal similarity (Jaccard's coefficient) of molluscs on the coast of California delineate provinces that are repeatable in the fossil record (Valentine 1966). Using similarity comparisons alone, modern provinces can be resolved at the generic and, excepting some contiguous provinces, at the family level in bivalves and gastropods (Campbell and Valentine 1977).

Gradients.———Gradients are increasingly recognized as useful tools in explaining spatial patterns in species distributions. The environmental conditions that usually define biogeographic boundaries typically vary along a gradient rather than in discrete intervals, for example, temperature, depth, substrate, and salinity (Spalding et al. 2007). As a result, biogeographic provincial boundaries are often not sharp, and they shift through time (Adey and Steneck 2001). Discrete borders between contiguous provinces can be especially difficult to resolve even in modern environments. For example intermediate provinces in the western Atlantic are difficult to delineate and do not meet classically defined provincial thresholds that describe adjacent provinces (Campbell and Valentine 1977). This pattern is consistent with overlaying provinces, or divisions, along a continuous gradient.

The case for environmental gradients controlling taxonomic distributions is well established but underutilized. Temperature gradients are well known to be important factors in the distribution of benthic algae (Cambridge et al. 1990; Adey and Steneck 2001), and coral reefs and kelp beds (Mann 2000). Thermal gradients may drive more than species distribution but also diversity itself, and they are considered a driving factor in the latitudinal diversity gradient (Jablonski et al. 2013). Depth gradients are also important in describing faunal distributions (Rex 1983). Historically, depth-related zones have served as a first-order classification for marine faunal distributions, and depth is one of the primary driving factors in defining biogeographic realms today (Rex 1983;

Spalding et al. 2007). Substrate composition is also recognized to vary as a gradient and exert some control on the distribution of benthic taxa (Adey and Steneck 2001; Holland et al. 2001).

Provinces and gradients are not necessarily mutually exclusive. Gradients may be simplified or reduced to provinces. For example, the rainbow is a simplification of the visible light spectrum, a gradient. Assigning provinces to portions of gradients is easier when these gradients are steeper, such that species distributions may seem discontinuous, but becomes harder when gradients are more gradual such that characteristic species exhibit overlapping distributions (Springer and Bambach 1985). It may also be the case that provinces appear to be common when data resolution is too low to appreciate gradational change. Understanding the relationship between abiotic gradients and the faunal provinces superimposed upon them could have direct applications for predicting the reaction of provinces to today's changing climate. Steepening of the latitudinal thermal gradient in the Neogene, when higher latitudes cooled while the tropics warmed, led directly to an increase in diversity and provinciality (Jablonski et al. 1985).

Scientists are constantly evolving understanding of natural phenomena. Accepting gradients as an important control on the pattern of provincial distributions would not be unlike the use of gradients to understand community composition. Long-held beliefs in the concept that communities are local groups of interacting species have gradually given way to the idea that communities involve interactions between populations of an entire region over multiple spatial and temporal scales (Ricklefs 2008). Understanding patterns in diversity requires developing an understanding of regional-scale environmental factors and historical influences that can control species distributions across all spatial scales (Ricklefs 2004).

Provinces in the Late Ordovician of Laurentia.———In the Late Ordovician of Laurentia, there are four traditionally recognized provinces that are based on faunal distributions and environmental characteristics: the Appalachian, Midcontinent, Southern, and Western Provinces (Fig. 1). These provinces have variable support depending on what taxa are being used to define them. Considering water-depth, climate, and endemic fauna, while using conodonts, one continent-scale Early-Middle Ordovician Laurentian province has been identified that spans all of Laurentia (Zhen and Percival 2003). Using similar criteria, ostracods have been used to identify a Midcontinent and a Southern Marginal province in the Late Ordovician of Laurentia (Mohibullah et al. 2012). Multiple faunal variables can be combined to classify a provincial signature. For example, in bryozoans, combining summed percents of trepostomes, upper tier, endemic, and geographically restricted genera were used to identify a provincial signature of three Late Ordovician Laurentian provinces: the Red River-Stony Mountain, Cincinnati, and Reedsville-Lorraine (Antsey 1986). These correspond to the Western, combined Midcontinent and Southern, and Appalachian Provinces in this study.

Provinces defined by environmental characteristics in the Late Ordovician (Fig. 1) have been determined using geochemical and trace fossil occurrence data (Holmden et al. 1998; Jin et al. 2012) as proxies for water mass mixing. Neodymium isotopes measured on apatite from conodonts reflect the neodymium signature of the overlying water during deposition (Holmden et al. 1998). Neodymium signatures of Late Ordovician conodonts from across Laurentia differ significantly from those of conodonts from the Iapetus Ocean, indicating that Laurentian epicontinental seas did not mix appreciably with the Iapetan Ocean. In the same study, $\delta^{13}C$ varied systematically across different aquafacies, or provinces. Indicative of oxygen content and dissolved organic carbon input, the $\delta^{13}C$ signatures in this study decrease from south to north from the Midcontinent through the Southern and Appalachian aquafacies. When εNd, $\delta^{13}C$, and lithology are considered, the Midcontinent, Appalachian, and Southern provinces are distinguishable from one another, suggesting they represent relatively distinctive water masses that are defined by temperature and salinity (Holmden et al. 1998). The low degree of mixing among these water masses is taken to support provinciality.

Although the geochemical signatures of the Western Province are currently unknown, it has a distinctive *Thallassinoides* ichnofacies (Jin et al. 2012). Recognized faunal similarities in rugosan corals (Elias 1982), sponges (Carrera and Rigby 1999), conodonts (Sweet and Bergstrom 1984) and bryozoans (Anstey 1986) in the region also support the existence of the Western Province.

There is some precedent for recognition of a proximity gradient relative to siliciclastic source area in the Appalachians (Springer and Bambach 1985). Five communities dominated by lingulids, bivalves, *Rafinesquina*, *Onniella (Dalmanella)*, and *Sowerbyella* were recognized in the Appalachian Basin and are interpreted to represent a dual gradient of depth and environmental disruption paired with distance from a clastic source, the Taconic highlands. It is unclear to what extent this gradient is dominated by water depth rather than proximity to Taconic orogenesis.

Environmental Setting of the Late Ordovician of Laurentia.———Despite remaining in tropical latitudes during the Ordovician, eastern Laurentia experienced a shift in water temperature, seawater chemistry, siliciclastic supply, and faunal composition in the Late Ordovician (Holland and Patzkowsky 1996,1997). Changes in seawater temperature are inferred from the physical and chemical properties of carbonates preserved on the craton, but the direct cause of temperature change remains unclear. Tropical-type conditions return in the late Cincinnatian (C5-C6), before onset of the Hirnantian glaciation (Holland and Patzkowsky 1996,1997).

Temperature and seawater chemistry change across the M5 sequence boundary, over the transition from the Mohawkian to Cincinnatian Series. Carbonates below the M5 sequence boundary are rich in skeletal grains, ooids, peloids, and lime mud, an assemblage associated with carbonates in modern tropical environments. Carbonates above the M5 sequence boundary lose skeletal grain diversity, and have little to no ooids, peloids, and lime mud, an association typical of modern cooler water carbonates (Holland and Patzkowsky 1996; Pope and Read 1998).

Phosphatization in the Whiterockian through the Mohawkian is limited to hardgrounds in transgressive deposits, but in the M5-C4 strata, phosphatization becomes widespread, and occurs as replacements of skeletal grains and in phosphatic lags at sequence boundaries (Holland and Patzkowsky 1996; Pope and Read 1997).

During this time of temperate-type carbonate deposition, many characteristic eastern Laurentian fauna disappear from the Appalachian area, including *Oepikina, Glyptorthis,* and *Leptaena*. Some, but not all of this fauna, primarily rugosans and brachiopods, including the brachiopods *Glyptorthis* and *Leptaena*, return to eastern Laurentia later in the Cincinnatian (Patzkowsky and Holland 1996). Some of these disappearing faunal elements occur in the interim in the Southern Province to the west, which continues to record tropical-type carbonates through this time.

Cooler temperatures have been attributed to global sea water temperatures falling at the earliest onset of Gondwanan glaciation (Pope and Read 1998), cooler deep waters upwelling from the Sebree Trough in the midcontinent (Kolata et al. 2001), some combination of tectonic and climatic forcing (Ettensohn 2010), or from upwelling through the Appalachian Basin (Railsback et al. 1990; Holland and Patzkowsky 1997).

Two pulses of increased siliciclastic input are observed. The first is associated with the Whiterockian Blountian phase of the Taconic orogeny, and the second is associated with the mid-Mohawkian phase of the Taconic orogeny (Holland and Patzkowsky 1996). The second phase was of a greater magnitude and areal extent, and led to the deposition of shallow-water sands in the present-day western Appalachians. These depositional patterns correspond with the transition from a deep carbonate ramp to a turbidite basin with increased subsidence and sediment input (Holland and Patzkowsky 1996). Alternatively, increased siliciclastic input, decreased carbonate deposition, and concurrent loss of evaporites have also been interpreted to indicate a shift from semi-arid to cooler and more humid climatic conditions (Pope and Read 1998). Given that environmental conditions exert some control on faunal distribution, it seems possible that variable siliciclastic supply might produce a substrate gradient sufficient to drive a biogeographic gradient across Laurentia in the Ordovician.

Methods

The overall approach in this project is to test the similarity between faunal assemblages across Laurentia to determine if a biogeographic gradient is present. This is done by comparing the faunal similarity between each combination of provinces at the continental scale, and between each combination of regions at the regional scale. Similarity is measured in terms of the most abundant taxa in each province or region, and in terms of quantified similarity using a Jaccard coefficient. At the regional scale, patterns in similarity are examined using Jaccard coefficients along with an ordination.

Continent Scale.———Occurrence data for shallow subtidal collections from the Ordovician in modern North America with age and geographic information was downloaded from the Paleobiology Database (Paleobiology Database 2013; Appendix 1). Occurrence data was also downloaded for shallow-subtidal collections from the United Kingdom (Avolonia) in the Late Ordovician to serve as an outgroup for comparison. Collection**s** of occurrences were sorted into Early, Middle, and Late Ordovician based on epoch, stage, or million year bin when given. The Early Ordovician includes Stairsian, Tremadocian, Tulean, and Blackhillsian stages, as well as Paleobiology Database million year bins Ordovician 1 and some of Ordovician 2. The Middle Ordovician includes Rangerian, Chazyan, Darwillian, and Whiterockian stages and Paleobiology Database million year bins Ordovician 2 and 3. The Late Ordovician includes the Turinian, Chatfieldian, Maysvillian, Ashgill, Richmondian, Gamachian, and Hirnantian stages as well as Paleobiology Database million year bins Ordovician 4 and 5. When age fields were found blank, incorrect, or ambiguous, member and formation information was used to resolve the age of the collection with reference to correlation charts (Ross et al. 1982), and the USGS Lexicon (United States Geological Survey 2012). If a collection age could not be designated to one of these three time intervals, the collection was excluded from the study by virtue of never being called in analysis. Late Ordovician occurrence data in the Appalachian province was supplemented with data from Bretsky (1970: Table 3).

Collections were assigned to one of the four recognized Late Ordovician provinces. Latitude and longitude coordinates for every collection were entered into ArcGIS (ESRI 2009), and using the point-in-polygon tool, were assigned an attribute corresponding to which province the collection should belong to. These assignments used modern latitude and longitude coordinates and an approximation of these provincial boundaries plotted on a modern map of North America. The boundaries for these provinces are primarily based on the aquafacies delineated by Holmden et al. (1998) and the Western Province outlined by Jin et al. (2012). For this analysis, the polygons representing provinces were forced to share edges to ensure that all collections were assigned to a province.

Occurrence data were corrected in several ways before analysis. Collections with no environmental information or that had contradictory environmental information were removed. Collections associated with Dalve's (1948) compendium of fossils from the Cincinnati Arch were removed because these were considered uniquely thorough and deemed incomparable to collections for every other region in the database. Occurrences of "*Lingula*" were replaced with "lingulid" to standardize the treatment of linguliform brachiopods during this interval. Occurrences of *Schizambon*, camerates, and *Skolithos* were removed, and any observed spelling errors in genera were corrected.

The similarity among provinces across Laurentia was measured with the Jaccard coefficient of similarity (Jaccard 1912). Within each time interval, occurrence data from all collections within each province were summed to make one collection with presence-absence data representative of the entire province. These aggregated collections were compared to each other province within the same time interval using Jaccard's coefficient of similarity, computed with vegdist() in the vegan package of R (R core Team 2012). Vegdist gives the Jaccard's dissimilarity between collections, so this result was subtracted from 1 to express faunal similarity from 0 (no common genera) to 1 (identical). In the Late Ordovician, each province was also compared to the outgroup data from the United Kingdom to establish the level of similarity typical of well-established provinces.

Regional Scale.———Data for the regional scale study of similarity across the border of two adjacent provinces in the eastern United States was obtained through field work. Collections from the shallow subtidal deposits of the C1 and C2 sequences of the Cincinnati Arch and Nashville Dome were obtained from previous studies (Patzkowsky and Holland 1999; Holland and Patzkowsky 2007; Appendix 2). New faunal samples were collected from the shallow subtidal of the C1 and C2 sequences from five regions in the Appalachian Basin (Fig. 2; Appendices 3,4), following the same protocol used to obtain the existing samples.

Within each region of the Appalachians, localities were selected to represent different strike belts by selecting outcrops on different ridges in the Valley and Ridge. At each locality, sample locations were selected from the Reedsville and Martinsburg formations (Fig. 3). The shallow subtidal facies was identified in the field based on massively bedded or highly bioturbated sandstones, or bioturbated fining-upwards interbedded fossiliferous packstones or mudstones. Tops of parasequences were targeted, and when possible, sampling targeted the stratigraphically highest shallow subtidal packages below the transition to peritidal or terrestrial facies, particularly the tidal flat deposits of the overlying Juniata Formation.

Each bulk sample was roughly the size of one or two gallon-sized bags. Each sample was constrained to a bed as much as possible, and 2-4 replicate samples were taken from different beds at each locality. In the lab, every visible fossil in these samples was identified to the genus level when possible, such that whole-fauna abundance counts were made for each sample. Unless obvious diagnostic features were readily visible, bryozoans were identified by morphological groups: thin ramose, thick ramose, thin bifoliate, thick bifoliate, encrusting, and massive trepostome following Holland and Patzkowsky (2007).

Samples containing only a single taxon or fewer than two dozen individuals were excluded from the study. In total, 36 samples were collected from 13 localities in the Appalachians. These were compared to 49 samples obtained from 11 localities in the Cincinnati Arch, and 13 samples collected from 8 localities in the Nashville Dome.

Analysis for the regional scale study of similarity in the eastern United States included similarity comparisons using presence-absence and relative abundance data. Using both types of data allows these approaches to be compared. Collections from every combination of two regions from the two Southern Province (Nashville Dome and Cincinnati Arch) and the five Appalachian Province regions were compared using both presence-absence and relative abundance (Appendix 5). Every pairwise comparison of collections from two regions was compared to make a distance matrix. Jaccard's coefficient was used for presence-absence data, and a quantified Jaccard's coefficient (Chao et al. 2005) was used for relative-abundance data. These dissimilarities were subtracted from 1 to make similarity coefficients, and a logit transformation (Ashton 1972) was applied to the matrices to account for these values being bounded by 0 and 1. This logit transformation is in the car package in R; it allows one to 'bump' 0 and 1 values to prevent errors in statistical tests. Values of 0 and 1 were altered by ±.0001 to prevent overlapping with raw values that are close to 0 or 1.

Student's t-tests were used to determine the mean Jaccard coefficient for each comparison as well as 95% confidence interval. These values were back-transformed from the logit scale using the inverse-logit function (boot package of R). The similarity between each pairwise comparison between regions was plotted against the great circle distance between the centroid of localities in both regions to quantify how similarity relates to distance.

A non-metric multidimensional scaling (NMDS) ordination was applied to the data to assess spatial trends in the faunal composition of samples. This ordination is based on the relative abundance data from all of the collections and results are shown later coded by region. This NMDS was calculated using metaMDS() in the vegan package in R, which provides taxon scores as well as collection scores. A scree plot was generated to determine that three axes should be used in the ordination to maximize simplicity and reduction in stress of the ordination (R code available in Appendix 6).

Results

Continent Scale.———Magnitude and spatial patterns in similarity support provinces and gradients that are dynamic over the length of the Ordovician (Fig. 4; Appendix 5). A few abundant taxa characterize each province (Tables 1-3). Values of similarity among the provinces through the entire Ordovician are low (.051-.25), but there is a spatial pattern in the similarity among the provinces. By the Late Ordovician, the Appalachian province becomes less similar to the rest of Laurentia, while similarities between the other regions remain intermediate.

Data are sparse in the Early Ordovician, making spatial comparisons difficult to assess. Where data exist, the patterns fit what is typical of the rest of the Ordovician (Fig. 4, Table1)**.** The Appalachian and Western Provinces are not very similar. In the Early Ordovician, cephalopods dominate the Appalachian Province and trilobites dominate the Western Province (Table 1). The Appalachian and Western Provinces exhibit low values of similarity (Fig. 4). Early Ordovician data for the Midcontinent Province are absent and only one useable collection exists, that contains only cephalopods in the Southern Province, making the data insufficient for this study.

In the Middle Ordovician, Laurentian Provinces begin to show spatial patterns indicative of a gradient, while remaining well-differentiated (Fig. 4, Table 2). The Appalachian Province is represented overwhelmingly by bryozoans, and the Southern

Province is largely characterized primarily by brachiopods, but bryozoans, gastropods, and trilobites are also common (Table 2). The Midcontinent has a similar makeup to the Southern Province at a higher taxonomic level, but without common bryozoan representatives. The Western Province in the Middle Ordovician is dominated by trilobite occurrences, but with some brachiopods and ostracods. The Western Province is the least similar to other Laurentian provinces. The Southern and Midcontinent provinces are the most similar, and they are also the most similar of any pair of provinces in any time interval (.25). Similarity values between the Appalachian and Midcontinent, and between the Appalachian and Southern are intermediate.

Spatial patterns in similarity are well established by the Late Ordovician (Fig 4, Table 3). The Appalachian province becomes the least similar to the rest of Laurentia, while comparisons between the Western and Midcontinent and Western and Southern province remain intermediate. The Appalachian province can be characterized primarily by its bivalves and brachiopods (Table 3). Brachiopod genera are the most represented genera in the Southern province, while bryozoans are the most represented in the Midcontinent. The Western province is dominated by coral genera, while trilobite genera no longer rank among the 10 most reported genera in the Western Province. In the Late Ordovician, the Appalachian and Western provinces are the least similar to each other (.051), and they are also the least similar of any two Laurentian provinces in any time interval (.051). This Jaccard similarity value is comparable to those between the United Kingdom outgroup and all of the Laurentian provinces (.036-.056). The Southern and Midcontinent provinces remain the most similar (.228). In the Late Ordovician, the

Appalachian Province is most similar to the Southern Province, which is most similar to the Midcontinent Province, which is the most similar province to the Western Province (Fig. 4).

Regional Scale.———Regional-scale results also indicate a gradational pattern in similarity (Fig. 5). This pattern is evident in the taxa that characterize each region (Table 4), the similarity between regions (Fig.5; Appendix 5) , and in ordination (Fig. 6). Similarity between regions is related to distance, but distance alone does not account for all of the variation in similarity (Fig. 8).

Abundance among genera and higher taxa show systematic spatial trends at the regional scale (Table 4). Bryozoans, especially ramose bryozoans, tend to be well-represented among all regions except the northernmost Appalachians. Articulate brachiopods are more abundant and diverse in the Cincinnati Arch and Nashville Dome collections, and become less abundant and less diverse northward in the Appalachian regions. Appalachian region 1 contains five genera of articulate brachiopods, while Appalachian region 5 contains only two brachiopod genera. Gastropods are present, but are not among the most abundant genera in the Southern Province. Gastropods are more abundant and more diverse in the Appalachian collections, particularly in the northernmost Appalachian region 5, where there are four genera of gastropods, and two of these are the most abundant genera. Bivalves are present in the Nashville and Cincinnati collections, but are not among the most abundant taxa. Bivalves are increasingly well represented from south to north in the Appalachian regions.

Among Appalachian collections, the northernmost and southernmost collections are the least similar. Between Appalachian and Southern province collections, similarity decreases northward along the Appalachian province, that is, the southern Appalachian collections are more similar to those of the Southern province than are northern Appalachian collections. Appalachian collections are more similar to collections from the Cincinnati Arch than to collections from the Nashville Dome.

Presence-absence data and relative abundance data display similar patterns. Comparisons using both data types show a south to north decline in similarity between the Appalachians and both Southern Province regions. Both types of data show Nashville collections are less similar to Appalachian collections than they are to Cincinnati collections, and Nashville collections are less similar to Appalachian collections than Cincinnati collections are to Appalachian collections. Among the Appalachian collections, comparisons using both types of data show the same trend of adjacent regions exhibiting higher similarity, while regions that are farther apart exhibit lower similarity. Appalachian regions 1 and 2 are anomalously similar for both types of data.

Presence-absence comparisons exhibit higher similarity with a larger range and greater uncertainty than relative abundance comparisons. Presence-absence comparisons yield slightly higher values (.021-.336) for similarity than do comparisons based on relative abundance (.010-.256). There is a higher range in similarity values using presence-absence (.316) than relative abundance (.246). Presence-absence comparisons; that is, the 95% confidence interval is larger for presence-absence comparisons. The 95% confidence interval on presence-absence similarity is 1.08-2.52 times greater than the confidence interval on the same comparison using relative abundance data, except for the comparison between Appalachian region 1 and the Cincinnati collections, for which the confidence intervals are nearly the same.

Ordination of these collections indicates a gradational spatial pattern in faunal composition among Southern and Appalachian collections, manifested along NMDS axis 1 (Fig. 6). NMDS1 scores increase from Nashville and Cincinnati collections to southern Appalachian collections to northern Appalachian collections. Overlap among Appalachian collections and Southern Province collections suggest that the boundary between these regions is gradational.

Appalachian collections are closer in NMDS1 and NMDS2 scores to Cincinnati collections than Nashville collections, excepting two anomalously high-scoring Nashville collections. These collections are found to have an unusually high abundance of *Orthorhynchula*, a brachiopod typically characteristic of northern Appalachian collections. Taxon scores in this ordination space (Fig. 7) show that taxa that typically prefer siliciclastic substrates including bivalves and gastropods score higher on NMDS1 than more typically carbonate substrate dwelling organisms.

Cincinnati collections plot higher on NMDS axis 2 than Nashville collections. Cincinnati collections and Appalachian collections have similar NMDS axis 2 scores. There is little overlap between the Cincinnati collections and the Nashville collections, or between the Appalachian collections and the Nashville collections. It is unclear what, if any, faunal patterns are involved in NMDS axis 2 separation.

Distance.———Overall similarity decreases with distance, but distance does not explain the majority of the trend in similarity (R^2 =0.242, Fig. 8a). Each set of comparisons exhibits an inverse relationship between distance and similarity, but there is considerable scatter in similarity measured at shorter distances compared to longer distances. Variability in measured similarity decreases with distance, particularly at distances exceeding 600 km. The lines of best fit differ among each set of comparisons, indicating that similarity relates to distance differently for each set. Distance explains more variation in similarity for Cincinnati to Appalachian collections (R^2=0.593, Fig. 8b) than for Nashville to Appalachian comparisons (R^2=0.148, Fig. 8c) or within-Appalachian comparisons (R^2= 0.121, Fig. 8d). Cincinnati to Appalachian comparisons consistently plot above the line of best fit for the entire data set, that is, they exhibit higher similarity than is expected for the distance between collections. Nashville to Appalachian comparisons consistently plot below the line of best fit for the entire data set, and they exhibit lower similarity than is expected given the distance between these collections. Comparisons between regions in the Appalachian province are better approximated by the line of best fit for the entire data set, this is expected as there are more within-Appalachian comparisons in the data set so the fit line should tend to lie close to these points. Collections in Appalachian regions 1 and 2 are anomalously similar relative to all other combinations and to what could be expected given the distance between the two collections. Distance alone is not sufficient to predict levels of similarity.

Discussion

Continent-scale gradient.———Results suggest the presence of a continental scale gradient rather than discrete provinces. The Appalachian and Western Provinces are the farthest and most dissimilar of the regions (Fig. 4), and are taken to represent the ends of this gradient. The Southern and Midcontinent regions are in the middle of the continent and the gradient. The Appalachian and Western Provinces are more similar to both the Southern and Midcontinent than they are to each other, and the Southern and Midcontinent regions are most similar to each other. This is consistent with these regions being divisions along a gradient. Though the Appalachian and Western regions are sufficiently distinct to classify these two as provinces, given that these have comparable similarity values to the comparisons with the U.K. outgroup, high similarity in the Southern and Midcontinent regions makes delineating discrete boundaries difficult. This is not to say that there are not provinces in the Late Ordovician of Laurentia, but rather that spatial patterns in faunal similarity are better described as a gradient (Fig. 9).

Support from regional study.———Support for a gradient also comes from the regional study. Brachiopods dominate the Cincinnati, Nashville, and southernmost Appalachian collections and become less abundant to the north (Table 4). Bivalves are not among the most abundant taxa in the Southern region, but become increasingly abundant to the north in the Appalachian collections. Similarity to the Southern region increases along the Appalachian region from North to South (Fig. 5). Collections in the Appalachian region are more similar to the Cincinnati Arch subregion than to the

Nashville Dome subregion, suggesting there may be additional support for a gradient within the Southern region as well as in the Appalachian.

Evidence for the gradient expressed at this scale is most apparent in ordination space (Fig. 7). Collections from both the Southern regions have similar NMDS1 scores, and Appalachian collections span NMDS1 with more positive scores to the north. Collections from adjacent regions often overlap and there is considerable overlap between southern Appalachian collections and Cincinnati collections along NMDS1. This pattern is indicative of a gradient rather than discrete provinces. Cincinnati collections separate from Nashville collections on NMDS2, which coincides with differential Jaccard's similarities and adds additional support for a gradient within the Southern region.

Both region-by-region abundance patterns (Table 4) and the taxon scores in MDS space (Fig. 7) show that more articulate brachiopods are associated with Southern Province and southern Appalachian collections. *Orthorhynchula* tends to be more characteristic of northern Appalachian collections and is often associated with siliciclastic substrates (Bretsky 1970). Gastropods and bivalves are more diverse and abundant in the northern Appalachian regions, and many of these are also associated with siliciclastic substrates. This agrees with a proposed substrate-driven gradient hypothesis for the Appalachians (Springer and Bambach 1985). These distributions suggest that the south-north gradient that plots along NMDS1 is largely substrate driven. It is unclear what is driving NMDS2.

Gradient changes through time.———The presence of a continent-scale gradient is supported during the Middle Ordovician and Late Ordovician, but the magnitude and pattern of this gradient changes over time. In the Middle Ordovician, the Western region is the most dissimilar to the rest of Laurentia, but by the Late Ordovician, the Western region becomes more similar to the Southern and Midcontinent provinces. In turn, the Appalachian province was more similar to the rest of Laurentia during the Middle Ordovician, but it becomes more distinct from the rest of the continent by the Late Ordovician. Enhanced disparity in faunal composition between the Appalachian Province and the other Laurentian provinces is broadly coincident with orogenic activity in the Taconic highlands and subsequent influx of siliciclastic sediment to the basin.

The merits of relative abundance data versus presence absence data.———Both presence-absence and relative abundance data produce similar patterns in similarity between the Appalachian and Southern areas, but the presence-absence data produce larger uncertainties and higher similarity values. These data were collected such that environment, age, and sampling strategy are controlled for such that differences in these results are due to the methodology.

Presence-absence data is expected to give higher values of similarity because common taxa in one province merely have to be present in the second province to increase similarity. If a taxon common in the first province is rare in the second province, similarity added by the presence of that taxa will be less for relative abundance comparisons than in presence-absence comparisons. Considering that mean similarity when using presence-absence data must be larger given the same two communities than relative abundance, it is no surprise that error is typically larger for presence-absence based comparisons than in relative abundance based comparisons. The more similar the relative abundance of genera in both communities, the closer to the presence-absence value the relative abundance value can get, and the smaller the differences in error will be. Because both data types produce similar patterns, using presence-absence data is sufficient for studies like this, although relative-abundance data is ideal and may be required for other research questions.

The relationship between distance and similarity.———There is an inverse relationship between distance and similarity, but distance alone does not predict levels of similarity. Observed variability in similarity measured at shorter distances is likely driven by variable environmental conditions (e.g. substrate) that would make one region more similar to each other regardless of proximity. Variability in similarity decreases at higher distances, and this is unsurprising as many factors that control faunal distributions could be expected to change over great distances. Each set of comparisons (Cincinnati collections vs. Appalachian collections, etc.) are better fit by different lines, suggesting some degree of separation or differentiation among these regions. If these areas were well connected or mixed, one line of fit would be expected to describe all of the data adequately. This suggests the relationship between distance and similarity is more or less complicated in different areas of Laurentia. Similarity values for comparisons involving Cincinnati collections and Appalachian collections are higher than average for the data set, in other words, these plot above the line of best fit for the data set. These collections are more similar to each other given the distance between them than would be predicted considering the observed relationship between distance and similarity for the data set as a whole. Conversely, similarity between Nashville collections and Appalachian collections are lower than would be predicted, and these are less similar than would be predicted given the distance between them. This could be explained by environmental conditions that control faunal distribution being more similar between Cincinnati and the Appalachians than between Nashville and the Appalachians. Distance accounts for the least amount of variation in similarity for comparisons between collections within the Appalachian Province. This suggests there could be environmental factors that are more important than distance, for example, substrate composition.

Caveats about using Paleobiology Database data for biogeographic studies.—— The Paleobiology Database is a powerful tool, without which projects like this would not be possible. To optimize the usefulness of this database, one must be aware of biases that arise from the nature of the data sources in the database, as well as what steps should be taken to minimize problems stemming from the amount and quality of data.

In compiled data such as those from the Paleobiology Database, trends in the data may reflect real natural phenomena as well as biases from the sources of these data. The higher taxonomic break-down of the top ten most reported genera raises the possibility that this data is biased by the sources. It is unlikely that the Appalachian Province in the Middle Ordovician, for example, is truly dominated by bryozoans to the extent that this list might suggest. It is more likely that the workers who have studied this interval were more detailed in their treatment of bryozoans than other taxa. The difference in number of bryozoan genera reported in different provinces reflects the propensity for some authors, but not others, to identify bryozoans to generic level (e.g. Bretsky 1970 vs. Holland and Patzkowsky 2007), rather than a real ecological trend. Fortunately, the use of presence-absence comparisons mitigates possible overrepresentation of some higher taxa, but this does not address potential underreporting of other groups.

Monographic effects can artificially overrepresent or underrepresent diversity compared to other collections in the same area. When considering multiple phyla, collections drawn from papers that exclusively focus on one taxon (e.g. trilobites) are not meaningfully comparable to a detailed compendium of all taxa known from a location, such as Dalve's (1948) exhaustive list of fossils of the Cincinnati region. This can also alter what appears to be the makeup of communities in a region. For example, particular genera of bryozoans may seem unusually abundant in one province and artificially absent in another if workers in the first have done a more thorough classification.

When considering age or environment, missing or mislabeled fields can become especially problematic. Many occurrences downloaded for this study included epochs in the place of stage data, or were lacking stage data entirely. A sobering number of occurrences were labeled shallow subtidal but lithology fields indicated these were black shales, or comment fields indicated these were assigned BA4-BA6 environments.

Misspelled genera is a fairly common problem, and it artificially inflates diversity and differences between collections. Finally, the database is a work in progress. Some classic papers have yet to be entered into the database, for example Bretsky's (1970) collections and Springer and Bambach's (1985) collections from the Appalachians, and we should all, as active researchers in the field, continue to improve this resource.

Conclusions

1) Results support the presence of a continental-scale gradient rather than discrete provinces. This gradient is also evident at the regional scale in the eastern United States. Although distance is partly the source of this gradient, the west to east and south to north transition from carbonates to siliciclastics is more important.

2) Increased disparity over time of the Appalachian region relative to the rest of Laurentia suggests this gradient was intensified by the Taconic orogeny, most likely due to increased siliciclastic input during tectonic activity.

3) Presence/absence and relative abundance data produce similar patterns, although presence/absence data have higher values of similarity and greater uncertainty.

4) Care and consideration need to be taken when determining if and how data from the Paleobiology Database can be used to investigate paleoecological and paleobiogeographical questions.

CHAPTER 3

CONCLUSIONS

Spatial patterns in similarity among provinces in the Late Ordovician of Laurentia support the presence of a continental-scale gradient rather than independent, discrete provinces. Spatial trends in similarity at the regional scale in the eastern United States also support the presence of this gradient. Although similarity between communities decreases with distance, the west to east and the south to north changes from carbonate substrate to siliciclastic substrate is more important to distribution patterns. The presence of a gradient where provinces have previously been inferred suggests that gradients may be insufficiently documented and underused as a tool in paleobiogeography.

Increased disparity by the Late Ordovician between the Appalachian region and the rest of Laurentia suggests this gradient was intensified by the Taconic orogeny. This intensification was likely driven by increased siliciclastic input and related environmental effects during orogenesis.

Data structure and source must be considered carefully when undertaking paleobiogeographical studies. Presence/absence and relative abundance data produce similar patterns, although presence/absence data have higher values of similarity and greater uncertainty. Data from the Paleobiology Database may need cleaning prior to use, and may not be suited for some paleoecological and paleobiogeographical questions.

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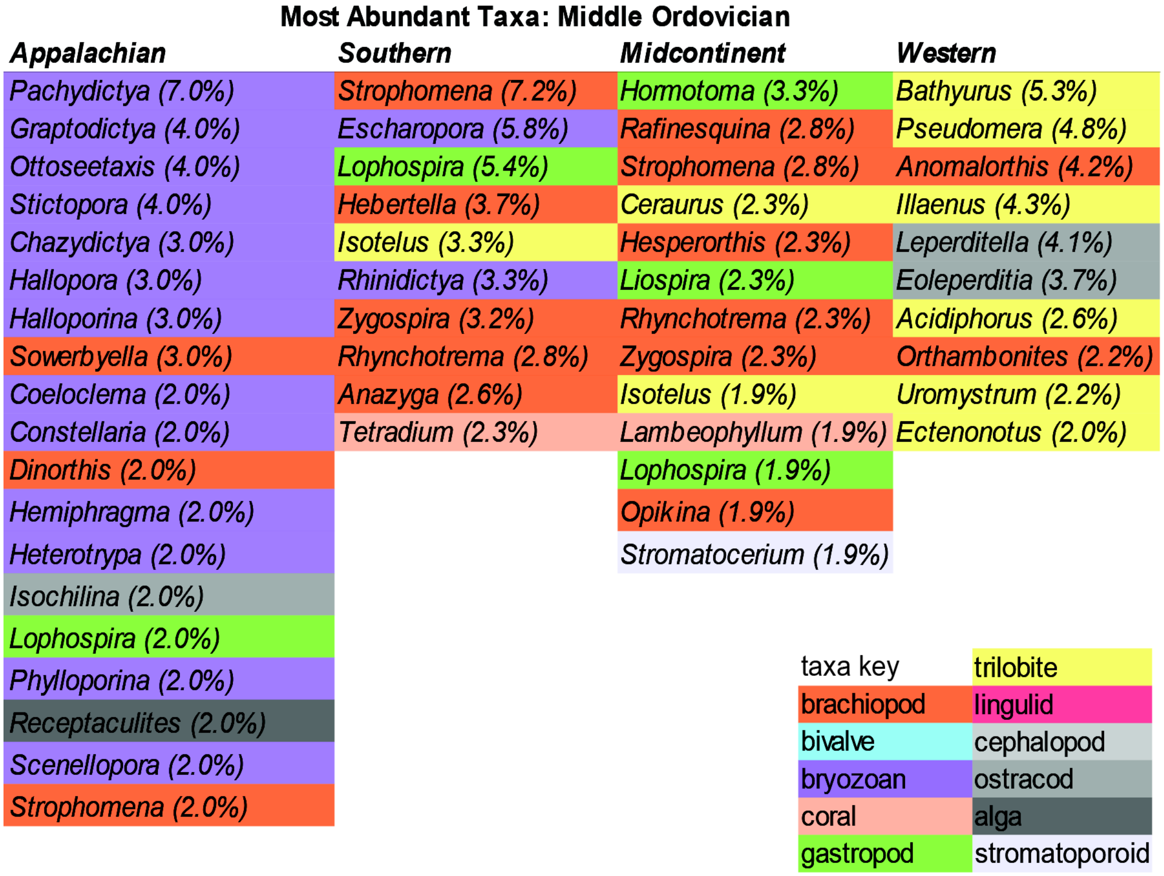
Table 1. Genera reported are color coded by higher taxon (key in lower right). Percentages reported indicate what percentage of occurrences in each province that genera represents.

Most Abundant Taxa: Early Ordovician

Appalachian	***Southern***	***Midcontinent***	***Western***
Protocycloceras (5.5%)	No data	*Ellesmeroceras (50%)*	*Petigurus (2.5%)*
Campbelloceras (4.7%)		*Woosteroceras (50%)*	*Isoteloides (2.3%)*
Bassleroceras (3.9%)			*Symphysurina (2.3%)*
Centrotarphyceras (3.9%)			*Hystricurus (2.2%)*
Eurystomites (3.9%)			*Strigigenalis (2.2%)*
Curtoceras (3.2%)			*Hesperonomia (2.1%)*
Lawrenceoceras (3.2%)			*Psalikilus (2.1%)*
Paraendoceras (3.2%)			*Carolinites (2.0%)*
Cassinoceras (2.4%)			*Genalaticurus (2.0%)*
Clitendoceras (2.4%)			*Anomalorthis (1.9%)*
Dakeoceras (2.4%)			
Proterocameroceras (2.4%)			
Tarphyceras (2.4%)			

taxa key	trilobite
brachiopod	lingulid
bivalve	cephalopod
bryozoan	ostracod
coral	alga
gastropod	stromatoporoid

Table 2. See Table 1 for explanation.

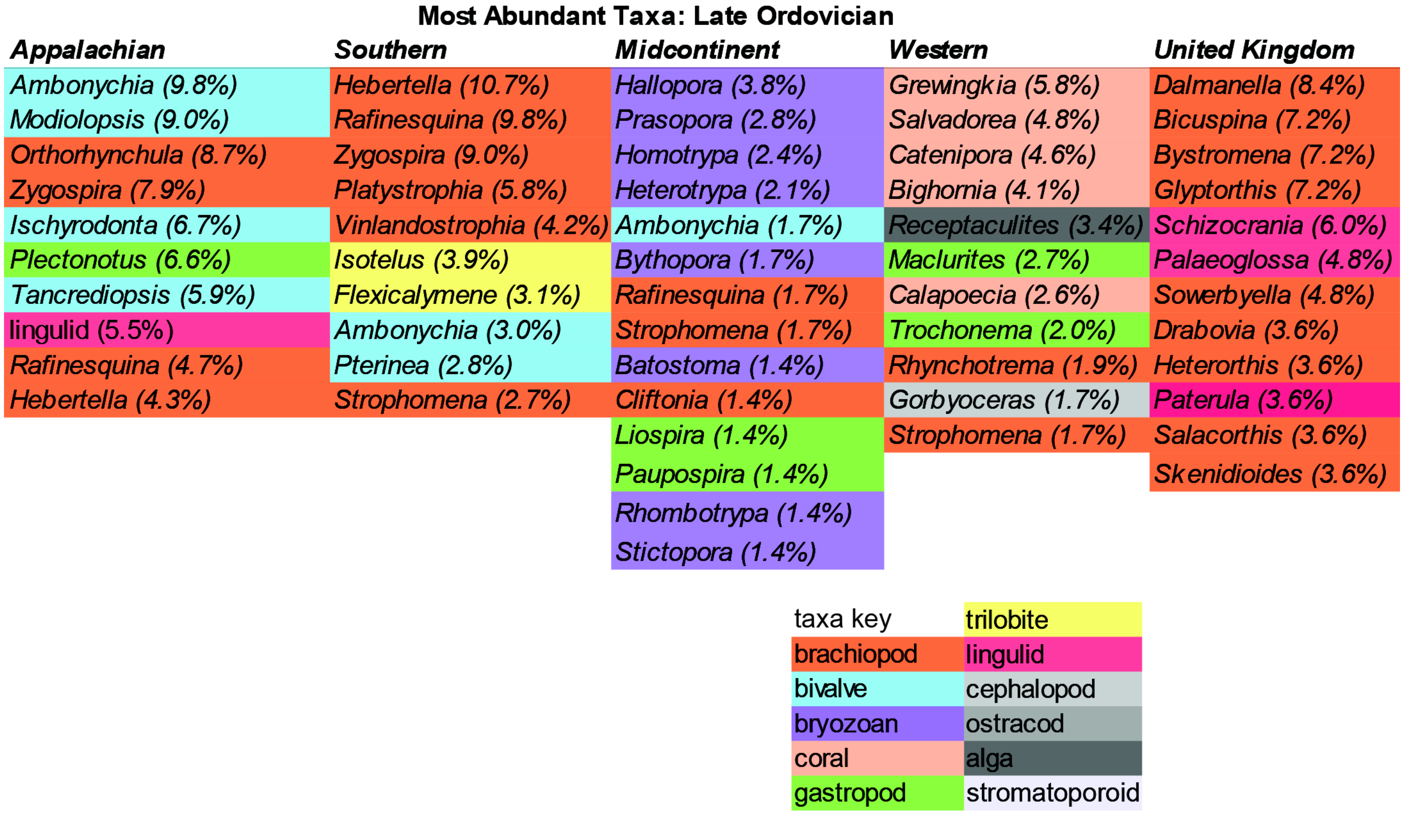


Most Abundant Taxa: Middle Ordovician

Appalachian	***Southern***	***Midcontinent***	***Western***
Pachydictya (7.0%)	*Strophomena (7.2%)*	*Hormotoma (3.3%)*	*Bathyurus (5.3%)*
Graptodictya (4.0%)	*Escharopora (5.8%)*	*Rafinesquina (2.8%)*	*Pseudomera (4.8%)*
Ottoseetaxis (4.0%)	*Lophospira (5.4%)*	*Strophomena (2.8%)*	*Anomalorthis (4.2%)*
Stictopora (4.0%)	*Hebertella (3.7%)*	*Ceraurus (2.3%)*	*Illaenus (4.3%)*
Chazydictya (3.0%)	*Isotelus (3.3%)*	*Hesperorthis (2.3%)*	*Leperditella (4.1%)*
Hallopora (3.0%)	*Rhinidictya (3.3%)*	*Liospira (2.3%)*	*Eoleperditia (3.7%)*
Halloporina (3.0%)	*Zygospira (3.2%)*	*Rhynchotrema (2.3%)*	*Acidiphorus (2.6%)*
Sowerbyella (3.0%)	*Rhynchotrema (2.8%)*	*Zygospira (2.3%)*	*Orthambonites (2.2%)*
Coeloclema (2.0%)	*Anazyga (2.6%)*	*Isotelus (1.9%)*	*Uromystrum (2.2%)*
Constellaria (2.0%)	*Tetradium (2.3%)*	*Lambeophyllum (1.9%)*	*Ectenonotus (2.0%)*
Dinorthis (2.0%)		*Lophospira (1.9%)*	
Hemiphragma (2.0%)		*Opikina (1.9%)*	
Heterotrypa (2.0%)		*Stromatocerium (1.9%)*	
Isochilina (2.0%)			
Lophospira (2.0%)			
Phylloporina (2.0%)			
Receptaculites (2.0%)			
Scenellopora (2.0%)			
Strophomena (2.0%)			

taxa key	trilobite
brachiopod	lingulid
bivalve	cephalopod
bryozoan	ostracod
coral	alga
gastropod	stromatoporoid

Table 3. See Table 1 for explanation.

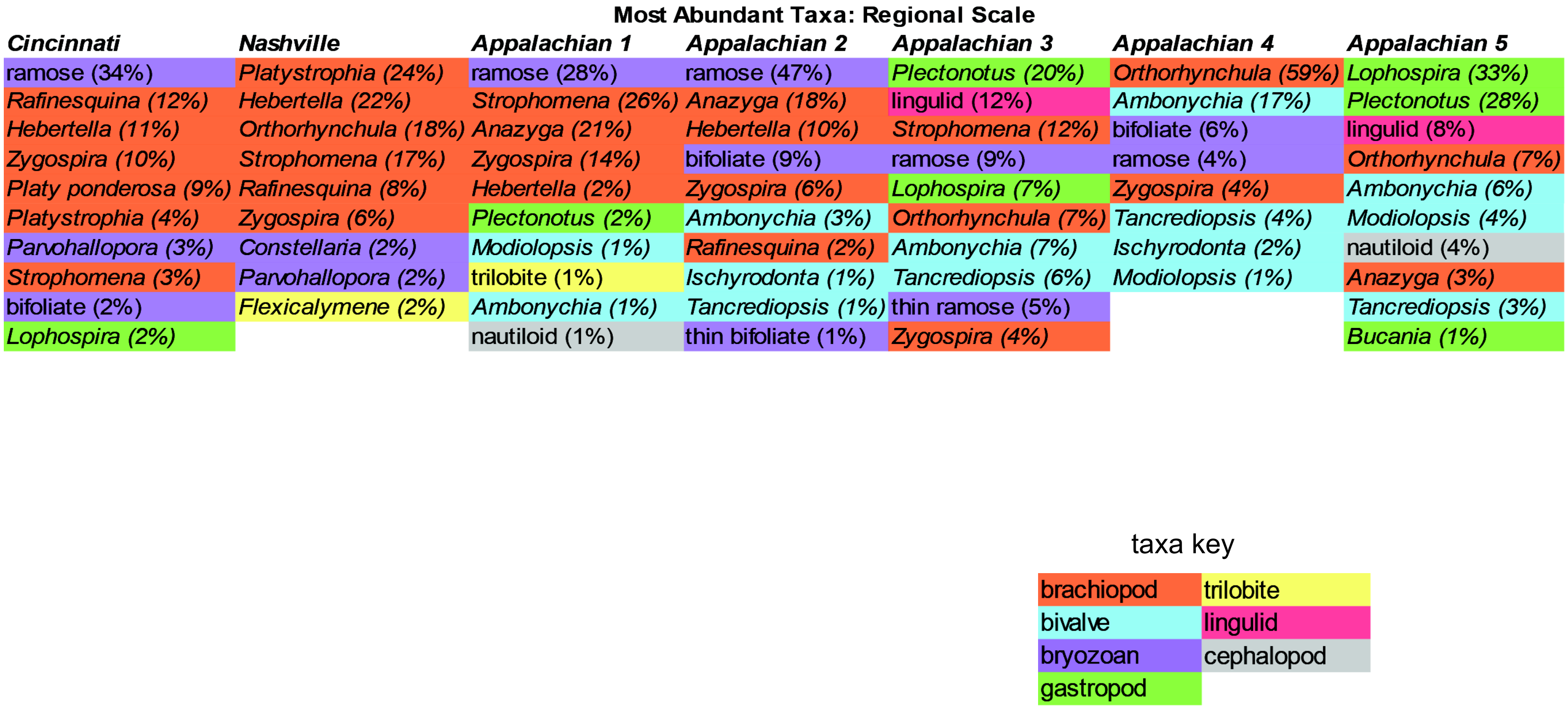


Most Abundant Taxa: Late Ordovician

Appalachian	***Southern***	***Midcontinent***	***Western***	***United Kingdom***
Ambonychia (9.8%)	*Hebertella* (10.7%)	*Hallopora* (3.8%)	*Grewingkia* (5.8%)	*Dalmanella* (8.4%)
Modiolopsis (9.0%)	*Rafinesquina* (9.8%)	*Prasopora* (2.8%)	*Salvadorea* (4.8%)	*Bicuspina* (7.2%)
Orthorhynchula (8.7%)	*Zygospira* (9.0%)	*Homotrypa* (2.4%)	*Catenipora* (4.6%)	*Bystromena* (7.2%)
Zygospira (7.9%)	*Platystrophia* (5.8%)	*Heterotrypa* (2.1%)	*Bighornia* (4.1%)	*Glyptorthis* (7.2%)
Ischyrodonta (6.7%)	*Vinlandostrophia* (4.2%)	*Ambonychia* (1.7%)	*Receptaculites* (3.4%)	*Schizocrania* (6.0%)
Plectonotus (6.6%)	*Isotelus* (3.9%)	*Bythopora* (1.7%)	*Maclurites* (2.7%)	*Palaeoglossa* (4.8%)
Tancrediopsis (5.9%)	*Flexicalymene* (3.1%)	*Rafinesquina* (1.7%)	*Calapoecia* (2.6%)	*Sowerbyella* (4.8%)
lingulid (5.5%)	*Ambonychia* (3.0%)	*Strophomena* (1.7%)	*Trochonema* (2.0%)	*Drabovia* (3.6%)
Rafinesquina (4.7%)	*Pterinea* (2.8%)	*Batostoma* (1.4%)	*Rhynchotrema* (1.9%)	*Heterorthis* (3.6%)
Hebertella (4.3%)	*Strophomena* (2.7%)	*Cliftonia* (1.4%)	*Gorbyoceras* (1.7%)	*Paterula* (3.6%)
		Liospira (1.4%)	*Strophomena* (1.7%)	*Salacorthis* (3.6%)
		Paupospira (1.4%)		*Skenidioides* (3.6%)
		Rhombotrypa (1.4%)		
		Stictopora (1.4%)		

taxa key	trilobite
brachiopod	lingulid
bivalve	cephalopod
bryozoan	ostracod
coral	alga
gastropod	stromatoporoid

Table 4. See Table 1 for explanation.



Most Abundant Taxa: Regional Scale

Cincinnati	***Nashville***	***Appalachian 1***	***Appalachian 2***	***Appalachian 3***	***Appalachian 4***	***Appalachian 5***
ramose (34%)	*Platystrophia (24%)*	ramose (28%)	ramose (47%)	*Plectonotus (20%)*	*Orthorhynchula (59%)*	*Lophospira (33%)*
Rafinesquina (12%)	*Hebertella (22%)*	*Strophomena (26%)*	*Anazyga (18%)*	lingulid (12%)	*Ambonychia (17%)*	*Plectonotus (28%)*
Hebertella (11%)	*Orthorhynchula (18%)*	*Anazyga (21%)*	*Hebertella (10%)*	*Strophomena (12%)*	bifoliate (6%)	lingulid (8%)
Zygospira (10%)	*Strophomena (17%)*	*Zygospira (14%)*	bifoliate (9%)	ramose (9%)	ramose (4%)	*Orthorhynchula (7%)*
Platy ponderosa (9%)	*Rafinesquina (8%)*	*Hebertella (2%)*	*Zygospira (6%)*	*Lophospira (7%)*	*Zygospira (4%)*	*Ambonychia (6%)*
Platystrophia (4%)	*Zygospira (6%)*	*Plectonotus (2%)*	*Ambonychia (3%)*	*Orthorhynchula (7%)*	*Tancrediopsis (4%)*	*Modiolopsis (4%)*
Parvohallopora (3%)	*Constellaria (2%)*	*Modiolopsis (1%)*	*Rafinesquina (2%)*	*Ambonychia (7%)*	*Ischyrodonta (2%)*	nautiloid (4%)
Strophomena (3%)	*Parvohallopora (2%)*	trilobite (1%)	*Ischyrodonta (1%)*	*Tancrediopsis (6%)*	*Modiolopsis (1%)*	*Anazyga (3%)*
bifoliate (2%)	*Flexicalymene (2%)*	*Ambonychia (1%)*	*Tancrediopsis (1%)*	thin ramose (5%)		*Tancrediopsis (3%)*
Lophospira (2%)		nautiloid (1%)	thin bifoliate (1%)	*Zygospira (4%)*		*Bucania (1%)*

taxa key

brachiopod	trilobite
bivalve	lingulid
bryozoan	cephalopod
gastropod	

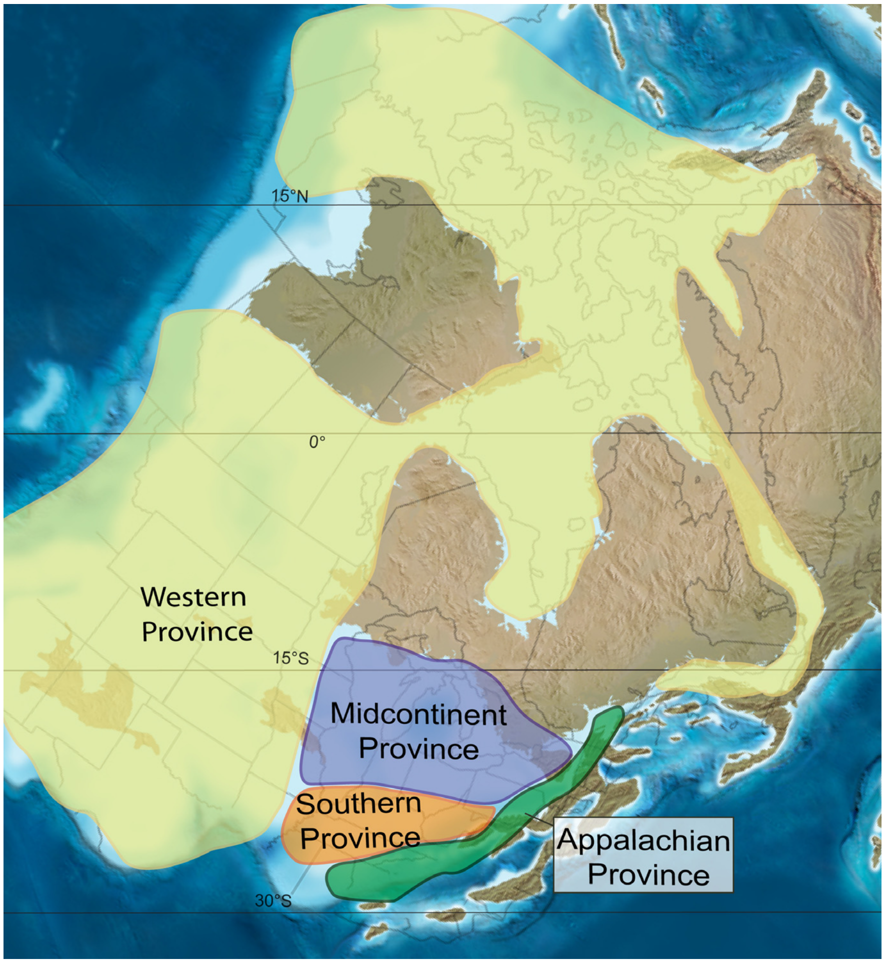


Figure 1. Recognized provinces in the Late Ordovician of Laurentia, based primarily on the geochemically defined aquafacies of Holmden et al. (1998) and the ichnofacies classification of Jin et al. (2012).

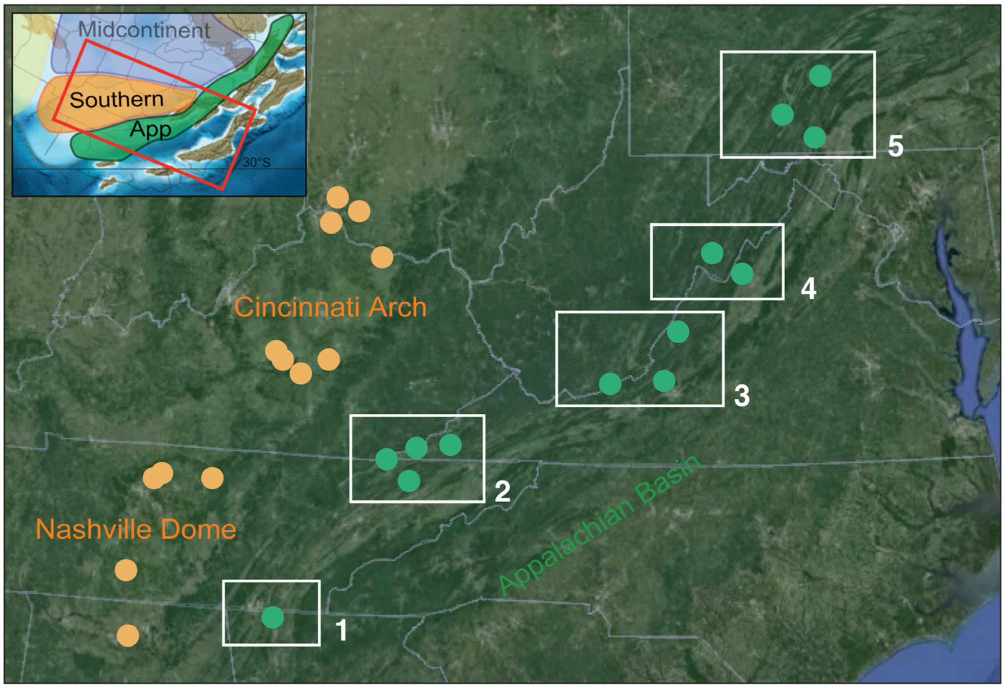


Figure 2. Sample localities in the Southern Province (orange) and the Appalachian Province (green). Appalachian collections are divided into subregions numbered 1-5 from south to north (white). Inset map shows provincial border.

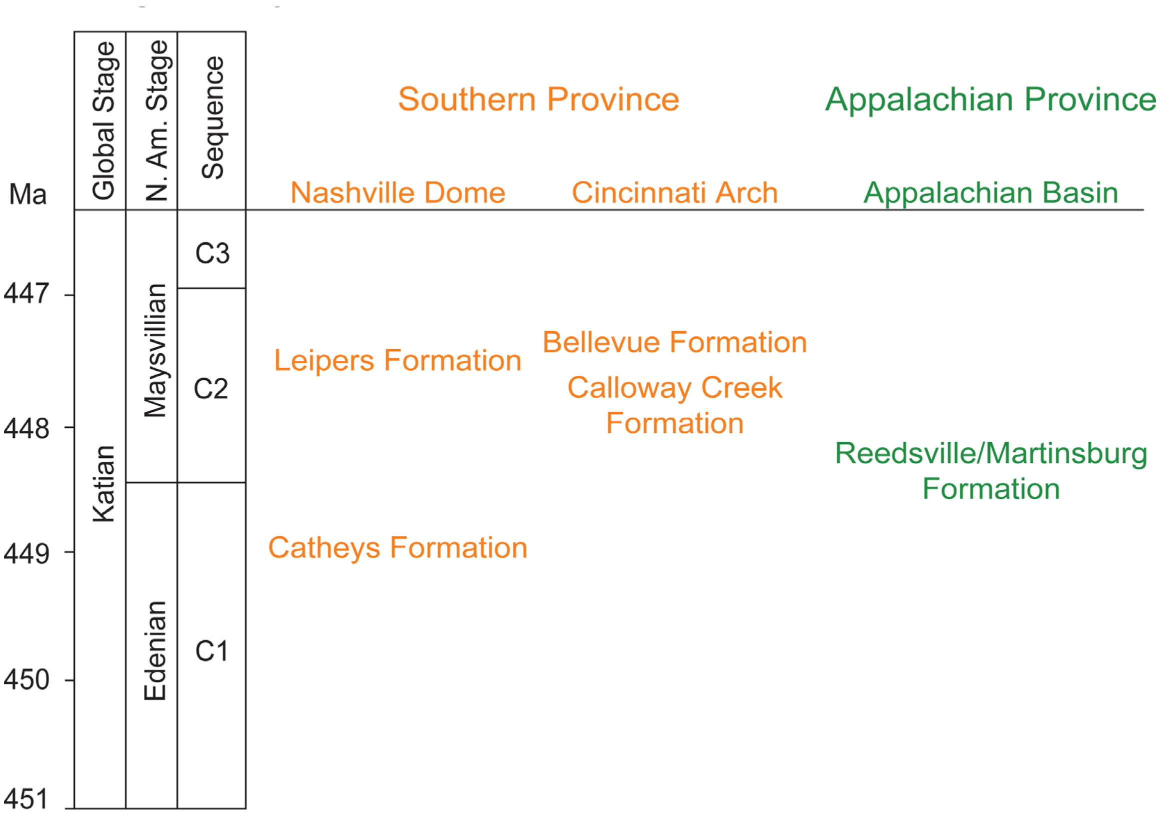


Figure 3. Stratigraphic distribution of samples. All samples were collected from the shallow subtidal facies (see Patzkowsky and Holland 1999; Holland and Patzkowsky 2007).

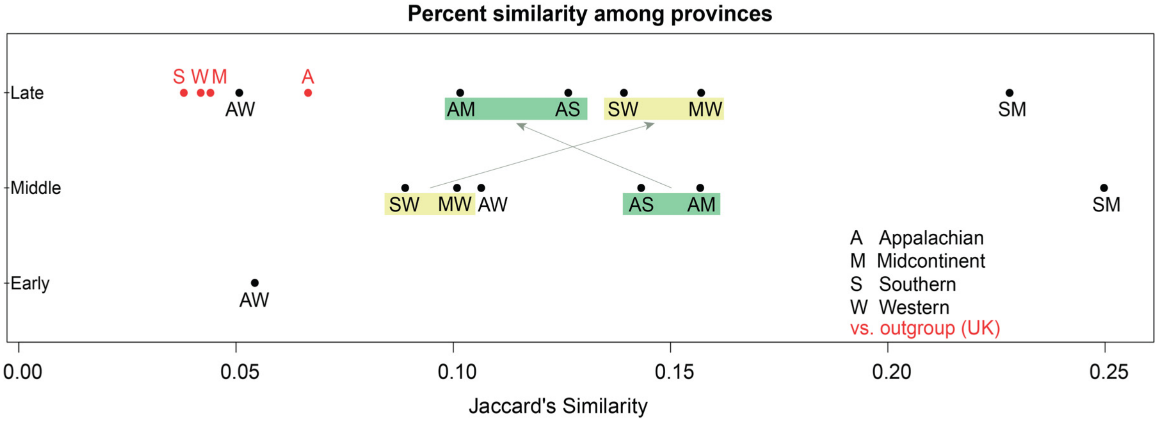


Figure 4. Jaccard's similarity values (x-axis) for each combination of provinces in the Early, Middle, and Late Ordovician (y-axis). Letters designate pair of provinces each data point represents. Red points compare the outgroup to the designated Laurentian province. Comparisons between the Appalachian and Midcontinent or Southern provinces are highlighted in green and comparisons between the Western and Midcontinent or Southern provinces are highlighted in yellow to depict the change in similarity patterns from the Middle to Late Ordovician.

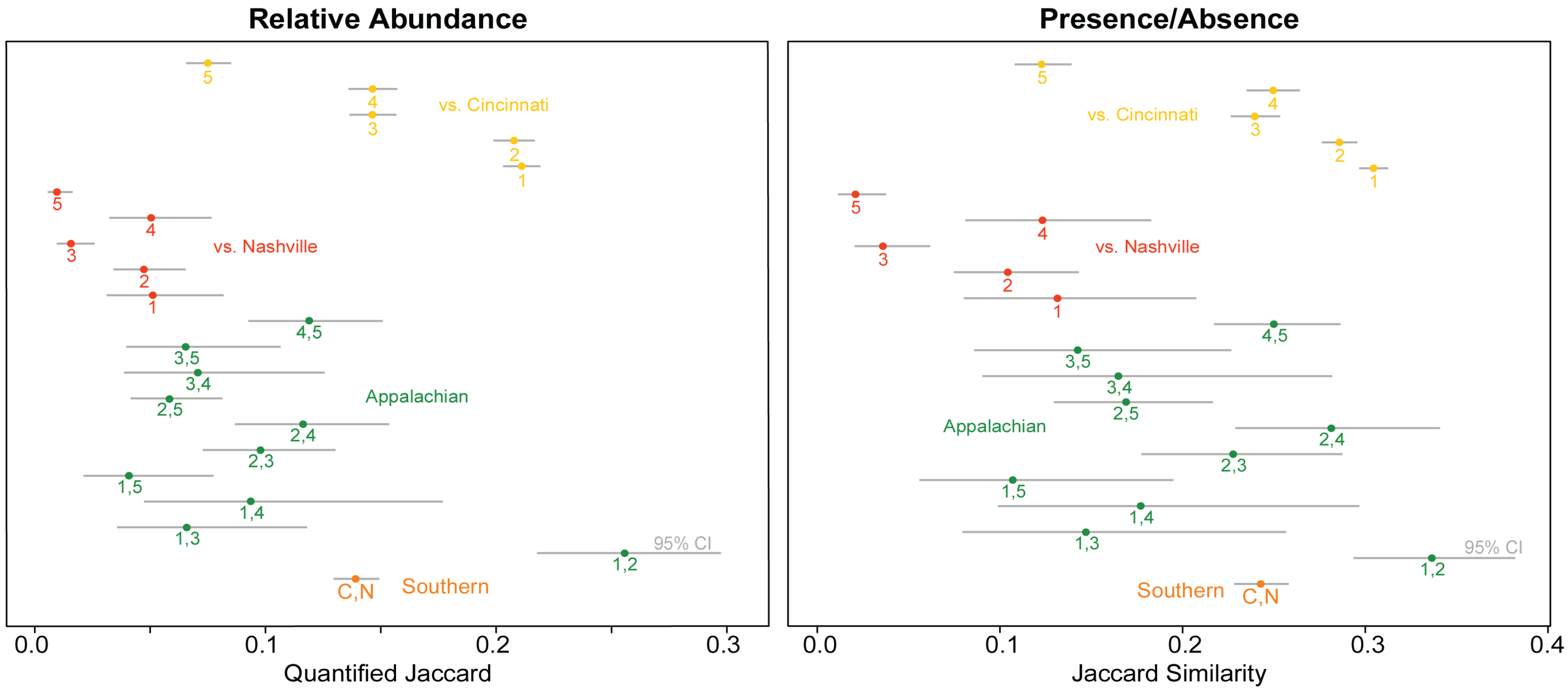


Figure 5. Jaccard Similarity (x-axis) values for each pairwise-comparison among collections in subregions. Within- Appalachian comparisons are in green. Appalachian vs. Cincinnati comparisons are in darker orange, Appalachian vs. Nashville comparisons are in lighter orange. Numbers correspond to which Appalachian subregion is involved in the comparison. Grey bars represent the 95% confidence interval. South to north decrease in similarity among comparisons between Appalachian and Southern Province collections is apparent for both types of data.

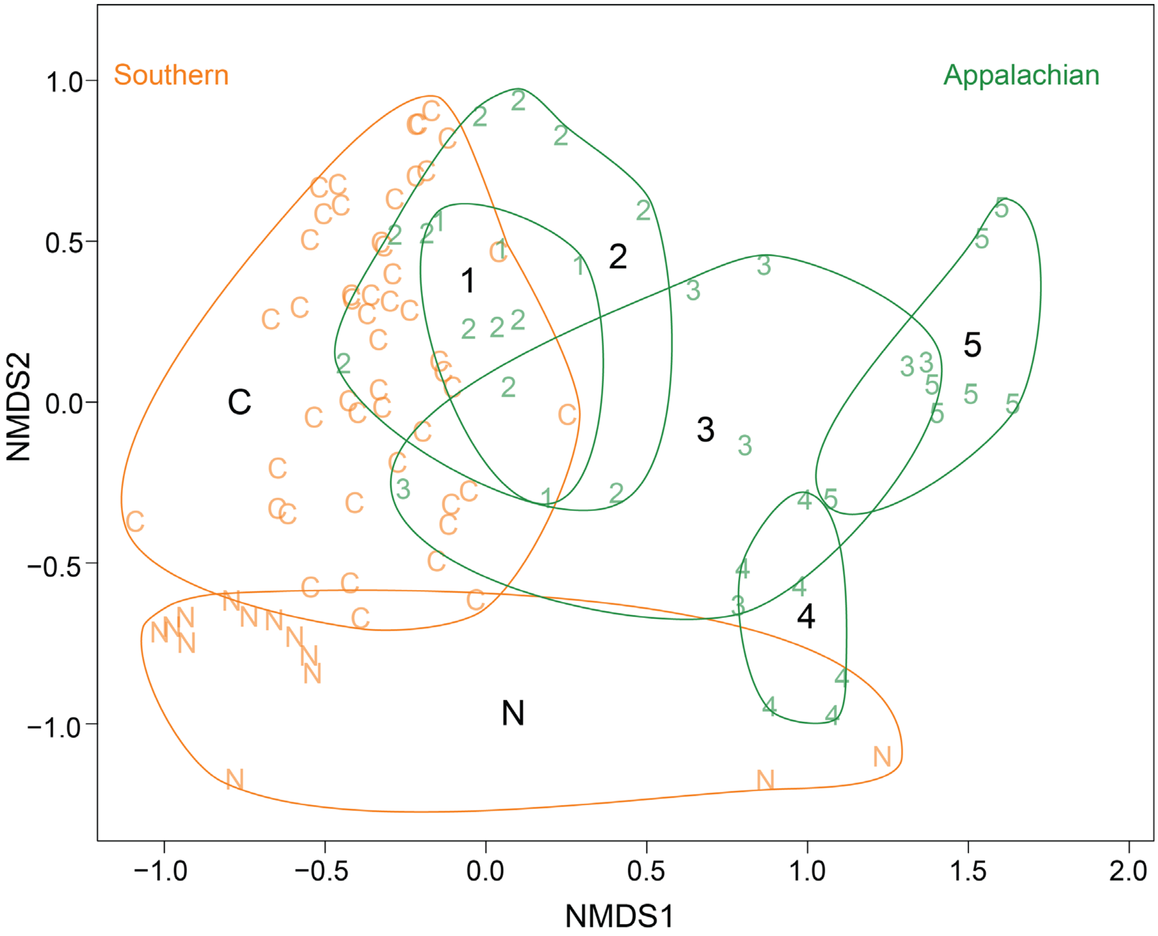


Figure 6. Ordination of collections in the regional-scale study. Southern Province collections (orange) exhibit lower NMDS1 scores than Appalachian (green) collections. NMDS1 scores become more positive to the north within the Appalachian regions. Collections from Nashville have lower NMDS2 scores than Cincinnati collections.

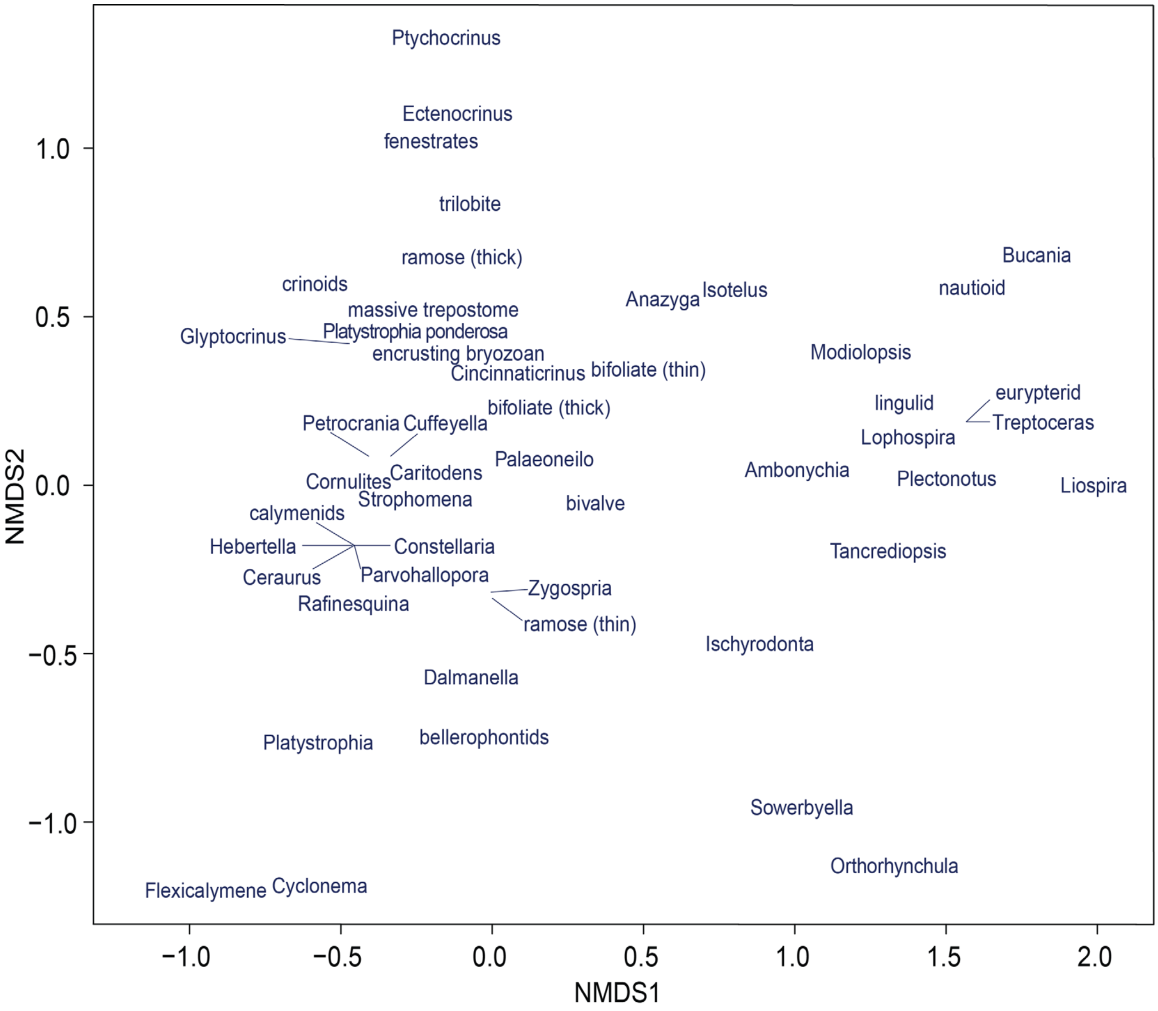


Figure 7. Taxon scores from the regional scale ordination. *Orthorhynchula,* gastropods, and bivalves typical of sandier substrates and the northern Appalachian collections have the most positive NMDS1 scores.

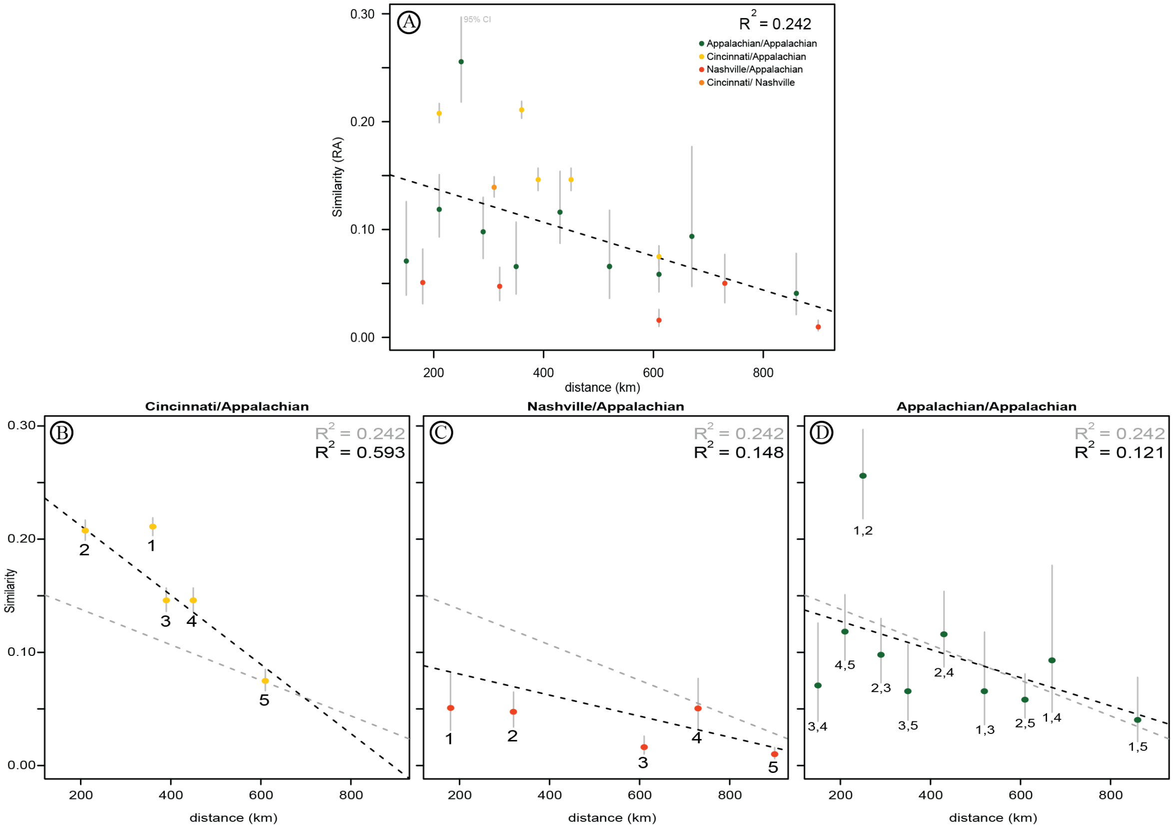


Figure 8. Jaccard's similarity (y-axis) vs. distance between the centroid of each set of collections (x-axis). Grey segments are 95% confidence intervals. Similarity decreases with distance. Fit is not particularly strong for any of the regression models. A. contains the entire data set, color coded by comparison, dashed line is the fitted model. B. Cincinnati/Appalachian comparisons. Grey dashed line shows fit for the whole data set, black dashed line shows the fit line for Cincinnati/Appalachian collections only. Numbers correspond to which Appalachian subregion the datum represents. C. Nashville/Appalachian comparisons.D. Within-Appalachian comparisons.

Figure 9. A schematic representation of the proposed gradient in the Late Ordovician of Laurentia (basemap from Blakey 2013)

Appendix 1. Paleobiology Database collection numbers used in this study, sorted by age and province.

Age: Early
Province: Appalachian
290 6971 6980 7105 42782 42793 42798 85184
88887 89489 89490 89491 89492 89501 89502 90082
90194 90195 98439 101293 119376 119377

Age:Early
Province: Midcontinent
101016

Age: Early
Province: Southern
N/A

Age: Early
Province: Western
429 11033 11034 11036 11039 11046 11047 11048
11050 11060 11063 11064 11072 56140 64502 66828
66832 66837 66841 66842 66843 66845 66847 66848
66849 66851 66852 66853 66854 66855 66856 66857
66858 66859 66860 66861 66864 69261 77844 77845
88805 88827 88838 88939 89013 103540 103784 103785
103786 103787 103788 103789 103790 103791 103792 103799
103800 103801 103803 103805 103806 103809 103810 103813
103814 103816 103817 103819 103820 103821 103822 103823
103824 103825 103826 103827 103829 103831 103888 103889
103891 103905 103906 103907 103908 103911 103912 103913
103916 103917 103918 103919 103920 104058 104059 104060
104061 104062 104063 104066 104067 104070 104071 104072
104073 104075 104076 104077 104079 104081 104082 104083
104084 104085 104086 104087 104089 104090 104091 104092
104094 104096 104097 104099 104100 104101 104102 104103
104104 104105 104106 104109 104110 104113 104115 104116
104118 104119 104121 104122 104123 104124 104126 104127
104128 104129 104130 104131 104132 104133 104134 104135
104137 104138 104141 104144 104145 104146 104147 104152
104153 104157 104158 104159 104160 104161 104162 104163
104164 104165 104167 104168 104169 104170 104171 104172
104173 104174 104175 104176 104177 104178 104180 104181
104183 104184 104185 104187 104188 104189 104190 104191
104262 104263 104264 104265 104266 104278 104279 104280
104281 104282 104283 104284 104285 104286 104287 104289
104290 104299 104301 104303 104304 104305 104306 104307

104308 104312 104314 104315 104360 104361 104363 104364
104433 104434 104436 104438 104439 104440 104441 104467
104468 104469 104470 104471 104472 104475 104476 104478
104558 104561 104563 104565 104568 104570 104571 104630
104631 104632 104633 104636 104638 104639 104640 104641
105090 105094 105776 105777 105779 105780 106370 106373
106374 106375 106387 106389 106390 106391 106392 106393
106394 106397 106398 106399 106420 106421 106422 106743
106745 106750 106751 106754 106755 106761 106763 106764
106765 106766 106770 106777 106778 106784 106788 106789
106790 106792 106794 106796 106799 106800 106801 106803
106806 106811 106818 106819 106822 106825 106834 106835
106836 106935 106936 106937 106939 106941 106942 106943
106946 106948 106949 106952 106954 106955 106957 106958
106960 106962 106964 143889

Age: Middle
Province: Appalachian
319 329 6984 6989 6990 6991 6992 7093
7095 7096 7097

Age: Middle
Province: Midcontinent
333 336 416 417 26174 26175 26188
26191

Age: Middle
Province: Southern
1697 1698 1700 1706 1916 1922 1923
1925 1928 1940 1941 1944 1945 1946
1947 1955 1956 1957 1958 5327 5329
5333 5346 5351 5352 5355 5356 5357
5361 6707 6708 6709 85803 86054 86055
86056 86057 86058 86059 86081 86084 86087
86088 86089 86090 86091 86095 86096 86097
86101 86102 86103 86106 86124 86126 86128
86130 86133 86134 86135 86136 86137 86141
86142 86144 86145 86146 86191 86192 86193
86194 86195 86196 87734 87737 87739

Age: Middle
Province: Western
296 301 305 310 311 318
425 13605 14229 25172 25173 25177
25857 25861 65131 65136 65141 65147

65151 80618 80619 102232 102233 102234
102236 102251 102252 102253 102255 102256
102258 102259 102261 102262 102263 102264
102265 102266 102267 102478 102479 102480
102485 103781 103909 103910 103914 103915
104268 104369 104370 104372 104373 104374
104375 104376 104378 104379 104380 104381
104383 104384 104386 104388 104389 104390
104391 104392 104393 104394 104395 104397
104398 104399 104400 104401 104402 104403
104404 104406 104408 104409 104410 104413
104417 104418 104423 104424 104426 104427
104429 104430 104431 104634 104653 104654
104655 104863 104870 104871 104873 104874
104875 104876 104877 104878 104879 104880
104881 104882 104883 104884 104885 104886
104887 104888 105612 105615 105635 105636
105641 105647 105648 105654

Age: Late
Province: Appalachian
*Collections from Bretsky (1970: Table 3) begin with B.
*Hyphenated collections are from the fieldwork of this study.
32398 32402 32456 32457 32458 32462 32465
32466 32467 B100 B101 B108 B110 B111
B112 B120 B123 B125 B126 B127 B128
B130 B131 B132 B133 B135 B136 B137
B138 B139 B140 B141 B142 B143 B144
B145 B147 B148 B149 B150 B151 B152
B153 B160 B161 B162 B163 B164 B166
B167 B168 B169 B170 B171 B172 B173
B174 B175 B177 B178 B179 B181 B182
B183 B184 B185 B186 B187 B188 B189
B190 B191 B192 B193 B194 B195 B196
B197 B199 B200 B201 B202 B203 B204
B205 B206 B32 B33 B37 B45 B47
B49 B60 B62 B63 B66 B68 B70
B71 B78 B81 B82 B84 B86 B87
B92 B93 B94 B95 B96 B97 B98
B99 RNG-3 CAT-3 CPM-3 STK-3 TH-3 CAT-1
TIP-1 CPM-2 NFM-1 STK-1 NAR-2 H16-2 AIR-1
ROY-3 CAT-2 H16-4 NFM-3 TIP-3 ROY-1 AL-3
NFM-2 RNG-4 RNG-1 H16-3 HAG-2 RNG-2 AIR-2
STK-2 HAG-1 ROY-2 TH-2 TH-1 NAR-1 TIP-2
CPM-1 HAG-3

Age: Late
Province: Midcontinent
356 357 396 421 6901 6902 6903
6904 6905 6906 6907 6908 6909 6910
6911 6913 13156 13200 22954 22956 22957
22961 26303 26304 55456 55457 55458 55459
55999

Age: Late
Province: Southern
350 354 361 374 375 382 398
399 1699 1710 1892 1893 1895 1918
1921 1927 1929 1930 1963 1972 1973
1974 1975 1976 1977 1978 1979 5323
5324 5325 5372 5373 5374 5392 5394
6900 34558 34559 34561 37833 48743 48749
48751 48752 48753 48754 48755 48756 48757
48758 48759 48765 48766 48767 48782 48783
48784 48785 48786 48787 48796 48797 48798
48799 48800 48802 48804 48807 48809 48810
48811 48812 48813 48818 48819 48820 48821
64166 64167 64169 64416 64417 64418 64419
64420 72427 72428 72429 72444 72445 72446
72447 72448 72449 72450 72454 72455 72456
72457 72458 72459 72460 72461 72462 72463
72464 72465 72466 72467 72468 72469 72470
72471 72522 72525 72528 72529 72530 72531
72532 72535 72536 72537 72538 72539 72540
72579 72580 72581 72582 72583 72584 72585
72586 72587 72588 72589 72590 72603 72604
72605 72606 72627 72628 72629 72630 72631
72632 72633 72634 72635 72636 72670 72671
72672 72673 72681 72682 72683 72684 72685
72686 72687 72688 72689 72690 72691 72692
72693 72694 72698 72699 72700 72701 72702
72703 72704 72705 72706 72707 72720 72722
72723 72724 72725 72737 72747 72748 72749
72750 72751 72752 72753 72754 72793 72794
72795 72796 72797 72798 72799 72800 72801
72802 72803 72812 72813 72814 72815 72816
72817 72818 72819 72820 72821 72822 72823
72824 72825 72826 72827 72829 72830 72831
72832 72841 72842 72844 72845 72846 72847
72848 72849 72850 72851 72863 72864 72865
72867 72868 72869 72888 72889 72924 72925

72936 72943 72944 72945 72946 72947 72948
72949 72950 72951 72952 72953 72964 72965
72966 72967 72984 72985 72986 72987 72988
72989 72990 73024 73025 73026 73027 73028
73029 73036 73037 73038 73039 73040 73042
73044 73045 73048 73049 73050 73051 73052
73083 73084 73085 73086 73103 73104 73105
73106 73115 73116 73117 73118 73119 73120
73121 73125 73127 73128 73129 73130 77144
85804 85805 85806 85810 85811 85812 85818
85820 85821 85822 85823 85824 85966 85974
85975 85976 85977 85979 85980 85990 85992
85993 85994 85995 85998 86004 86005 86008
86049 86050 86051 86052 86053 86060 86061
86062 86063 86064 86065 86066 86076 86077
86078 86079 86197 86198 86199 86200 86201
86202 86203 86204 86205 86206 86207 86208
86209 86210 86211 86212 86213 86214 86215
86216 86217 86218 86219 86220 86221 86222
86223 86224 86225 86226 86227 86228 86230
86231 86232 86233 86234 87813 87820 87821
87822 87825 87915 87932 87959 89538

Age: Late
Province: Western
10338 10442 10638 24124 24166 25319
25320 25321 25493 25506 25508 25514
25552 26070 26071 26921 26937 26938
26939 26940 26941 26942 26943 26944
26945 26946 26947 26948 26949 26950
26951 26952 26953 26954 26955 26956
26957 27246 27248 27251 27252 27253
27255 27256 27257 27258 27259 27280
27281 27283 27284 27286 27288 27291
27301 27302 27303 27305 27306 27307
27308 27309 27310 27426 27427 27428
27429 27430 27488 27489 27490 27494
28019 55455 55460 65153 65155 65235
80620 101902 101984 104326 104327 104329
104331 104332 104333 104522 109064 109065
109070 109071 113017

Age: Late
Province: United Kingdom (Outgroup)
3370 45273 45274 45275 45276 45277 45278
45279

Appendix 2. Southern Province collections used in the regional scale analysis (Patzkowsky and Holland 1999; Holland and Patzkowsky 2007)

Cincinnati Collections (Holland and Patzkowsky 2007)
2S002, 2S003, 2S004, 2S005, 2S006, 2S007, 2S008, 2S009, 2S010, 2S011, 2S012, 2S013, 2S014, 2S015, 2S016, 2S017, 2S018, 2S019, 2S020, 2S021, 2S022, 2S023, 2S024, 2S025, 2S026, 2S027, 2S028, 2S029, 2S030, 2S031, 2S032, 2S033, 2S034, 2S035, 2S036, 2S037, 2S038, 2S039, 2S040, 2S041, 2S042, 2S043, 2S044, 2S045, 2S046, 2S047, 2S048, 2S049

Nashville Collections (Patzkowsky and Holland 1999)
95PUW1, 95DF1, 95DF2, 95DF4, 95VVW12, 95VVW13, 95SCD8, 94HT2, 93VVW2, 95VVW13, 95SCD8, 94HT2, 93VVW2, 93SCD2, 95PU1, 95PUW10, 97GC6

Appendix 3: Faunal census of Appalachian collections

	Box	Ambonychia	Anazyga	bifoliate	Bucanella	Caritodens	Cuffeyella
RNG-1	1	0	23	0	0	0	0
RNG-2	1	3	27	0	0	0	0
RNG-3	1	0	11	0	0	0	0
RNG-4	1	0	0	0	0	0	0
HAG-1	2	1	101	22	0	0	0
HAG-2	2	0	22	0	0	0	0
HAG-3	2	2	2	7	1	2	0
STK-1	2	7	13	30	0	0	0
STK-2	2	20	6	2	0	0	0
STK-3	2	0	11	3	0	0	0
TH-1	2	1	0	37	0	0	0
TH-2	2	2	108	54	0	0	0
TH-3	2	27	86	3	0	0	0
TIP-1	2	1	11	22	0	0	0
TIP-2	2	1	10	0	0	0	0
TIP-3	2	2	4	2	0	0	0
AIR-1	3	18	0	2	0	3	0
AIR-2	3	0	0	0	0	0	0
CAT-1	3	0	5	0	0	0	3
CAT-2	3	13	0	0	3	1	0
CAT-3	3	8	0	2	0	1	0
NAR-1	3	9	0	5	0	0	0
NAR-2	3	18	0	25	0	0	0
CPM-1	4	9	0	0	0	0	0
CPM-2	4	2	0	0	0	0	0
CPM-3	4	0	0	0	0	0	0
NFM-1	4	77	0	10	0	1	0
NFM-2	4	19	0	4	0	1	0
NFM-3	4	7	0	24	0	0	0
AL-3	5	0	3	0	0	0	0
H16-2	5	1	0	0	1	0	0
H16-3	5	3	0	0	0	0	0
H16-4	5	5	2	0	0	0	0
ROY-1	5	4	0	0	0	0	0
ROY-2	5	0	2	0	1	0	0
ROY-3	5	0	0	0	0	0	0

	encrusting	eurypterid	Hebertella	Ischyrodonta	Isotelus	lingulid	Liospira
RNG-1	0	0	0	0	0	0	0
RNG-2	1	0	1	0	0	0	0
RNG-3	0	0	6	0	0	0	0
RNG-4	0	0	0	0	0	0	0
HAG-1	2	0	0	0	0	0	0
HAG-2	0	0	0	0	0	0	0
HAG-3	1	0	11	0	0	0	0
STK-1	0	0	43	1	0	0	0
STK-2	2	0	39	18	0	0	0
STK-3	0	0	8	3	0	0	0
TH-1	0	0	39	0	0	0	0
TH-2	1	0	0	0	0	0	0
TH-3	2	0	4	0	0	0	0
TIP-1	1	0	32	0	0	0	0
TIP-2	1	0	38	0	0	0	0
TIP-3	0	0	2	0	0	0	0
AIR-1	0	0	0	0	0	4	0
AIR-2	1	0	0	2	0	51	0
CAT-1	0	0	5	0	0	0	0
CAT-2	0	0	0	0	0	26	0
CAT-3	0	1	0	3	0	32	0
NAR-1	0	0	0	1	0	0	0
NAR-2	0	0	0	1	0	0	0
CPM-1	0	0	0	4	0	0	0
CPM-2	0	0	0	3	0	0	0
CPM-3	0	0	0	3	0	0	0
NFM-1	0	0	0	0	0	0	0
NFM-2	1	0	0	2	0	0	0
NFM-3	0	0	1	0	0	0	0
AL-3	0	0	0	0	0	0	0
H16-2	0	0	0	0	0	0	0
H16-3	0	0	0	0	1	0	0
H16-4	0	0	0	0	0	0	2
ROY-1	0	0	0	0	0	8	0
ROY-2	0	0	0	0	0	2	0
ROY-3	0	0	0	1	0	6	0

	Lophospira	Modiolopsis	nautiloid	Orthorhynchula	Palaeonella
RNG-1	0	0	0	0	0
RNG-2	1	3	0	0	0
RNG-3	0	0	3	0	0
RNG-4	1	1	0	0	0
HAG-1	0	0	0	0	0
HAG-2	0	0	0	0	0
HAG-3	2	0	0	0	0
STK-1	0	0	0	0	0
STK-2	0	5	0	0	5
STK-3	0	3	0	0	0
TH-1	0	0	0	0	0
TH-2	0	0	0	0	0
TH-3	0	1	0	0	0
TIP-1	0	0	0	0	0
TIP-2	0	0	0	0	0
TIP-3	0	1	0	0	0
AIR-1	3	3	1	19	0
AIR-2	0	2	2	0	0
CAT-1	0	0	0	0	0
CAT-2	13	1	0	0	0
CAT-3	49	2	0	3	0
NAR-1	2	0	0	13	0
NAR-2	1	1	0	33	0
CPM-1	0	1	0	85	0
CPM-2	0	1	0	33	0
CPM-3	3	0	0	40	0
NFM-1	0	4	2	66	0
NFM-2	0	4	0	123	0
NFM-3	0	0	0	53	0
AL-3	1	0	0	1	0
H16-2	2	2	0	0	0
H16-3	1	1	2	0	0
H16-4	55	0	7	8	0
ROY-1	5	3	0	2	0
ROY-2	6	0	0	2	0
ROY-3	0	3	0	1	0

	Platystrophia	Plectonotus	Rafinesquina	ramose	Sowerbyella
RNG-1	0	0	2	26	0
RNG-2	0	6	0	26	0
RNG-3	0	0	0	25	0
RNG-4	0	0	0	4	0
HAG-1	0	0	0	236	0
HAG-2	0	0	0	0	0
HAG-3	5	4	0	28	0
STK-1	0	1	0	47	0
STK-2	0	0	0	38	0
STK-3	0	0	0	160	0
TH-1	0	1	34	41	0
TH-2	0	0	2	135	0
TH-3	0	0	1	54	0
TIP-1	0	0	0	100	0
TIP-2	0	0	0	101	0
TIP-3	3	0	0	31	0
AIR-1	0	26	0	52	0
AIR-2	0	23	0	10	0
CAT-1	0	0	0	0	0
CAT-2	0	38	0	0	0
CAT-3	0	78	0	4	0
NAR-1	0	6	0	3	2
NAR-2	0	11	0	17	0
CPM-1	0	0	0	0	0
CPM-2	0	0	0	0	0
CPM-3	0	0	0	0	0
NFM-1	0	1	0	12	0
NFM-2	0	2	0	11	0
NFM-3	0	0	0	7	0
AL-3	0	0	0	0	0
H16-2	0	0	0	0	0
H16-3	0	0	0	0	0
H16-4	0	1	0	0	0
ROY-1	0	25	0	0	0
ROY-2	0	15	0	0	0
ROY-3	0	18	1	0	0

	Strophomena	Tancrediopsis	thin bifoliate	thin ramose	Treptostome
RNG-1	17	0	0	0	0
RNG-2	37	0	0	0	0
RNG-3	12	0	0	0	0
RNG-4	8	0	0	0	0
HAG-1	0	0	0	0	0
HAG-2	0	0	0	0	0
HAG-3	0	8	6	1	0
STK-1	0	0	0	0	0
STK-2	0	0	0	0	0
STK-3	4	5	0	0	0
TH-1	0	0	0	2	0
TH-2	0	0	0	4	0
TH-3	0	0	6	2	0
TIP-1	0	0	0	0	0
TIP-2	0	0	0	0	0
TIP-3	0	0	0	0	0
AIR-1	0	26	0	0	0
AIR-2	0	6	0	0	0
CAT-1	106	0	0	0	0
CAT-2	5	10	0	0	0
CAT-3	0	10	0	0	1
NAR-1	0	0	0	40	0
NAR-2	0	5	0	3	0
CPM-1	0	1	0	0	0
CPM-2	0	0	0	0	0
CPM-3	0	26	0	0	0
NFM-1	0	0	0	0	0
NFM-2	0	0	0	0	0
NFM-3	0	0	2	0	0
AL-3	0	0	0	0	0
H16-2	0	0	0	0	0
H16-3	0	1	0	0	0
H16-4	0	0	0	0	0
ROY-1	0	5	0	0	0
ROY-2	0	0	0	0	0
ROY-3	0	0	0	0	0

	trilobite	Zygospira
RNG-1	1	5
RNG-2	0	0
RNG-3	3	0
RNG-4	0	35
HAG-1	0	0
HAG-2	0	21
HAG-3	0	7
STK-1	0	9
STK-2	0	16
STK-3	0	3
TH-1	0	0
TH-2	0	0
TH-3	0	0
TIP-1	0	8
TIP-2	0	8
TIP-3	0	42
AIR-1	0	7
AIR-2	0	0
CAT-1	0	0
CAT-2	0	0
CAT-3	0	0
NAR-1	0	22
NAR-2	0	7
CPM-1	0	4
CPM-2	0	12
CPM-3	0	5
NFM-1	0	2
NFM-2	0	3
NFM-3	0	3
AL-3	0	0
H16-2	0	0
H16-3	0	0
H16-4	0	0
ROY-1	0	0
ROY-2	0	0
ROY-3	0	0

Appendix 4. Locality information for Appalachian collections

Region 1

Ringgold (RNG): Large (multistory) road cut on south side of Georgia Route 75, east of Catoosa. It is not accessible from the highway, must park behind the carpet factories and hike back. 34.908° N, 85.105°W.

Region 2

Hagan (HAG): Railroad cut on the east side of the railroad tracks at Hagan, Virginia. 36.702°N, 83.289°W.

Stickleyville (STK): Road cut on south side of Virginia Route 58, .2 miles west of junction between Route 58 and Route 726. 36.711°N, 82.877°W.

Thorn Hill (TH): Road cut on the south side of Tennessee Route 25, just west of the intersection between Old Mountain Road and Route 25. 36.35232°N, 83.400°W.

Tiprell Road (TIP): Railroad cut at the foot of a hill below Tiprell Road, just beyond (less than .1 miles) where Tiprell Road forks and turns up that same hill, south of Cumberland Gap, Tennessee. 36.567°N, 83.676°W.

Region 3

Airport Road (AIR): Roadcut on Route 606, just below junction with Route 703 (Airport Road) on Warm Springs Mountain. 37.876°N, 79.888°W.

Catawba (CAT): Roadcut on the south side of Virginia Route 311, just uphill from the guardrail, near Catawba, Virginia. 37.380°N, 80.090°W.

Narrows (NAR): Roadcut on the east side of Virginia Route 460, northbound, on the east side of the river near Narrows, Virginia . 37.352°N, 80.809°W.

Region 4

North Fork Mountain (NFM): Roadcut on south side of 33-W, western side of North Fork Mountain, West Virginia, about .6 miles past the antenna at the top of the mountain, heading west. 38.708°N, 79.411°W.

Coopers Mountain (CPM): Roadcut on the east side of Virginia Route 732 (Coopers Mountain Road) approximately 1.4 miles south of Route 33. 38.480°N, 79.026°W.

Region 5

Allensville (AL): Roadcut on Allensville Mountain Road, .65 miles after (north of) the intersection with Barr Road with near Allensville, Pennsylvania. 40.557°N, 77.821°W.

Highway 16 (H16): Roadcut on Highway 16 on Tuscarora Mountain, SE of McConnellsburg, Pennsylvania. 39.905°N, 77.966°W.

Loysburg (ROY): Roadcut on the north side of Pennsylvania Route 36 (Woodbury Pike), less than .1 miles east of junction with Town Hill Road, near Loysburg, Pennsylvania. 40.160°N, 78.373°W.

Appendix 5.

Continent-Scale Similarity

Age	**Provinces**		**Jaccard's Similarity**
Early	Appalachian	Midcontinent	N/A
	Appalachian	Southern	N/A
	Appalachian	Western	0.055
	Midcontinent	Southern	N/A
	Midcontinent	Western	0.009
	Southern	Western	N/A
Middle	Appalachian	Midcontinent	0.157
	Appalachian	Southern	0.144
	Appalachian	Western	0.107
	Midcontinent	Southern	0.250
	Midcontinent	Western	0.101
	Southern	Western	0.089
Late	Appalachian	Midcontinent	0.102
	Appalachian	Southern	0.127
	Appalachian	Western	0.051
	Midcontinent	Southern	0.228
	Midcontinent	Western	0.158
	Southern	Western	0.140
	Appalachian	U.K.	0.067
	Midcontinent	U.K.	0.044
	Southern	U.K.	0.038
	Western	U.K.	0.042

Regional Scale Similarity

Relative Abundance

Subregions		*Jaccard's Similarity*	*Lower Confidence Limit*	*Upper Confidence Limit*	*Distance (km)*
C	N	0.139	0.13	0.149	310
1	2	0.256	0.218	0.297	250
1	3	0.066	0.036	0.118	520
1	4	0.094	0.047	0.177	670
1	5	0.041	0.021	0.078	860
2	3	0.098	0.073	0.13	290
2	4	0.116	0.087	0.154	430
2	5	0.058	0.042	0.081	610
3	4	0.071	0.039	0.126	150
3	5	0.066	0.04	0.107	350
4	5	0.119	0.093	0.151	210
1	N	0.051	0.031	0.082	180
2	N	0.047	0.034	0.065	320
3	N	0.016	0.01	0.026	610
4	N	0.050	0.032	0.077	730
5	N	0.010	0.006	0.016	900
1	C	0.211	0.203	0.219	360
2	C	0.208	0.199	0.217	210
3	C	0.146	0.136	0.157	390
4	C	0.146	0.136	0.157	450
5	C	0.075	0.066	0.085	610

Regional Scale Similarity
Presence Absence

Subregions		*Jaccard's Similarity*	*Lower Confidence Limit*	*Upper Confidence Limit*	*Distance (km)*
1	2	0.336	0.294	0.382	250
1	3	0.147	0.079	0.257	520
1	4	0.177	0.099	0.297	670
1	5	0.107	0.056	0.195	860
2	3	0.228	0.177	0.287	290
2	4	0.281	0.229	0.341	430
2	5	0.169	0.13	0.217	610
3	4	0.165	0.09	0.282	150
3	5	0.142	0.086	0.227	350
4	5	0.250	0.217	0.286	210
1	N	0.131	0.08	0.207	180
2	N	0.104	0.075	0.143	320
3	N	0.036	0.021	0.062	610
4	N	0.123	0.081	0.183	730
5	N	0.021	0.011	0.038	900
1	C	0.305	0.297	0.313	360
2	C	0.286	0.276	0.296	210
3	C	0.240	0.226	0.253	390
4	C	0.249	0.235	0.264	450
5	C	0.123	0.108	0.139	610

```
##Appendix 6
#Continental Scale then regional scale

#Load Libraries
library(vegan)
library(boot)
library(car)
#Read in data
Laurentia<-
read.csv("Ord_occs.csv",header=TRUE,sep=",",as.is=TRUE)
provremod<-
read.csv("provremod.csv",header=TRUE,sep=",",as.is=TRUE)
col_age<-read.csv("col_age.csv",header=TRUE,sep=",",as.is=TRUE)
outgroup<-read.csv("UK-culled.csv",header=T,sep=",")
bretsky<-
read.csv("BretskyAppCollCull.csv",header=TRUE,sep=",",row.names=1
)
app2013<-
read.csv("Appalachian_2013.csv",header=TRUE,sep=",",row.names=1)
AbundanceMatrix<-
read.csv("AbundanceMatrix.csv",header=TRUE,sep=",",row.names=1)
paradist<-read.csv("paradist.csv")

##############CONTINENTAL SCALE################################
#prep data

#check rows, should be 0
which(Laurentia$collection_no!=provremod$collection)

#put province data in occurrence table
Laurentia<-cbind(Laurentia,provremod)

#Clean up the data
#Nix the Lingula (but not Lingulasma)
Laurentia$occurrence.genus_name<-
gsub("Lingula$","Lingulid",Laurentia$occurrence.genus_name)

#Nix the blank environments
Laurentia<-Laurentia[which(Laurentia$environment!=""),]

#Oust Dalve
Laurentia<-Laurentia[which(Laurentia$collection_no!
=389&Laurentia$collection_no!=391&Laurentia$collection_no!=394),]

#Nix Schizambon
Laurentia<-Laurentia[which(Laurentia$occurrence.genus_name!
="Schizambon"),]

#check collections still match (should = 0)
which(Laurentia$collection_no != col_age$collection_no)

#Put ages in now, this table was built off the culled Laurentia
```

```
Laurentia<-cbind(Laurentia,col_age)

#Correct Misspellings
Laurentia$occurrence.genus_name<-
gsub("Apheorthis","Apheoorthis",Laurentia$occurrence.genus_name)
Laurentia$occurrence.genus_name<-
gsub("Cerurinella","Ceraurinella",Laurentia$occurrence.genus_name
)
Laurentia$occurrence.genus_name<-
gsub("Cymatonata","Cymatonota",Laurentia$occurrence.genus_name)
Laurentia$occurrence.genus_name<-
gsub("Drepanodos","Drepanodus",Laurentia$occurrence.genus_name)
Laurentia$occurrence.genus_name<-
gsub("Heterotrpya","Heterotrypa",Laurentia$occurrence.genus_name)
Laurentia$occurrence.genus_name<-
gsub("Hormotelus","Homotelus",Laurentia$occurrence.genus_name)
Laurentia$occurrence.genus_name<-
gsub("Missiquoia","Missisquoia",Laurentia$occurrence.genus_name)
Laurentia$occurrence.genus_name<-
gsub("Paterulus","Paterula",Laurentia$occurrence.genus_name)
Laurentia$occurrence.genus_name<-
gsub("Pauposira","Paupospira",Laurentia$occurrence.genus_name)
Laurentia$occurrence.genus_name<-
gsub("Pionodema","Pianodema",Laurentia$occurrence.genus_name)

#Nix Camerates
Laurentia<-Laurentia[which(Laurentia$occurrence.genus_name!
="Camerate"),]

#Nix Skolithos
Laurentia<-Laurentia[which(Laurentia$occurrence.genus_name!
="Skolithos"),]

#Add outgroup
Laur<-Laurentia[,c(1,3,5,11,12,17,21,27,29)]
Out<-outgroup[,c(1,4,6,17,18,23,30)]
Prov<-replicate(length(rownames(Out)),5)
Age<-replicate(length(rownames(Out)),3)
Out<-cbind(Out,Prov,Age)

occdata<-rbind(Laur,Out)

#######

#Generate the Occurrence Matrix
#make sure province and age column are called "Prov" and "Age"

#If you are trying to add data to the occurrence matrix you need
to put your collections in here

addnames<-sort(unique(c(names(bretsky),names(app2013))))
addrows<-c(rownames(bretsky),rownames(app2013))
```

```
GenerateOccurrenceMatrix<-function(pbdbdata,addins){
     if (addins=="TRUE"){
           UniqueGenera<-
sort(unique(c(pbdbdata$occurrence.genus_name,addnames)))
           UniqueCollections<-
unique(c(pbdbdata$collection_no,addrows))
     }
     else {
     UniqueGenera<-sort(unique(pbdbdata$occurrence.genus_name))
     UniqueCollections<-unique(pbdbdata$collection_no)
     }

     Occurrences <- matrix(data=0,
nrow=length(UniqueCollections), ncol=length(UniqueGenera)+2,
dimnames=list(UniqueCollections,c(UniqueGenera,"Province","Age"))
)

     for (i in 1:nrow(pbdbdata)){
           CollectionNumber <-
which(UniqueCollections==pbdbdata$collection_no[i])
           GenusNumber <-
which(UniqueGenera==pbdbdata$occurrence.genus_name[i])
           Occurrences[CollectionNumber,GenusNumber] <-1
           Occurrences[CollectionNumber,length(UniqueGenera)+1]<-
as.numeric(pbdbdata$Prov[i])
           Occurrences[CollectionNumber,length(UniqueGenera)+2]<-
as.numeric(pbdbdata$Age[i])

     }
     Occurrences<-as.data.frame(Occurrences)
     Occurrences
}
OccurrenceMatrix<-GenerateOccurrenceMatrix(occdata,TRUE)

#Make sure nothing got weird (should be 0)
which(rownames(OccurrenceMatrix) !=
unique(c(occdata$collection_no,addrows)))

#Fill in added rows
OccurrenceMatrix[which(rownames(OccurrenceMatrix)%in
%addrows),names(OccurrenceMatrix)=="Province"]<-1
OccurrenceMatrix[which(rownames(OccurrenceMatrix)%in
%addrows),names(OccurrenceMatrix)=="Age"]<-3

for (i in 1:nrow (bretsky)){
           colnumber<-which(rownames(bretsky)
[i]==rownames(OccurrenceMatrix))
           filllist<-names(bretsky)[which(bretsky[i,]>0)]
           GenusNumbers<-which(names(OccurrenceMatrix)%in
%filllist)
           OccurrenceMatrix[colnumber,GenusNumbers]<-1
     }
```

```
for (i in 1:nrow (app2013)){
          colnumber<-which(rownames(app2013)
[i]==rownames(OccurrenceMatrix))
          filllist<-names(app2013)[which(app2013[i,]>0)]
          GenusNumbers<-which(names(OccurrenceMatrix)%in
%filllist)
          OccurrenceMatrix[colnumber,GenusNumbers]<-1
     }

#Eliminate morpho-bryozoan (unique to added app collections) and
"nautiloid"
OccurrenceMatrix<-OccurrenceMatrix[,names(OccurrenceMatrix)!
="nautiloid"]
bryos<-grep("Bryozoan.",names(OccurrenceMatrix))
OccurrenceMatrix<-OccurrenceMatrix[,names(OccurrenceMatrix)[-
bryos]]

#Eliminate singleton collections
OccurrenceMatrix<-
OccurrenceMatrix[which(rowSums(OccurrenceMatrix[,c(names(Occurren
ceMatrix)!="Province" & names(OccurrenceMatrix)!="Age")])>1),]

#################################################################

####Aggregate, continent scale, Early/Middle/Late

P11<-OccurrenceMatrix[which(OccurrenceMatrix$Province==1 &
OccurrenceMatrix$Age==1),]
     P11<-rbind(P11,colSums(P11))
     AggP11<-P11[nrow(P11),]
     AggP11$Province<-1
     AggP11$Age<-1

P21<-OccurrenceMatrix[which(OccurrenceMatrix$Province==2 &
OccurrenceMatrix$Age==1),]
     P21<-rbind(P21,colSums(P21))
     AggP21<-P21[nrow(P21),]
     AggP21$Province<-2
     AggP21$Age<-1

if(length(which(OccurrenceMatrix$Province==3 &
OccurrenceMatrix$Age==1))==0)
     {AggP31<-AggP21
     AggP31[,which(names(AggP31)=="Province")]<-3
     AggP31[1,1:(length(names(AggP31))-2)]<-
replicate(length(names(AggP31))-2,0)
     }
if(length(which(OccurrenceMatrix$Province==3 &
OccurrenceMatrix$Age==1))>0){
     P31<-OccurrenceMatrix[which(OccurrenceMatrix$Province==3 &
OccurrenceMatrix$Age==1),]
     P31<-rbind(P31,colSums(P31))
```

```
      AggP31<-P31[nrow(P31),]
      AggP31$Province<-3
      AggP31$Age<-1
      }

P41<-OccurrenceMatrix[which(OccurrenceMatrix$Province==4 &
OccurrenceMatrix$Age==1),]
      P41<-rbind(P41,colSums(P41))
      AggP41<-P41[nrow(P41),]
      AggP41$Province<-4
      AggP41$Age<-1

P12<-OccurrenceMatrix[which(OccurrenceMatrix$Province==1 &
OccurrenceMatrix$Age==2),]
      P12<-rbind(P12,colSums(P12))
      AggP12<-P12[nrow(P12),]
      AggP12$Province<-1
      AggP12$Age<-2

P22<-OccurrenceMatrix[which(OccurrenceMatrix$Province==2 &
OccurrenceMatrix$Age==2),]
      P22<-rbind(P22,colSums(P22))
      AggP22<-P22[nrow(P22),]
      AggP22$Province<-2
      AggP22$Age<-2

P32<-OccurrenceMatrix[which(OccurrenceMatrix$Province==3 &
OccurrenceMatrix$Age==2),]
      P32<-rbind(P32,colSums(P32))
      AggP32<-P32[nrow(P32),]
      AggP32$Province<-3
      AggP32$Age<-2

P42<-OccurrenceMatrix[which(OccurrenceMatrix$Province==4 &
OccurrenceMatrix$Age==2),]
      P42<-rbind(P42,colSums(P42))
      AggP42<-P42[nrow(P42),]
      AggP42$Province<-4
      AggP42$Age<-2

P13<-OccurrenceMatrix[which(OccurrenceMatrix$Province==1 &
OccurrenceMatrix$Age==3),]
      P13<-rbind(P13,colSums(P13))
      AggP13<-P13[nrow(P13),]
      AggP13$Province<-1
      AggP13$Age<-3

P23<-OccurrenceMatrix[which(OccurrenceMatrix$Province==2 &
OccurrenceMatrix$Age==3),]
      P23<-rbind(P23,colSums(P23))
      AggP23<-P23[nrow(P23),]
      AggP23$Province<-2
```

```
      AggP23$Age<-3

P33<-OccurrenceMatrix[which(OccurrenceMatrix$Province==3 &
OccurrenceMatrix$Age==3),]
      P33<-rbind(P33,colSums(P33))
      AggP33<-P33[nrow(P33),]
      AggP33$Province<-3
      AggP33$Age<-3

P43<-OccurrenceMatrix[which(OccurrenceMatrix$Province==4 &
OccurrenceMatrix$Age==3),]
      P43<-rbind(P43,colSums(P43))
      AggP43<-P43[nrow(P43),]
      AggP43$Province<-4
      AggP43$Age<-3

P53<-OccurrenceMatrix[which(OccurrenceMatrix$Province==5 &
OccurrenceMatrix$Age==3),]
      P53<-rbind(P53,colSums(P53))
      AggP53<-P53[nrow(P53),]
      AggP53$Province<-5
      AggP53$Age<-3

Aggregates<-
rbind(AggP11,AggP21,AggP31,AggP41,AggP12,AggP22,AggP32,AggP42,Agg
P13,AggP23,AggP33,AggP43,AggP53)
rownames(Aggregates)<-c(11,21,31,41,12,22,32,42,13,23,33,43,53)

interprovincesimilarityAgg<-function(ProvinceAn,ProvinceBn,Agen){

      provinceageA<-Aggregates[Aggregates$Province==ProvinceAn &
Aggregates$Age==Agen,colnames(Aggregates)!
="Province"&colnames(Aggregates)!="Age"]
      provinceageB<-Aggregates[Aggregates$Province==ProvinceBn &
Aggregates$Age==Agen, colnames(Aggregates)!="Province" &
colnames(Aggregates)!="Age"]

      provinceage<-rbind(provinceageA,provinceageB)

      similarity<-1-vegdist(provinceage, method="jaccard",
binary=TRUE)

      similarity
      }

#Aggregate Table

AggregateTable<-
as.data.frame(matrix(data=9,nrow=22,ncol=4,dimnames=list(1:22,c("
ProvinceA","ProvinceB","Age","similarity"))))

row <- 1
```

```
for (Age in 1:3){
    for (ProvinceA in 1:3){
        for (ProvinceB in (ProvinceA+1):4){

        if (ProvinceA==3 & Age==1|ProvinceB==3 & Age==1){  #no
data
        ips <- 9
        } else {
                ips<-
interprovincesimilarityAgg(ProvinceA,ProvinceB,Age)
                }


        #fill in row
        AggregateTable[row,1] <- ProvinceA
        AggregateTable[row,2] <- ProvinceB
        AggregateTable[row,3] <- Age
        AggregateTable[row,4] <- ips


        # increment row number
        row <- row+1

        }
    }
}
    row<-19
    for (ProvinceA in 1:4){
        ProvinceB<-5
        Age<-3
        ips<-
interprovincesimilarityAgg(ProvinceA,ProvinceB,Age)

        AggregateTable[row,1] <- ProvinceA
        AggregateTable[row,2] <- ProvinceB
        AggregateTable[row,3] <- Age
        AggregateTable[row,4] <- ips

        # increment row number
        row <- row+1
        }
AggregateTable
write.csv(AggregateTable,"AggregateSimilarity.csv")

###PLOT
plotagr<-AggregateTable[AggregateTable$similarity<9,]

stripchart(plotagr$similarity~plotagr$Age,
xlim=c(0,max(plotagr$similarity)+.01), ylim=c(.5,3.5),
xlab="Jaccard's Similarity",ylab="Age",las=1, pch=16,
col="white", main="Aggregated Similarity")
points(plotagr$similarity[plotagr$ProvinceB==5],
```

```
plotagr$Age[plotagr$ProvinceB==5], pch=16, col="firebrick2")
points(plotagr$similarity[plotagr$ProvinceB!=5],
plotagr$Age[plotagr$ProvinceB!=5], pch=16, col="black")
points(plotagr$similarity[plotagr$Age==1&(plotagr$ProvinceA==2|
plotagr$ProvinceB==2)],plotagr$Age[plotagr$Age==1&(plotagr$Provin
ceA==2|plotagr$ProvinceB==2)],pch=16,col="white")

labelsage23<-
c("AM","AS","AW","MS","MW","SW","AM","AS","AW","MS","MW","SW")
simsage23<-plotagr$similarity[plotagr$ProvinceB!=5&plotagr$Age!
=1]
agesage23<-plotagr$Age[plotagr$ProvinceB!=5&plotagr$Age!=1]-.15
text(c(simsage23),c(agesage23),col="black",cex=.8,label=c(labelsa
ge23))

labelsage1<-c("AW")
simsage1<-
plotagr$similarity[plotagr$Age==1&plotagr$ProvinceA==1&plotagr$Pr
ovinceB==4]
agesage1<-
plotagr$Age[plotagr$Age==1&plotagr$ProvinceA==1&plotagr$ProvinceB
==4]-.15
text(c(simsage1),c(agesage1),col="black",cex=.8,label=c(labelsage
1))

labelsoutgroup<-c("A","M","S","W")
simsoutgroup<-plotagr$similarity[plotagr$ProvinceB==5]
agesoutgroup<-plotagr$Age[plotagr$ProvinceB==5]+.15
text(c(simsoutgroup),c(agesoutgroup),col="fire brick
1",cex=.8,label=c(labelsoutgroup))

text(.2,1.4,col="black",cex=.8,label="A Appalachian")
text(.2,1.2,col="black",cex=.8,label="M Midcontinent")
text(.2,1.0,col="black",cex=.8,label="S Southern")
text(.2,.8,col="black",cex=.8,label="W Western")
text(.2,.6,col="fire brick 2",cex=.8,label=" outgroup (UK)")


##############################################
#Ranked Lists
AbundanceList13<-sort(P13[nrow(P13),],decreasing=TRUE)
AbundanceList23<-sort(P23[nrow(P23),],decreasing=TRUE)
AbundanceList33<-sort(P33[nrow(P33),],decreasing=TRUE)
AbundanceList43<-sort(P43[nrow(P43),],decreasing=TRUE)
AbundanceList53<-sort(P53[nrow(P53),],decreasing=TRUE)
List13<-AbundanceList13[,AbundanceList13>0]
List23<-AbundanceList23[,AbundanceList23>0]
List33<-AbundanceList33[,AbundanceList33>0]
List43<-AbundanceList43[,AbundanceList43>0]
List53<-AbundanceList53[,AbundanceList53>0]

sum13<-sum(List13[,names(List13)!="Province"&names(List13)!
```

```
="Age"])
p13<-List13[,names(List13)!="Province"&names(List13)!
="Age"]/sum13
sum23<-sum(List23[,names(List23)!="Province"&names(List23)!
="Age"])
p23<-List23[,names(List23)!="Province"&names(List23)!
="Age"]/sum23
sum33<-sum(List33[,names(List33)!="Province"&names(List33)!
="Age"])
p33<-List33[,names(List33)!="Province"&names(List33)!
="Age"]/sum33
sum43<-sum(List43[,names(List43)!="Province"&names(List43)!
="Age"])
p43<-List43[,names(List43)!="Province"&names(List43)!
="Age"]/sum43
sum53<-sum(List53[,names(List53)!="Province"&names(List53)!
="Age"])
p53<-List53[,names(List53)!="Province"&names(List53)!
="Age"]/sum53
write.csv(p13,"abundancelistAL.csv")
write.csv(p23,"abundancelistML.csv")
write.csv(p33,"abundancelistSL.csv")
write.csv(p43,"abundancelistWL.csv")
write.csv(p53,"abundancelistUL.csv")

AbundanceList12<-sort(P12[nrow(P12),],decreasing=TRUE)
AbundanceList22<-sort(P22[nrow(P22),],decreasing=TRUE)
AbundanceList32<-sort(P32[nrow(P32),],decreasing=TRUE)
AbundanceList42<-sort(P42[nrow(P42),],decreasing=TRUE)
List12<-AbundanceList12[,AbundanceList12>0]
List22<-AbundanceList22[,AbundanceList22>0]
List32<-AbundanceList32[,AbundanceList32>0]
List42<-AbundanceList42[,AbundanceList42>0]

sum12<-sum(List12[,names(List12)!="Province"&names(List12)!
="Age"])
p12<-List12[,names(List12)!="Province"&names(List12)!
="Age"]/sum12
sum22<-sum(List22[,names(List22)!="Province"&names(List22)!
="Age"])
p22<-List22[,names(List22)!="Province"&names(List22)!
="Age"]/sum22
sum32<-sum(List32[,names(List32)!="Province"&names(List32)!
="Age"])
p32<-List32[,names(List32)!="Province"&names(List32)!
="Age"]/sum32
sum42<-sum(List42[,names(List42)!="Province"&names(List42)!
="Age"])
p42<-List42[,names(List42)!="Province"&names(List42)!
="Age"]/sum42

write.csv(p12,"abundancelistAM.csv")
```

```
write.csv(p22,"abundancelistMM.csv")
write.csv(p32,"abundancelistSM.csv")
write.csv(p42,"abundancelistWM.csv")

AbundanceList11<-sort(P11[nrow(P11),],decreasing=TRUE)
AbundanceList21<-sort(P21[nrow(P21),],decreasing=TRUE)
AbundanceList31<-sort(P31[nrow(P31),],decreasing=TRUE)
AbundanceList41<-sort(P41[nrow(P41),],decreasing=TRUE)
List11<-AbundanceList11[,AbundanceList11>0]
List21<-AbundanceList21[,AbundanceList21>0]
List31<-AbundanceList31[,AbundanceList31>0]
List41<-AbundanceList41[,AbundanceList41>0]

sum11<-sum(List11[,names(List11)!="Province"&names(List11)!
="Age"])
p11<-List11[,names(List11)!="Province"&names(List11)!
="Age"]/sum11
sum21<-sum(List21[,names(List21)!="Province"&names(List21)!
="Age"])
p21<-List21[,names(List21)!="Province"&names(List21)!
="Age"]/sum21
sum31<-sum(List31[,names(List31)!="Province"&names(List31)!
="Age"])
p31<-List31[,names(List31)!="Province"&names(List31)!
="Age"]/sum31
sum41<-sum(List41[,names(List41)!="Province"&names(List41)!
="Age"])
p41<-List41[,names(List41)!="Province"&names(List41)!
="Age"]/sum41

write.csv(p11,"abundancelistAE.csv")
write.csv(p21,"abundancelistME.csv")
write.csv(p31,"abundancelistSE.csv")
write.csv(p41,"abundancelistWE.csv")

#############REGIONAL SCALE#########################
#Set up Data

RAmatrix1<-decostand(AbundanceMatrix[,names(AbundanceMatrix)!
="Box"],"total")
#Convert abundance matrix to relative abundance
Box<-AbundanceMatrix$Box
RAmatrix<-cbind(RAmatrix1,Box)

#########Abundance lists: Most abundant taxa in each box########

#Make a table of the sums of each genera in a box, divided by the
number of individuals, this is basically relative abundance of
the aggregate collections of each box. At the end this will spit
out a list of the most abundant taxa in each collection

AggBoxTable<-
```

```
as.data.frame(matrix(data=9,nrow=7,ncol=length(names(AbundanceMat
rix)), dimnames=list(1:7,c(names(AbundanceMatrix)))))
for (i in 1:7){
      Box<-AbundanceMatrix[which(AbundanceMatrix$Box==i),]
      Box<-rbind(Box,colSums(Box))
      aggBox<-Box[nrow(Box),]
      aggBox$Box<-i
      AggBoxTable[i,]<-aggBox
      }

#Convert this to relative abundance
AggBoxTableBox<-AggBoxTable$Box
AggBoxTable<-AggBoxTable[,names(AggBoxTable)!="Box"]
RAagg<-decostand(AggBoxTable,"total")
Boxes<-c(1:7)
RAaggbox<-cbind(RAagg,Boxes)
names(RAaggbox)[which(names(RAaggbox)=="Boxes")]<-"Box"

AbundanceListBox1<-
round(sort(RAaggbox[RAaggbox$Box==1,],decreasing=TRUE),digits=2)
AbundanceListBox2<-
round(sort(RAaggbox[RAaggbox$Box==2,],decreasing=TRUE),digits=2)
AbundanceListBox3<-
round(sort(RAaggbox[RAaggbox$Box==3,],decreasing=TRUE),digits=2)
AbundanceListBox4<-
round(sort(RAaggbox[RAaggbox$Box==4,],decreasing=TRUE),digits=2)
AbundanceListBox5<-
round(sort(RAaggbox[RAaggbox$Box==5,],decreasing=TRUE),digits=2)
AbundanceListBox6<-
round(sort(RAaggbox[RAaggbox$Box==6,],decreasing=TRUE),digits=2)
AbundanceListBox7<-
round(sort(RAaggbox[RAaggbox$Box==7,],decreasing=TRUE),digits=2)
(ListBox1<-AbundanceListBox1[,AbundanceListBox1>0])
(ListBox2<-AbundanceListBox2[,AbundanceListBox2>0])
(ListBox3<-AbundanceListBox3[,AbundanceListBox3>0])
(ListBox4<-AbundanceListBox4[,AbundanceListBox4>0])
(ListBox5<-AbundanceListBox5[,AbundanceListBox5>0])
#Nashville
(ListBoxN<-AbundanceListBox6[,AbundanceListBox6>0])
#Cinci
(ListBoxC<-AbundanceListBox7[,AbundanceListBox7>0])


######Similarity######

#Combines collections from the two called regions, calculates
Jaccard's similarity
#binary=1 for PA, binary=0 for RA

betweenBoxsimilarity<-function(BoxnA,BoxnB,binary){

      boxA<-RAmatrix[RAmatrix$Box==BoxnA,colnames(RAmatrix)!
```

```
="Box"]
      boxB<-RAmatrix[RAmatrix$Box==BoxnB,colnames(RAmatrix)!
="Box"]
      twoboxes<-rbind(boxA,boxB)

      if (binary=="FALSE"|binary==0){
      similarity<-1-vegdist(twoboxes, method="jaccard",
binary=FALSE)
      } else{
      similarity<-1-vegdist(twoboxes, method="jaccard",
binary=TRUE)
      }
      logitsim<-car::logit(similarity,adjust=.0001)
      ttest<-t.test(logitsim)
      sd<-sd(logitsim)
      results<-c(ttest,sd)
      names(results)[10]<-"sd"
      intresults<-c(ttest,sd)
      names(intresults)[10]<-"sd"
      results<-
c(inv.logit(intresults$estimate),inv.logit(intresults$conf.int[1]
),inv.logit(intresults$conf.int[2]),inv.logit(intresults$sd))
      names(results)<-c("estimate","LCL","UCL","sd")
      results
    }


#Fill table:PA

PAbetweenBoxtable<-as.data.frame(matrix(data=9,nrow=21, ncol=6,
dimnames=list(1:21, c("BoxA","BoxB","mean","LCL","UCL","sd"))))

      row<-1

      for (BoxA in 1:6) {
           for (BoxB in (BoxA+1):7){
                bBs<-betweenBoxsimilarity(BoxA,BoxB,1)
                PAbetweenBoxtable[row,1]<-BoxA
                PAbetweenBoxtable[row,2]<-BoxB
                PAbetweenBoxtable[row,3]<-bBs[1]
                PAbetweenBoxtable[row,4]<-bBs[2]
                PAbetweenBoxtable[row,5]<-bBs[3]
                PAbetweenBoxtable[row,6]<-bBs[4]

           #increment row counter
           row<-row+1
           }
      }

write.csv(PAbetweenBoxtable,"PAbetweenBoxtable.csv")
(PAbetweenBoxtableRound<-round(PAbetweenBoxtable,3))
```

```
#Fill table:RA
RAbetweenBoxtable<-as.data.frame(matrix(data=9,nrow=21, ncol=6,
dimnames=list(1:21, c("BoxA","BoxB","mean","LCL","UCL","sd"))))

     row<-1

     for (BoxA in 1:6) {
          for (BoxB in (BoxA+1):7){
               bBs<-betweenBoxsimilarity(BoxA,BoxB,0)
               RAbetweenBoxtable[row,1]<-BoxA
               RAbetweenBoxtable[row,2]<-BoxB
               RAbetweenBoxtable[row,3]<-bBs[1]
               RAbetweenBoxtable[row,4]<-bBs[2]
               RAbetweenBoxtable[row,5]<-bBs[3]
               RAbetweenBoxtable[row,6]<-bBs[4]

          #increment row counter
          row<-row+1
          }
     }

write.csv(RAbetweenBoxtable,"RAbetweenBoxtable.csv")
(RAbetweenBoxtableRound<-round(RAbetweenBoxtable,3))


####Plots

#Within-Box PA#
windows()
plot(rownames(PAwithinBoxtable)~PAwithinBoxtable$mean,type="n",la
s=1,main="Within-Box P/A",ylab="Box",xlab="Jaccard
Similarity",xlim=c(0,max(PAwithinBoxtable$UCL)+.05))
#Add confidence intervals, r is simply a row counter
for (r in 1:nrow(PAwithinBoxtable)){

segments(PAwithinBoxtable[r,2],r,PAwithinBoxtable[r,3],r,col="gre
y")
}
points(PAwithinBoxtable$mean[1:5],rownames(PAwithinBoxtable)
[1:5],pch=16,col="steel blue 2")
points(PAwithinBoxtable$mean[6],rownames(PAwithinBoxtable)
[6],pch=16,col="orchid3")
points(PAwithinBoxtable$mean[7],rownames(PAwithinBoxtable)
[7],pch=16,col="orchid4")
text(.12,6,col="orchid3",cex=.8,label="Nashville")
text(.25,7,col="orchid4",cex=.8,label="Cincinnati")


#Within-Box: RA#
windows()
plot(rownames(RAwithinBoxtable)~RAwithinBoxtable$mean,type="n",la
s=1,main="Within-Box RA",ylab="Box",xlab="Jaccard
```

```
Similarity",xlim=c(0,max(RAwithinBoxtable$UCL)+.05))
#Add confidence intervals, r is simply a row counter
for (r in 1:nrow(RAwithinBoxtable)){

segments(RAwithinBoxtable[r,2],r,RAwithinBoxtable[r,3],r,col="gre
y")
}
points(RAwithinBoxtable$mean[1:5],rownames(RAwithinBoxtable)
[1:5],pch=16,col="steel blue 2")
points(RAwithinBoxtable$mean[6],rownames(RAwithinBoxtable)
[6],pch=16,col="orchid3")
points(RAwithinBoxtable$mean[7],rownames(RAwithinBoxtable)
[7],pch=16,col="orchid4")
text(.26,6,col="orchid3",cex=.8,label="Nashville")
text(.3,7,col="orchid4",cex=.8,label="Cincinnati")



#####PA Plot
#Grey lines are 95% confidence intervals; plotted is mean jaccard
similarity between labeled collections;

withinpa<-rbind(PAbetweenBoxtable[PAbetweenBoxtable$BoxA>5 &
PAbetweenBoxtable$BoxB>5,],PAbetweenBoxtable[PAbetweenBoxtable$Bo
xA<6 & PAbetweenBoxtable$BoxB<6,])

betweenpa<-PAbetweenBoxtable[PAbetweenBoxtable$BoxA<6 &
PAbetweenBoxtable$BoxB>5,]

rownames(withinpa)<-c(1:11)
betweenSortpa<-betweenpa[c(1,3,5,7,9,2,4,6,8,10),]
rownames(betweenSortpa)<-c(12:21)

combonamespa<-c(rownames(withinpa),rownames(betweenSortpa))
combomeanspa<-c(withinpa$mean,betweenSortpa$mean)

windows()
plot(combonamespa~combomeanspa,ylim=c(0,21),type="n",xlim=c(0,max
(c(max(withinpa$mean),max(betweenSortpa$mean)))
+.05),main="Presence/Absence",ylab="",xlab="Jaccard Similarity")

for (r in 1:nrow(withinpa)){
     segments(withinpa[r,4],r,withinpa[r,5],r,col="grey")
}
for (q in 1:nrow(betweenSortpa)){

segments(betweenSortpa[q,4],11+q,betweenSortpa[q,5],11+q,col="gre
y")
}

points(withinpa$mean[withinpa$BoxA>5 &
withinpa$BoxB>5],rownames(withinpa)[withinpa$BoxA>5 &
```

```
withinpa$BoxB>5],pch=16,col="darkorange3")
points(withinpa$mean[withinpa$BoxA<6 &
withinpa$BoxB<6],rownames(withinpa)[withinpa$BoxA<6 &
withinpa$BoxB<6],pch=16,col="forestgreen")
points(betweenSortpa$mean[betweenSortpa$BoxB==6],rownames(between
Sortpa)[betweenSortpa$BoxB==6],pch=16,col="darkorange1")
points(betweenSortpa$mean[betweenSortpa$BoxB==7],rownames(between
Sortpa)[betweenSortpa$BoxB==7],pch=16,col="darkorange2")

text(withinpa$mean[withinpa$BoxA>5 &
withinpa$BoxB>5],.5,col="darkorange3",cex=.6,label="C,N")
withinpalabels<-
c("1,2","1,3","1,4","1,5","2,3","2,4","2,5","3,4","3,5","4,5")
text(c(withinpa$mean[withinpa$BoxA<6 &
withinpa$BoxB<6]),c(seq(1.5,10.5,1)),cex=.6,col="forestgreen",lab
el=c(withinpalabels))
betweenpalabels<-c(1:5)
text(c(betweenSortpa$mean[betweenSortpa$BoxB==6]),c(seq(11.5,15.5
,1)),cex=.6,col="darkorange1",label=c(betweenpalabels))
text(c(betweenSortpa$mean[betweenSortpa$BoxB==7]),c(seq(16.5,20.5
,1)),cex=.6,col="darkorange2",label=c(betweenpalabels))
text(.18,14,cex=.6,col="darkorange1",label="vs. Nashville")
text(.17,19,cex=.6,col="darkorange2",label="vs. Cincinnati")
text(.09,7,cex=.6,col="forestgreen",label="Appalachian")
text(.19,1,cex=.6,col="darkorange3",label="Southern")

#####RA Plot

withinra<-rbind(RAbetweenBoxtable[RAbetweenBoxtable$BoxA>5 &
RAbetweenBoxtable$BoxB>5,],RAbetweenBoxtable[RAbetweenBoxtable$Bo
xA<6 & RAbetweenBoxtable$BoxB<6,])

betweenra<-RAbetweenBoxtable[RAbetweenBoxtable$BoxA<6 &
RAbetweenBoxtable$BoxB>5,]

rownames(withinra)<-c(1:11)
betweenSortra<-betweenra[c(1,3,5,7,9,2,4,6,8,10),]
rownames(betweenSortra)<-c(12:21)

combonamesra<-c(rownames(withinra),rownames(betweenSortra))
combomeansra<-c(withinra$mean,betweenSortra$mean)

windows()
plot(combonamesra~combomeansra,ylim=c(0,21),type="n",xlim=c(0,max
(c(max(withinra$mean),max(betweenSortra$mean)))
+.05),main="Relative Abundance",ylab="",xlab="Jaccard
Similarity")

for (r in 1:nrow(withinra)){
     segments(withinra[r,4],r,withinra[r,5],r,col="grey")
}
for (q in 1:nrow(betweenSortra)){
```

```
segments(betweenSortra[q,4],11+q,betweenSortra[q,5],11+q,col="gre
y")
}

points(withinra$mean[withinra$BoxA>5 &
withinra$BoxB>5],rownames(withinra)[withinra$BoxA>5 &
withinra$BoxB>5],pch=16,col="darkorange3")
points(withinra$mean[withinra$BoxA<6 &
withinra$BoxB<6],rownames(withinra)[withinra$BoxA<6 &
withinra$BoxB<6],pch=16,col="forestgreen")
points(betweenSortra$mean[betweenSortra$BoxB==6],rownames(between
Sortra)[betweenSortra$BoxB==6],pch=16,col="darkorange1")
points(betweenSortra$mean[betweenSortra$BoxB==7],rownames(between
Sortra)[betweenSortra$BoxB==7],pch=16,col="darkorange2")

text(withinra$mean[withinra$BoxA>5 &
withinra$BoxB>5],.5,col="darkorange3",cex=.6,label="C,N")
withinralabels<-
c("1,2","1,3","1,4","1,5","2,3","2,4","2,5","3,4","3,5","4,5")
text(c(withinra$mean[withinra$BoxA<6 &
withinra$BoxB<6]),c(seq(1.5,10.5,1)),cex=.6,col="forestgreen",lab
el=c(withinralabels))
betweenralabels<-c(1:5)
text(c(betweenSortra$mean[betweenSortra$BoxB==6]),c(seq(11.5,15.5
,1)),cex=.6,col="darkorange1",label=c(betweenralabels))
text(c(betweenSortra$mean[betweenSortra$BoxB==7]),c(seq(16.5,20.5
,1)),cex=.6,col="darkorange2",label=c(betweenralabels))

text(.10,14,cex=.6,col="darkorange1",label="vs. Nashville")
text(.25,19,cex=.6,col="darkorange2",label="vs. Cincinnati")
text(.16,8,cex=.6,col="forestgreen",label="Appalachian")
text(.18,1,cex=.6,col="darkorange3",label="Southern")

###################################

###MDS###
#MDS

#Run MDS
mMds1<-metaMDS(RAmatrix[,names(RAmatrix)!="Box"],k=1)
mMds2<-metaMDS(RAmatrix[,names(RAmatrix)!="Box"],k=2)
mMds3<-metaMDS(RAmatrix[,names(RAmatrix)!="Box"],k=3)
mMds4<-metaMDS(RAmatrix[,names(RAmatrix)!="Box"],k=4)
mMds5<-metaMDS(RAmatrix[,names(RAmatrix)!="Box"],k=5)
mMds6<-metaMDS(RAmatrix[,names(RAmatrix)!="Box"],k=6)
mMds7<-metaMDS(RAmatrix[,names(RAmatrix)!="Box"],k=7)

#Scree plot, pick number of axes
stressvector<-
c(mMds1$stress,mMds2$stress,mMds3$stress,mMds4$stress,mMds5$stres
s,mMds6$stress,mMds7$stress)
```

```
windows()
plot(stressvector,pch=16,las=1,xlab="k",ylab="stress")
#deciding to use k=3

#Species effects
windows()
plot(mMds3, type="t", display=c("species"),cex=.7)

#plot(mMds4, type="t", display=c("species"),cex=.7)


#MDS sites numbered (k=4)
windows()
plot(mMds4,type="n")
text(mMds4$points[which(rownames(mMds4$points)%in
%rownames(RAmatrix)
[RAmatrix$Box==6]),],col="darkorange2",labels="N",cex=.8)
text(mMds4$points[which(rownames(mMds4$points)%in
%rownames(RAmatrix)[RAmatrix$Box==7]),], col="darkorange2",
labels="C",cex=.8)
text(mMds4$points[which(rownames(mMds4$points)%in
%rownames(RAmatrix)[RAmatrix$Box==2]),],
col="forestgreen",labels="2",cex=.8)
text(mMds4$points[which(rownames(mMds4$points)%in
%rownames(RAmatrix)[RAmatrix$Box==3]),],
col="forestgreen",labels="3",cex=.8)
text(mMds4$points[which(rownames(mMds4$points)%in
%rownames(RAmatrix)[RAmatrix$Box==4]),],
col="forestgreen",labels="4",cex=.8)
text(mMds4$points[which(rownames(mMds4$points)%in
%rownames(RAmatrix)[RAmatrix$Box==5]),],
col="forestgreen",labels="5",cex=.8)
text(mMds4$points[which(rownames(mMds4$points)%in
%rownames(RAmatrix)[RAmatrix$Box==1]),],
col="forestgreen",labels="1",cex=.8)
text(-.3,-1.2,label="Southern",col="darkorange2",cex=.8)
text(1.7,-.5, label="Appalachian",col="forestgreen",cex=.8)

#MDS sites numbered (k=3)
#windows()
plot(mMds3,type="n")
text(mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)
[RAmatrix$Box==6]),],col="darkorange2",labels="N",cex=.8)
text(mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)[RAmatrix$Box==7]),], col="darkorange2",
labels="C",cex=.8)
text(mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)[RAmatrix$Box==2]),],
col="forestgreen",labels="2",cex=.8)
text(mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)[RAmatrix$Box==3]),],
```

```
col="forestgreen",labels="3",cex=.8)
text(mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)[RAmatrix$Box==4]),],
col="forestgreen",labels="4",cex=.8)
text(mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)[RAmatrix$Box==5]),],
col="forestgreen",labels="5",cex=.8)
text(mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)[RAmatrix$Box==1]),],
col="forestgreen",labels="1",cex=.8)
text(-.3,-1.2,label="Southern",col="darkorange2",cex=.8)
text(1.7,-.5, label="Appalachian",col="forestgreen",cex=.8)

#MDS chull
plot(mMds3,type="n")

mdspointsn<-mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)[RAmatrix$Box==6]),]
mdspointsc<-mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)[RAmatrix$Box==7]),]
mdspoints2<-mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)[RAmatrix$Box==2]),]
mdspoints3<-mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)[RAmatrix$Box==3]),]
mdspoints4<-mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)[RAmatrix$Box==4]),]
mdspoints5<-mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)[RAmatrix$Box==5]),]
mdspoints1<-mMds3$points[which(rownames(mMds3$points)%in
%rownames(RAmatrix)[RAmatrix$Box==1]),]

mdspn<-mdspointsn[,1:2]
mdspc<-mdspointsc[,1:2]
mdsp2<-mdspoints2[,1:2]
mdsp3<-mdspoints3[,1:2]
mdsp4<-mdspoints4[,1:2]
mdsp5<-mdspoints5[,1:2]
mdsp1<-mdspoints1[,1:2]

circlesn<-chull(mdspn)
circlesn<-c(circlesn,circlesn[1])
circlesc<-chull(mdspc)
circlesc<-c(circlesc,circlesc[1])
circles2<-chull(mdsp2)
circles2<-c(circles2,circles2[1])
circles3<-chull(mdsp3)
circles3<-c(circles3,circles3[1])
circles4<-chull(mdsp4)
circles4<-c(circles4,circles4[1])
circles5<-chull(mdsp5)
circles5<-c(circles5,circles5[1])
circles1<-chull(mdsp1)
```

```
circles1<-c(circles1,circles1[1])



text(mdspointsn,col="darkorange1",labels="N",cex=.8)
text(mdspointsc, col="darkorange1", labels="C",cex=.8)
text(mdspoints2, col="forestgreen",labels="2",cex=.8)
text(mdspoints3, col="forestgreen",labels="3",cex=.8)
text(mdspoints4, col="forestgreen",labels="4",cex=.8)
text(mdspoints5, col="forestgreen",labels="5",cex=.8)
text(mdspoints1, col="forestgreen",labels="1",cex=.8)
text(-.3,-1.2,label="Southern",col="darkorange1",cex=.8)
text(1.7,-.5, label="Appalachian",col="forestgreen",cex=.8)

lines(mdspn[circlesn,])
lines(mdspc[circlesc,])
lines(mdsp1[circles1,])
lines(mdsp2[circles2,])
lines(mdsp3[circles3,])
lines(mdsp4[circles4,])
lines(mdsp5[circles5,])

###########################################
#Distance
paradist<-read.csv("paradist.csv")
attach(paradist)

windows()
plot(RA~distr,pch=16,type="n",las=1,ylim=c(0,max(paradist$RAUCL))
,ylab="Similarity (RA)", xlab="distance (km)")

#Add confidence intervals, r is simply a row counter
for (r in 1:nrow(paradist)){

segments(paradist[r,4],paradist[r,7],paradist[r,4],paradist[r,8],
col="grey")
}

points(distr[box1=="C"|box2=="C"],RA[box1=="C"|
box2=="C"],pch=16,col="orange")
points(distr[box1=="N"|box2=="N"],RA[box1=="N"|
box2=="N"],pch=16,col="orangered")
points(distr[box2!="C"&box2!="N"],RA[box2!="C"&box2!
="N"],pch=16,col="darkgreen")
abline(lm(RA~distr),lty=2)

averageR2<-summary(lm(RA~distr))$adj.r.squared

text(800,.3,label= paste("R  =",round(averageR2,3)))

#####
windows()
```

```
par(mfrow=c(1,3))
plot(RA~distr,pch=16,type="n",las=1,ylim=c(0,max(paradist$RAUCL))
,ylab="Similarity (RA)", xlab="distance (km)",
main="Cincinnati/Appalachian")

#Add confidence intervals, r is simply a row counter
for (r in 1:nrow(paradist)){
if (box1[r]=="C"|box2[r]=="C"){

segments(paradist[r,4],paradist[r,7],paradist[r,4],paradist[r,8],
col="grey")
}
}

points(distr[box1=="C"|box2=="C"],RA[box1=="C"|
box2=="C"],pch=16,col="orange")
abline(lm(RA~distr),lty=2,col="grey")
abline(lm(RA[box1=="C"|box2=="C"]~distr[box1=="C"|
box2=="C"]),lty=2)

cinR2<-summary(lm(RA[box1=="C"|box2=="C"]~distr[box1=="C"|
box2=="C"]))$adj.r.squared

text(800,.3,label= paste("R  =",round(averageR2,3)),col="grey")
text(800,.28,label= paste("R  =",round(cinR2,3)))
#####
plot(RA~distr,pch=16,type="n",las=1,ylim=c(0,max(paradist$RAUCL))
,ylab="Similarity (RA)", xlab="distance (km)",
main="Nashville/Appalachian")

#Add confidence intervals, r is simply a row counter
for (r in 1:nrow(paradist)){
if (box1[r]=="N"|box2[r]=="N"){

segments(paradist[r,4],paradist[r,7],paradist[r,4],paradist[r,8],
col="grey")
}
}

points(distr[box1=="N"|box2=="N"],RA[box1=="N"|
box2=="N"],pch=16,col="orangered")
abline(lm(RA~distr),lty=2,col="grey")
abline(lm(RA[box1=="N"|box2=="N"]~distr[box1=="N"|
box2=="N"]),lty=2)
nashR2<-summary(lm(RA[box1=="N"|box2=="N"]~distr[box1=="N"|
box2=="N"]))$adj.r.squared
text(800,.3,label= paste("R  =",round(averageR2,3)),col="grey")
text(800,.28,label= paste("R  =",round(nashR2,3)))
```