Integrating GIS and Phylogenetic Biogeography to Assess Species-Level Biogeographic Patterns

A Case Study of Late Devonian Faunal Dynamics

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CONTENTS

5.1 Introduction .................................................................................................. 114
5.2 Quantifying Geographic Ranges of Fossil Taxa .......................................... 115
5.3 Geographic Information Systems in Palaeobiogeography ........................... 116
5.3.1 Palaeobiogeographic Potential of GIS............................................... 116
5.3.2 Overview of GIS Analyses in Palaeontology ....................................... 116
5.3.3 Practical Considerations for Implementing GIS in Palaeobiogeographic Studies ............................................................ 117
5.3.4 Effects of Taphonomic Biases on Palaeobiogeographic Patterns ........... 119
5.4 Relating Geographic Range, Ecology, and Evolution ............................... 120
5.5 Case Study: Species-Level Analyses of Late Devonian Biogeographic Patterns ...................................................................................... 122
5.5.1 Impact of Geographic Range on Species Survival ............................ 123
5.5.2 Biogeographic Patterns in a Phylogenetic Context ............................ 128
5.5.3 Speciation Rate and Mode Analysis ................................................. 128
5.5.4 Phylogenetic Biogeography .............................................................. 132
5.6 Discussion .................................................................................................. 133
5.7 Conclusions ................................................................................................ 134
Acknowledgements .......................................................................................... 134
Literature Cited .................................................................................................. 135
5.1 INTRODUCTION

The fossil record contains a rich history of shifting geographic ranges of species in the ancient past (Lieberman, 2003). Quantifying the geographic ranges of species in the fossil record is currently an underdeveloped yet promising area of study. Palaeobiogeographic studies have typically examined shifts in geographic range over large timescales (stages or periods), mainly of higher taxa (Boucot, 1975). Range reconstruction methods using Geographic Information Systems (GIS), however, provide promising new opportunities to quantify ranges of individual fossil species in addition to higher taxa across temporal intervals approximating that of biostratigraphic zones (Rode and Lieberman, 2004, 2005; Stigall Rode and Lieberman, 2005a, 2005b). Recent use of GIS in palaeontology, including reconstructing the species ranges of Palaeozoic invertebrates through multiple temporal intervals (Rode and Lieberman, 2000, 2004, 2005), has begun to surpass cataloguing species occurrences and to produce data to test palaeoecological and palaeobiogeographic hypotheses. Palaeobiogeographic ranges of higher taxa, such as families and orders, contribute important information about the evolutionary history of clades and their co-evolution with the Earth.

Characterisation of the ranges of individual fossil species, however, provides additional insight into evolutionary processes such as speciation and extinction. Because species are the entities through which the macroevolutionary phenomena of speciation and extinction occur, quantification of species ranges provides key information for assessing evolutionary patterns. In particular, quantifying changes in the spatial distribution of species ranges through time can provide insight into biogeographic feedback onto palaeoecology and macroevolution. The geographic range of a fossil species, as for a modern species, represents the geographic limits of the realised niche of that taxon (Brooks and McLennan, 1991, 2002; Lomolino et al., 2006). Quantifying the spatial shifts in these distributions over geologic time, therefore, can provide information about changing environmental tolerances or (more commonly) habitat tracking of a stable species through time (Stigall Rode and Lieberman, 2005b). Studying ranges of individual species, therefore, provides direct information on the interplay between biogeographic and palaeoecological processes.

Furthermore, species ranges when combined with species-level phylogenetic information can provide insight into the relationship amongst the macroevolutionary processes of speciation, extinction, and biogeography. A robust species-level phylogenetic hypothesis will provide a rigorous evolutionary framework in which to interpret specific shifts in geographic ranges of closely related species (Wiley and Mayden, 1985). In addition, the use of species-level phylogenies within a phylogenetic biogeographic framework further provides analytical data on the interaction between biogeography and evolution. In particular, style of speciation, episodes of vicariance or dispersal, and the role of tectonic or environmental drivers of biodiversity change during intervals of biodiversity crisis may be quantified (Lieberman and Eldredge, 1996; Rode and Lieberman, 2005; Stigall Rode and Lieberman, 2005a).

Quantifying the interaction between species range expansion and contraction and macroevolution in the fossil record has the potential to provide insight into the long-term effects of range changes, such as expansion and contraction, during the modern
biodiversity crisis. The fossil record provides a rich history of range expansions and interbasinal species invasions that can be studied as analogues of modern events to characterise the long-term effects of modern ecosystem threats such as invasive species. Monitoring and understanding the reasons for geographic range expansion and contraction are crucial in examining the ecological and evolutionary history of both individual species and monophyletic clades (Enserink, 1999; Engler et al., 2004; Gurevitch and Padilla, 2004; Wilson et al., 2004). The importance of preserving geographic ranges of modern species is echoed throughout the modern biological conservation literature (Peterson and Vieglais, 2001; Johnson et al., 2004; Rushton et al., 2004; Thomas et al., 2004; Wilson et al., 2004). The long-term (thousands to hundreds of thousands of years) impact of expansions or contractions in geographic range (those effects requiring hundreds or thousands of years to manifest) can only be directly assessed by studying similar events in the geological past.

5.2 QUANTIFYING GEOGRAPHIC RANGES OF FOSSIL TAXA

Determining the geographic limits of taxon ranges has historically been a key feature of palaeobiogeography. Numerous studies have examined the geographic regions occupied by higher taxa, such as families and orders. Palaeobiogeographic analyses of this type commonly involve plotting taxonomic occurrences on continent or basin scale maps, and examining changes in geographic patterns at the temporal scale of stages (often 5–10 million years in duration) or greater. Biotic comparison based on presence or absence of taxa and perceived biogeographic barriers have contributed enormously to biogeography by documenting first-order biogeographic patterns in the fossil record through the delineation of biogeographic realms and provinces (Boucot et al., 1969; Boucot, 1975; Oliver, 1976; Webby, 1992).

Many palaeobiogeographic analyses concentrate on statistical patterns of similarity between areas using comparative methods, in which the overall similarity of all taxa within regions are considered together rather than investigating the geographic limits of single taxa. Methods for quantifying biogeographic differences range from studies based on similarity metrics and correspondence analysis (Lees et al., 2002; Shen and Shi, 2004) to those in which parsimony is used to determine nested patterns of endemism (Parsimony Analysis of Endemicity; Rosen and Smith, 1988). These types of analyses provide insight into biogeographic patterns operating at ecosystem and biosphere levels. Useful as these methods are, they are designed to identify biogeographic patterns between regions and cannot assess the multidimensional spatial distribution (irregular geographic limits and temporal relationships) of taxa within a region.

Species-level analyses provide a framework to assess the relationship amongst biogeographic, palaeoecological, and evolutionary patterns (Adrain et al., 2001). Analyses of species-level patterns would be prohibitively cumbersome if not for increases in both the availability of palaeontological databases (e.g., the Paleobiology Database, http://paleodb.org/cgi-bin/bridge.pl) and computing capabilities in the past decade. Recent studies have incorporated inferred geographic limits of individual species in several contexts. Roy et al. (2001, 2004) determined the latitudinal range of modern and Pleistocene Pacific coast bivalve species to examine range shifts in
response to climatic changes. Rode and Lieberman (2004) and Stigall Rode and Lieberman (2005b) reconstructed the ranges of individual brachiopod species across the Late Devonian mass extinction interval and found a significant biogeographic difference between victims and survivors. A similar biogeographic bias in range size and extinction also occurs in Late Triassic ammonoids (W. Kiessling, pers. comm.).

5.3 GEOGRAPHIC INFORMATION SYSTEMS IN PALAEOBIOGEOGRAPHY

5.3.1 PALAEOBIOGEOGRAPHIC POTENTIAL OF GIS

Simultaneous analysis of multiple species’ ranges can be readily accomplished within a GIS. GIS-based analysis has only recently been applied to palaeobiogeographic analyses, but it offers significant advantages over previous approaches for reconstructing ranges of fossil taxa (Stigall Rode, 2005b). Geographic information systems function as a series of digital maps in which different datasets are stored as independent layers (Theobald, 2003). GIS range maps are dynamic; layers can be shown or hidden and data updated instantly. The ability to efficiently and accurately update data within distribution maps is a significant advantage over traditional range creation methods. Furthermore, GIS databases can be designed to incorporate both temporal and spatial variability (Berry, 1995; Chou, 1997; Burrough and McDonnell, 1998; Stigall Rode, 2005b). This creates a quantitative framework in which to examine temporal and spatial patterns in the fossil record in a statistically rigorous manner. Moreover, creating GIS-based range maps requires a series of species occurrence points, georeferenced to latitude and longitude values. This type of data can potentially integrate seamlessly with large database projects, such as the Paleobiology Database. Species occurrence data can be both extracted from and donated to such databases, which ensures further utility of these data to other researchers.

The combination of these features indicates that GIS analysis of species ranges can result in the creation of hypotheses based on large datasets that can be tested statistically, a fundamental advance for palaeobiogeography. For example, testable hypotheses could be generated examining the relationship of geographic ranges to environmental variables or patterns of speciation and extinction (Stigall Rode, 2005b). In addition, the use of GIS methodology is widespread amongst biologists and ecologists; therefore, incorporation of GIS into the palaeontology ‘toolbox’ will further enhance opportunities for neo- and palaeobiogeographers to interact. Statistical analyses comparable to those used within the modern biota can then be applied to the fossil record. The use of parallel methods with modern and fossil taxa creates a common framework to compare the dynamics of shifting biogeographic ranges across multiple timescales.

5.3.2 OVERVIEW OF GIS ANALYSES IN PALAEOLOGY

Although many biological and geological subdisciplines routinely incorporate GIS into analyses, palaeontological use of GIS methods has been somewhat limited to date. The primary use of GIS in palaeontology has been to create geospatial
Integrating GIS and Phylogenetic Biogeography

databases of fossil localities (Benton et al., 2001; Ferguson et al., 2001; Lacruz et al., 2003; McKinney et al., 2003, 2004). These digital databases provide a tremendous opportunity for geospatial analysis that has not yet been exploited analytically. Spatially arrayed morphological features have also been analysed within a GIS including ontogenetic changes in mammalian molar cusps (Jernvall et al., 2000) and the distinctiveness of ammonite suture patterns (Yacobucci and Manship, 2003; Manship, 2004).

Relatively few studies have utilised GIS for analyses testing palaeobiogeographic hypotheses and most of these have analysed species distributions strictly by spatial analysis point data. Graham et al. (1996a) implemented the first palaeobiogeographic GIS analysis with the FAUNMAP database. The database included point occurrence data for Cenozoic mammals. Spatial occurrences of taxa were utilised to examine range shifts in relation to climate and to analyse community stability through episodes of climate change (Graham et al., 1996a, 1996b; Graham, 2000). Markwick (2002) utilised species occurrence data from the Cenozoic tetrapod fauna of Europe (digitised as point data overlain on polygon-based climate maps) to discern a relationship amongst climate, biogeography, and species diversity. A similar analysis conducted by Vermeersch (2005) analysed the geographic distribution of hominids during the last glacial cycle compared to climate and vegetation distributions. The most sophisticated use of point occurrence data to date was undertaken by Rayfield et al. (2005) who analysed the spatial and temporal occurrence of terrestrial vertebrates to assess the relative validity of vertebrate biochrons in the Middle to Late Triassic.

One of the most powerful aspects of GIS analysis is the ability to reconstruct geographic ranges in multidimensional space. Species occurrence data can be converted from point data into polygon coverages allowing the size and spatial position of geographic ranges to be quantified and compared using spatial statistics. Such studies have been limited to date, but offers incredible potential for palaeobiogeographic analysis (reviewed in ‘case studies’ below; Stigall and Lieberman, 2006). The use of computer learning-based genetic algorithms to predict species range limits based on environmental parameters offers additional potential to quantify and interpret the causes of species range shifts in the fossil record (Stigall Rode and Lieberman, 2005b).

5.3.3 Practical Considerations for Implementing GIS in Palaeobiogeographic Studies

The use of GIS in palaeontology offers great potential for increased quantification within palaeontological analyses. GIS provide the capacity to analyse large amounts of species occurrence data and produce quantitatively constrained geographic range reconstruction. The basic steps in GIS range reconstruction are database assembly (including taxonomic, geographic, and stratigraphic information for each specimen), mapping of species localities onto modern continental configurations, rotation of species occurrence data onto palaeocontinental reconstructions, and reconstruction of geographic ranges (Rode and Lieberman, 2004; Stigall Rode, 2005b).

The most important and time consuming of these steps is the first: database creation. GIS is a tool, and like all analytical tools, there are important theoretical issues
that must be considered. Spatial analysis routines only examine the data provided, and the quality of the output reflects the quality of the source data.

The primary data required to reconstruct a species’ range are the taxon identification, geographic location (in decimal degrees) of collection, and the temporal interval of occurrence. Mapping cannot be completed without these three pieces of information, however, a GIS database will have considerably enhanced utility for querying results if additional information can also be included. Recommended additional information includes detailed stratigraphic information (formation, member, zone), additional geographic information (country, state/province, county, city, locality description), systematic classification (higher or lower level classification than unit of interest), and the reference information (specimen ID number from museum/field collection).

Species occurrence data can be derived from a number of sources including new field collections, museum collections, literature, or archival palaeontological databases. Depending on the level of temporal or spatial accuracy desired to address a specific question, certain data sources may be more appropriate than others. New field collections can have the highest-level precision, because the investigator can validate the taxon ID, geographic coordinates, and stratigraphic horizon personally. Museum collections provide the opportunity to validate taxon ID (which is critical inasmuch as many collections’ identifications are several decades old), but locality and stratigraphic horizon must be assumed to be accurate and often have coarse resolution. Data extracted directly from databases often share the coarse stratigraphic and temporal resolution of museum collections and the investigator must also assume taxon identifications are accurate. Data extracted from the literature must be assumed to contain accurate stratigraphic and locality information but may provide opportunity for verification of species ID if specimens are illustrated or systematic descriptions are included.

Species distribution maps, which provide a basis for quantitative spatial analysis, are relatively simple to create within a GIS. Following database construction, species data can be mapped onto modern continental distributions within a GIS (ArcGIS 9.2 [ESRI®, 2006] is currently the industry standard) or rotated onto palaeocontinental positions using programs such as PaleoGIS (Ross and Scotese, 2000) or Point Tracker (Scotese, 2004; Figure 5.1). Once the data are rotated onto the palaeocontinental positions, the rotated point data and palaeocontinental maps can be imported into ArcGIS for manipulation. Range maps can then be constructed for each species during each time slice in which it was extant by digitising a polygon to enclose the distribution data for each species as illustrated in Figure 5.1C. More detailed discussion of methods and a stepwise guide to palaeobiogeographic reconstruction methods are published elsewhere (Stigall Rode, 2005b; Stigall, 2006a).

As with the construction of the occurrence database, practical considerations are important in range reconstruction. Multiple techniques could be envisioned for digitising polygons, so investigators should explicitly define the criteria followed when presenting results. It is suggested that when digitising polygons, a specific policy of polygon assembly be adopted by an investigator and that policy should be articulated in resulting publications. Aspects of the policy should include: (1) what distance buffer will be used around occurrence points; and (2) how are the outer boundaries of
the polygon determined (e.g., establishing a polygon with the smallest perimeter, the smallest internal area, or some other criterion). Parsimony principles should be followed where possible to reduce ad hoc assumptions. For example, the reconstructed polygon illustrated in Figure 5.1C in which some occurrences fall within the range is more parsimonious than an alternative polygon in which the range perimeter follows the outline of all occurrences.

5.3.4 Effects of Taphonomic Biases on Palaeobiogeographic Patterns

Of particular concern when reconstructing geographic ranges of fossil species are issues related to taphonomy and the fidelity of the fossil record. Although taphonomic filtering can affect the fossil record in numerous ways (see review in Kidwell and Flessa, 1996), the most significant taphonomic biases to consider within palaeobiogeographic studies are: (1) undersampling (e.g., species was present but not collected at a locality/strata); (2) out-of-habitat transport of specimens; and (3) secular changes in rock volume or facies in outcrop belts. Each of these processes can potentially result in incomplete or inaccurate biogeographic reconstructions if overlooked, but each can also be addressed or mitigated.

The potential for undersampling to affect palaeobiogeographic reconstructions is primarily a function of the abundance of a taxon within the ecosystem. Abundant taxa are more likely to be frequently collected and, consequently, reconstructed ranges for these taxa are more likely to approximate reality. For abundant organisms with strong skeletal elements, such as shallow marine bivalves, analyses have shown that up to 85% of species are preserved in the fossil record (Valentine, 1989). Detailed palaeobiogeographic analyses are, therefore, best suited to common or abundant taxa whose fossil records will exhibit high fidelity. The temporal and spatial limits of an investigation should be scaled appropriately to address this concern. For example, members of Devonian brachiopod species are much more abundant than Devonian phyllocarids (a group of predatory crustaceans); consequently, GIS-based analyses of

![FIGURE 5.1 Steps in GIS range reconstruction. (A) Distribution of all data points plotted onto a modern continental configuration. (B) Reconstruction of all data points present for a single biostratigraphic zone. (C) Reconstruction of the geographic range of the bivalve, Leptodesma (Leiopteria) nitida in the linguiformis zone (terminal Frasnian conodont zone), range is 30.0 × 10³ km². (Modified from Rode, A.L. and Lieberman, B.S. (2005), Journal of Paleontology, 79: 267–276.).](image-url)
these groups have been performed on differing spatial and temporal scales: fine scale for brachiopods (conodont zones and township level; Rode and Lieberman, 2004) and a coarser scale for phyllocarids (stages and county level; Rode and Lieberman, 2005), respectively.

Out-of-habitat transport has the potential to confound biogeographic patterns, particularly in studies attempting to link palaeobiogeography with palaeoecology. Studies of modern environments (both marine and continental), however, have repeatedly found that skeletal remains of organisms are rarely transported outside the range of the original habitat of the source population (Kidwell and Bosence, 1991; Kidwell and Flessa, 1996). The primary exceptions to this occur in environments with steep depositional slopes or episodic pulses of high energy which can transport large amounts of skeletal material (Kidwell and Bosence, 1991). Being aware of the depositional slope and energy regime of the sedimentary units under investigation will allow this potential bias to be removed or accounted for within analyses.

The most significant and potentially difficult bias to address in palaeobiogeographic studies is the effect of secular changes in outcrop volume and sedimentary environments within the study area. This type of bias, in fact, is likely to be present within all palaeobiogeographic studies that span a significant range in either time or space. It is critical for investigators to consider whether this type of effect is present within their data and then determine what types of data analysis are best suited to remove any taphonomic biases of this sort. Several statistical approaches can be used depending on the type of secular bias including degrading all data to the level of the lowest interval using subsampling routines, examining changes in area extent using relative or normalised rather than absolute areas, or other types of statistical analyses. In some instances, secular changes may not negatively affect an analysis. For example, Stigall Rode and Lieberman (2005b) recovered a pattern in which several species were increasing their geographic ranges even though the total outcrop area was decreasing. This source of potential bias should be addressed in all palaeobiogeographic studies, however, whether there is a direct link seems initially apparent.

5.4 RELATING GEOGRAPHIC RANGE, ECOLOGY, AND EVOLUTION

Characterising the geographic distribution and limits of species’ ranges and analysing biogeographic patterns across the entire biota provides a framework in which to examine palaeoecological and evolutionary patterns. Reconstructed range maps provide the basis for identifying expansions, contractions, or lateral shifts in geographic range of an individual species between temporal intervals (Rode and Lieberman, 2004). Species ranges, such as those described above, can be statistically analysed against environmental parameters within a GIS framework (Rode and Lieberman, 2004) including geostatistical analyses. Species-level analyses can be directly related to immigration or speciation events, emigration or extinction events, and phylogenetic hypotheses of evolutionary relationships (Stigall Rode, 2005b; Stigall Rode and Lieberman, 2005a). Combined analyses of temporal changes in numerous species or clades can shed further light on community level patterns.
Integrating GIS and Phylogenetic Biogeography

More advanced GIS-based methods involving range prediction have also been applied to model species ranges in the fossil record based on environmental preferences. Mensing et al. (2000) predicted the location of Pleistocene packrat (Neotoma) middens in Nevada by using a weights-of-evidence model based on geology, elevation, and slope aspect. Stigall Rode and Lieberman (2005b) used a genetic algorithm incorporating multiple environmental variables to predict the geographic extent of species ranges. This study modified an algorithm, GARP (Genetic Algorithm for Rule-Set Prediction), originally developed to approximate the fundamental niche of a species and then predict the geographic ranges of modern species based on ecological parameters (Stockwell and Peters, 1999; Sanchez-Cordero et al., 2004; Stigall Rode and Lieberman, 2005b). The geological record provides ample environmental data for niche modelling analyses. Environmental variables can be readily discerned from sedimentary structures and lithological parameters in the sedimentary record. This type of analysis, therefore, represents another way in which neo- and palaeobiogeographers can use compatible methods to produce testable hypotheses.

Comparison of species-level biogeographic patterns within a species-level phylogenetic framework provides insight into macroevolutionary processes. For example, observed spatial overlap between two species may be due to several causes including shared environmental tolerances or common ancestry (Wiley and Mayden, 1985; Brooks and McLennan, 1991). Comparing the biogeographic pattern with the evolutionary history of a group provides a method to choose between these alternatives (Stigall Rode, 2005b).

Furthermore, analysis of species-level biogeographic patterns within a phylogenetic context provides the ability to discern patterns of speciation by dispersal or vicariance (Lieberman, 2000, 2003). Several methods of phylogenetic biogeography have been designed to address this issue including parsimony-based analyses, such as Primary and Secondary Brooks Parsimony Analysis (BPA; Brooks et al., 2001). Secondary BPA, in fact, is designed specifically to recover episodes of dispersal and area reticulations in the history of a clade. Other methods developed after BPA include cost-matrix analyses such as Dispersal–Vicariance Analysis (DIVA; Ronquist, 1997) and tree reconciliation analyses such as TreeMap (Page, 1994). A newly developed method, which builds on secondary BPA using nodal analyses to examine specific speciation events across three or more clades, known as Phylogenetic Analysis for Comparing Trees (PACT), provides a direct way to assess vicariance and dispersal events at individual phylogenetic nodes (Wojcicki and Brooks, 2005; Brooks and Folinsbee, 2011). This method integrates seamlessly with examination of reconstructed species-level range reconstructions.

In addition, Lieberman-modified Brooks Parsimony Analysis (LBPA; Lieberman and Eldredge, 1996; Lieberman, 2000) analyses faunal patterns of vicariance and geodispersal exhibited by an entire clade or clades. The LBPA method is the only phylogenetic biogeographic method designed to relate recovered biogeographic patterns to identifiable earth history events, specifically whether cyclical events (e.g., relative sea-level change or climatic oscillations) or singular events (e.g., tectonic collisions or other noncyclical change) contribute more profoundly to the development of observed biogeographic patterns (Lieberman, 2000). By integrating individual
species patterns from range map reconstructions with clade patterns from LBPA, fine details of faunal dynamics can be teased apart (Stigall and Lieberman, 2006).

5.5 CASE STUDY: SPECIES-LEVEL ANALYSES OF LATE DEVONIAN BIOGEOGRAPHIC PATTERNS

The Late Devonian was a time of profound evolutionary and environmental change associated with the Frasnian–Famennian Biodiversity Crisis, including reduction in speciation rates, increased extinction rates, rampant species invasions, and ecosystem restructuring (Sepkoski, 1986; McGhee, 1996; Droser et al., 2000). The biodiversity crisis may have lasted as long as three million years with a final pulse of more severe extinction in the last few hundred thousand years of the Frasnian. To unravel the faunal dynamics of this complex crisis, it is critical to understand both the spatial and temporal patterns associated with biodiversity decline.

Prior to the mass extinction interval, a dramatic transition occurred from a highly endemic Middle Devonian fauna to a cosmopolitan biota by the late Frasnian (early Late Devonian; Oliver, 1976, 1990; McGhee, 1996). The expansion of geographic ranges and the transition to a Late Devonian cosmopolitan biota has been documented in many taxa including rugose corals (Oliver, 1976, 1990; Oliver and Pedder, 1994), brachiopods (McGhee, 1981, 1996), foraminifera (Kalvoda and Walliser, 1990), fishes (Young, 1987), conodonts (Klapper and Johnson, 1980; Klapper, 1995), trilobites (Feist, 1991), and land plants (Raymond and Metz, 1995). This changing pattern of geographic range, particularly range expansion events analogous to species invasions, during the Middle to Late Devonian transition, has been implicated in species survival during the biodiversity crisis interval (Rode and Lieberman, 2004).

The Late Devonian strata of Eastern North America, in particular, comprise an excellent record in which to examine changing geographic ranges. The extensive sedimentary record of the Appalachian basin was derived from weathering highlands uplifted during the Acadian Orogeny and preserves a detailed history of the Late Devonian (Frasnian/Famennian) mass extinction, widespread range expansion of species, and a dramatic reduction in speciation rates (Dineley, 1984; McGhee, 1996). The primary tectonic developments were related to the Acadian Orogeny on the eastern margin of the continent (Van der Voo, 1988; Dalziel et al., 1994; Murphy and Keppie, 1998; McKerrow et al., 2000; Figure 5.2). Overthrusting during pulses of the Acadian Orogeny affected the relative relief of the intracratonic basins and arches within Laurentia (Quinlan and Beaumont, 1984; Beaumont et al., 1988). Intracratonic arches were uplifted during episodes of tectonic quiescence, isolating the shallow epicontinental marine basins, and subsided during orogenic pulses (Figure 5.3). The relative relief of intracratonic arches directly influenced the potential for marine species to disperse between the shallow marine basins within Laurentia. Consequently, palaeobiogeographic analyses can address questions related to the relative timing of tectonic uplift and sea level changes because the relative separation of sedimentary basins is reflected directly in biotic exchange versus endemism of their associated faunas.
The combination of biotic overturn, geographic expansion, tectonic activity, and substantial fossil and sedimentary record make the Late Devonian of Eastern North America an excellent interval in which to implement GIS methods, assess their accuracy, and employ these methods to decipher the faunal dynamics of a key event in Earth's history. The case study presented below uses range reconstructions constrained by GIS or phylogenetic frameworks to address specific aspects of the Late Devonian Biodiversity Crisis.

5.5.1 Impact of Geographic Range on Species Survival

Using a GIS-based analysis of brachiopod and bivalve species from the Middle to Late Devonian in Laurentia, Rode and Lieberman (2004) investigated the relationship amongst biogeography, relative sea level, and environmental changes. For this analysis a database, including over 8,400 species occurrence points spanning 19 conodont zones from the Givetian to early Fammenian, was assembled from museum and (limited) field collections. The ranges of 341 species of the 28 most common brachiopod and bivalve genera of the Middle to Late Devonian in Laurentia (Rode and Lieberman, 2004) were reconstructed using the polygon boundary method discussed and outlined above (Figures 5.1 and 5.4). Species ranges were spatially quantified within temporal bins approximating conodont zones (approximately 0.5
Ma) within a GIS. The timing and extent of species invasions into new tectonic basins were also determined.

Rode and Lieberman (2004) uncovered statistically significant relationships amongst size of species ranges, relative sea-level changes, and species survival through the mass extinction interval. Interbasinal invasion events were not randomly distributed in time but were clustered in three episodes of elevated interbasinal species invasion (Figures 5.4 and 5.5). The timing of these events corresponds to the beginning of the Frasnian, onset of the biodiversity crisis in the mid-Frasnian, and the final stage of the biodiversity crisis in the Late Frasnian. These three pulses of invasion also coincide with transgressive (relative sea-level rise) events IIb, IIC, and IID of Johnson et al. (1985). In addition, species survival through the crisis interval exhibited a clear biogeographic pattern. A clear survival advantage was conferred on species with: (1) larger geographic ranges (t-test, \( p < 0.001 \)); (2) one or more episodes of interbasinal invasion in their history (t-test, \( p < 0.001 \)); or (3) that occupied middle- to outer-shelf environments (\( X^2 \) test, \( p = 0.004 \)). Conversely, species that were strictly endemic, had narrow geographic ranges, or lived in nearshore or basinal environments had statistically lower rates of survival into the Famennian.

The relationship between geographic range size and extinction survival was further examined using a genetic algorithm approach to predict the geographic range of a species by modelling the boundaries of its fundamental niche (Stigall Rode and Lieberman, 2005b). This study utilised the GARP modelling system (Stockwell and Peters, 1999), which predicts species ranges by estimating the fundamental ecological requirements (niche) of a species from a set of known occurrence sites each of

FIGURE 5.3 Intracratic arches that served as primary barriers to shallow marine dispersal within Laurentia during the Devonian. Abbreviations: A—Acadian highlands; C—Cincinnati Arch; F—Findley Arch; K—Kankakee Arch; O—Ozark Dome; S—Canadian Shield; T—Transcontinental Arch; W—Wisconsin Arch. (Reprinted from Stigall Rode, A.L. and Lieberman, B.S. (2005a). Palaeogeography, Palaeoclimatology, Palaeoecology, 222: 272-284. With permission from Elsevier.)
Figure 5.4 Palaeobiogeographic ranges of *Schizophoria impressa* in six biostratigraphic intervals of the Middle to Late Devonian indicating episodes of range expansion, contraction, and interbasinal invasion. (A) Lower *falsiovalis* zone, $3.9 \times 10^3$ km$^2$; (B) Upper *hassi* zone, $17.8 \times 10^3$ km$^2$; (C) *jamieae* zone, $142.4 \times 10^3$ km$^2$ (range expansion); (D) Lower *rhenana* zone, $143.2 \times 10^3$ km$^2$ (invasion into Iowa Basin marked by line); (E) *linguiformis* zone, $128.4 \times 10^3$ km$^2$, (F) Upper *triangularis* zone, $2.6 \times 10^3$ km$^2$ (post-Late Devonian biodiversity crisis reduction in range). (Modified from Stigall Rode, A.L. (2005a). *Journal of Systematic Palaeontology*, 3: 133–167.)
which is related to a set of environmental variables discerned by sedimentary analysis of the strata from which the fossils were collected. Genetic algorithms provide an alternative to standard regression modelling by including several algorithms in an iterative, artificial-intelligence-based approach. This approach automates decision making by repeatedly analysing a series of local rules that combine categorical, range-type, and logistic rules to obtain higher significance levels than global rules, such as those applied in regression modelling (Stockwell and Peters, 1999; Stockwell and Peterson, 2002). The computer-learning based approach allows the GARP modelling system to customise the set of rules utilised in estimating the ecological niche for each species (Peterson and Vieglas, 2001). The maximum geographic range for the species is then predicted to occupy regions within the study area that satisfy the conditions of the optimised rule set (Stockwell and Peters, 1999; Stigall Rode and Lieberman, 2005b). Niche modelling provides a method to directly utilise sedimentary parameters to predict the geographic region of a species’ fundamental niche.

GARP models were based on the dataset of Rode and Lieberman (2004); this allows direct comparison of niche-based range prediction and ranges reconstructed using the GIS method detailed above. GARP and GIS range reconstructions agree

closely (Figure 5.6). In most pairwise comparisons of polygon enclosure and GARP prediction models, the ranges are roughly consistent between the two outputs (Stigall Rode and Lieberman, 2005b). Often the predicted ranges quite closely match the polygon ranges, for example, in *Cyrtospirifer chemungensis* (Figure 5.6A,B), which may suggest both that GARP is accurately predicting known ranges and that the method of collection of data for the GIS polygon enclosure ranges may be sufficient to reasonably capture the actual species range. Commonly, although not always, the GARP predicted range encompasses the entire polygon enclosure range and predicts species to occur in additional areas adjacent to the polygon range, such as in *Praewaagenoconcha speciosa* (Figure 5.6C,D). Because the GARP algorithm-predicted species ranges are based on a ruleset that has been trained on the data and contains both internal and external tests, it should be expected to produce more refined estimates of species range than GIS enclosure models. In fact, predicted

![Maps showing GIS polygon enclosure range reconstructions and GARP distribution predictions.](image)

**FIGURE 5.6** Comparison of GIS polygon enclosure range reconstructions and GARP distribution predictions. For GARP ranges, black indicates areas where all of the best subset runs predict a species will occur, and white indicates none of the best runs predicting species occurrence; the gray scale indicates relative probability between these two end members. Note that the GIS range reconstructions are rotated onto palaeocontinental positions, whereas GARP ranges are in modern continental configuration. (A) GIS polygon enclosure range and (B) GARP prediction range for the brachiopod *Cyrtospirifer chemungensis* during the *linguiformis* Zone; (C) GIS polygon enclosure range; and (D) GARP prediction range for the brachiopod *Praewaagenoconcha speciosa* during the *linguiformis* Zone. (From Stigall Rode, A.L. and Lieberman, B.S. (2005a) *Palaeogeography, Palaeoclimatology, Palaeoecology*, 222: 272–284. With permission from Elsevier.)
ranges that exceed the known species occurrence-bounding polygon provide testable hypotheses for future work in assessing the boundaries of species ranges, predicting ranges of species groups and boundaries of community types, and also determining the quality of the fossil record.

Statistical patterns recovered from GARP analyses are congruent with those from GIS polygon analyses. Large geographic range is statistically associated with species survivorship across the crisis interval for species examined in the linguiformis Zone (terminal Frasnian conodont zone; ANOVA, $p = 0.002$; Stigall Rode and Lieberman, 2005b). The relationship of large geographic range and species invasion history with survival through the Late Devonian Biodiversity Crisis recovered in Rode and Lieberman (2004) is again substantiated in this analysis by detailed mapping of species ranges and statistical evaluation of patterns recovered.

### 5.5.2 Biogeographic Patterns in a Phylogenetic Context

To place the patterns of biogeographic change discussed above within an evolutionary context, species-level phylogenies were completed for four representative clades of Middle to Late Devonian marine invertebrates (Stigall Rode and Lieberman, 2005a). The taxa investigated include: the Archaeostraca, a suborder of phyllocarid crustaceans; Leptodesma (Leiopteria), a bivalve subgenus; Schizophoria (Schizophoria), an orthid brachiopod subgenus; and Floweria, a genus of orthothetid brachiopods. Species-level phylogenies are published in Rode and Lieberman (2002), Rode (2004), and Stigall Rode (2005a), respectively. These phylogenies formed the basis for speciation rate calculations and species-level phylogenetic biogeographic analysis.

### 5.5.3 Speciation Rate and Mode Analysis

To determine speciation mode at individual cladogenetic events, biogeographic areas were optimised onto internal nodes in the most parsimonious cladograms using the Fitch Parsimony Algorithm, which provides a framework to interpret speciation mode at individual speciation events (Lieberman, 2002; Wojcicki and Brooks, 2005). Of determinable speciation events within these Middle to Late Devonian clades, speciation by dispersal is the dominant mode (Stigall and Lieberman, 2006). Speciation events due to dispersal comprise 72% of events, whereas vicariance is only implicated in 28% of speciation events (Table 5.1; Rode and Lieberman, 2002; Rode, 2004; Stigall Rode, 2005a). This level of vicariance is greatly reduced compared to that observed in modern clades. Many analyses of speciation mode in the modern biota (Wiley and Mayden, 1985; Brooks and McLennan, 1991, 2002) indicate that the great majority of allopatric speciation occurs via vicariance (72% vicariance, 28% dispersal [cited in Brooks and McLennan, 1991]). Although these studies may underestimate the amount of speciation by dispersal (Cowie and Holland, 2006), other recent studies report similarly high levels of vicariance in marine invertebrate clades (McCartney et al., 2000; Dawson, 2005; Kelly et al., 2006), taxa which would be most comparable to the Devonian study. The reduction in vicariant speciation during this interval may be linked to the marked expansion in geographic range in many species at this time (discussed above). Allopatric speciation by vicariance
Integrating GIS and Phylogenetic Biogeography requires the isolation of previously adjacent populations (Mayr, 1942). The numerous range expansion events during this interval, however, would make it difficult to sustain isolation, thereby potentially cutting off the main mechanism of vicariant speciation. In addition, because species with smaller ranges are more likely to become extinct during this interval, the reduction in size from an ancestral range to that of an isolated population is more likely to increase extinction rate, rather than produce a speciation event during this interval.

When the timing of speciation events is constrained, a temporal distinction emerges (Stigall, 2006b). Species-level phylogenetic hypotheses from Rode (2004) and Stigall Rode (2005a) were converted to strato-cladograms following Smith (1994; Figure 5.7). This method assumes that sister groups diverge at the same time from cladogenetic nodes and creates ghost ranges to connect theoretical speciation and known range data. Rates of biodiversity change, speciation, and extinction were calculated from these data using a pure birth process model. The pure birth process is a deterministic exponential model of taxon growth used for calculating instantaneous rates of biodiversity change within a phylogenetic framework (Hulbert, 1993; Lieberman, 2001; Nee, 2004; Rode and Lieberman, 2005). Rates of biodiversity change were calculated with the following equations, where \( R \) is net biodiversity change, \( S \) is speciation rate, and \( E \) is extinction rate:

\[
R = (\ln N_1 - \ln N_0)/\Delta t \tag{5.1}
\]

\[
S = (\ln(N_0 + o_0) - \ln N_0)/\Delta t \tag{5.2}
\]

\[
E = (\ln(N_0 + o_0) - \ln N_1)/\Delta t \tag{5.3}
\]

In all equations, \( N_0 \) is the initial number of species in a clade at time \( t_0 \), \( N_1 \) is the number of species present at time \( t_1 \), \( \Delta t \) represents the duration of the interval \( t_1 - t_0 \).

### TABLE 5.1
Episodes of Speciation by Vicariance and Dispersal in Late Devonian Clades

<table>
<thead>
<tr>
<th>Clade</th>
<th>Number of Vicariance Events</th>
<th>Number of Dispersal Events</th>
<th>Percent Speciation by Vicariance (%)</th>
<th>Percent Speciation by Dispersal (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Schizophoria (Schizophoria)</td>
<td>2</td>
<td>17</td>
<td>11</td>
<td>89</td>
</tr>
<tr>
<td>Floweria</td>
<td>7</td>
<td>7</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td>Leptodesma (Leiopteria)</td>
<td>2</td>
<td>6</td>
<td>25</td>
<td>75</td>
</tr>
<tr>
<td>Archaeocytherea</td>
<td>6</td>
<td>13</td>
<td>32</td>
<td>68</td>
</tr>
<tr>
<td>Overall</td>
<td>17</td>
<td>43</td>
<td>28%</td>
<td>72</td>
</tr>
</tbody>
</table>


and $o_0$ is the number of speciation events during interval $t_1 - t_0$. Rates of biodiversity change are illustrated in Figure 5.8.

Results of rate calculation indicate several basic patterns. Net biodiversity loss during the Late Devonian biodiversity crisis occurs during the crisis interval (Late Frasnian). This loss is driven partly by extinction (Figure 5.8C), but not entirely. In fact, extinction rates for all clades were higher in preceding intervals than during the Late Frasnian. Speciation rates, however, decline from moderate rates during the Middle Devonian to near zero in the Frasnian (Figure 5.8B). Thus, it is probable that speciation decline was the key determinant in net biodiversity loss. The relative paucity of vicariant speciation discussed above may contribute significantly to the overall pattern of speciation decline because all but two documented vicariance events precede the Late Devonian (Stigall, 2006b).

**FIGURE 5.8** Instantaneous rates of taxonomic turnover. (A) Rate of net biodiversity change calculated from Equation (5.1), (B) speciation rate calculated from Equation (5.2), (C) extinction rate calculated from Equation (3). Taxon symbols: solid line, Schizophoria (Schizophoria); short dash, Floweria; long-short dash, Leptodesma (Leiopteria).
To discern the relationship between biogeographic areas occupied by these taxa, LBPA was conducted using the four species-level phylogenies discussed above (Stigall Rode and Lieberman, 2005a). Both the vicariance and geodispersal area cladograms have excellent tree support, but include incongruent biogeographic patterns (Figure 5.9; Stigall Rode and Lieberman, 2005a). Using this method, incongruent patterns are interpreted as relating causes of singular or noncyclical nature (at least on the time scale of speciation), such as tectonic events (Lieberman and Eldredge, 1996; Lieberman, 2000). Tectonic activity was prevalent in the Middle to Late Devonian of Laurentia and is a likely driver of observed biogeographic patterns. The development, uplift, and downwarp of the intracratonic arches have all been related to orogenic pulses during the Devonian: intracratonic arches experienced uplift during times of orogenic quiescence and downwarp during orogenic pulses (Quinlan and Beaumont, 1984; Beaumont et al., 1988).

The well-resolved vicariance pattern reflects faunal associations known to occur in the Early Devonian faunal provinces (Boucot, 1975; Oliver, 1976) and may reflect Early Devonian separation of basins caused by uplift of tectonic arches during a

![Vicariance Tree](image1)

![Geo-dispersal Tree](image2)

**FIGURE 5.9** Strict consensus trees recovered from Lieberman-modified BPA analysis. Vicariance tree indicates the relative order areas were separated. Vicariance tree is the strict consensus of three equally parsimonious resolutions; tree length is 238 steps, with consistency index of 0.85, retention index of 0.51, and $g_1$ value of –0.54. Geodispersal tree indicates the relative order areas were connected. Geodispersal tree is the strict consensus of eight equally parsimonious resolutions; tree length is 268 steps, with consistency index of 0.84, retention index of 0.42, and $g_1$ value of –0.55. Both trees rooted with ancestor as the out-group. (Reprinted from Stigall Rode, A.L. and Lieberman, B.S. (2005a), *Palaeogeography, Palaeoclimatology, Palaeoecology*, 222: 272-284. With permission from Elsevier.)
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quiescent phase of the Acadian Orogeny (Ettensohn, 1985; Beaumont et al., 1988). Conversely, the geodispersal cladogram indicates two events which probably occurred following a flexural downwarp of the Findlay and Kankakee arches during the Middle or Late Devonian associated with an Acadian orogenic pulse (Quinlan and Beaumont, 1984; Beaumont et al., 1988; Ver Straeten and Brett, 2000). This offset in perceived timing between vicariance and geodispersal patterns may indicate a fundamental change in the style of biogeographic patterns during the Middle Devonian to Late Devonian. This shift may reflect earlier eustastic versus later tectonic controls on biogeographic patterns, possibly resulting from the relative intensity of Acadian orogenic events.

Comparing the results of the phylogenetic biogeographic analysis with the species-level GIS analysis discussed above, parallel patterns emerge. The Middle to Late Devonian orogenic pulses, which are the likely promoters of the preserved geodispersal patterns, also coincide with transgressive events of the Johnson et al. (1985) sea-level curve. Interbasinal species invasions occur in concert with these transgressive pulses and clearly would have been facilitated by the downwarping of intracratonic arches. This relationship suggests that the interplay of tectonic pulses and transgressive events may have played a major factor in regulating biogeographic patterns and hence biodiversity dynamics during the Late Devonian.

5.6 DISCUSSION

The results of the analyses presented in the case studies above combine to provide a multifaceted insight into the complex interactions operating amongst biogeographic, ecological, and macroevolutionary processes in the time period leading to and including the Frasnian–Famennian biodiversity crisis. Previous studies have noted that although extinction rates were elevated, they were not statistically distinguishable from background rates (Bambach and Knoll, 2001; Bambach et al., 2002); much of the biodiversity lost in this interval must, therefore, be attributable to speciation decline (McGhee, 1996; Bambach et al., 2002). This finding occurs in the case study taxa (Figure 5.8), but the additional species-level analyses reviewed herein allow speciation decline to be examined in detail. Overall speciation decline in these taxa occurs in the Frasnian Stage and is associated with a concomitant decline in the relative amount of speciation by vicariance (Stigall, 2006b).

The case studies presented above illustrate several ways in which quantitative reconstruction of species ranges can be examined in concert with species-level phylogenetic hypotheses to examine the relationship between species ranges and faunal dynamics during the Late Devonian Biodiversity Crisis. In particular, these analyses illustrate that creation of a large set of geographic ranges (in this example with brachiopod and bivalve species) can facilitate examination of changes in geographic range with respect to environmental parameters, such as sea level, as well as the correlation of mass extinction survival with larger geographic ranges and a history of interbasinal invasion events (Rode and Lieberman, 2004; Stigall Rode and Lieberman, 2005b). Results of coordinating analyses of species-level phylogenetic biogeography further corroborate the importance of geodispersal (including interbasinal invasions) and a diminished role for vicariance in driving biogeographic
patterns during the Late Devonian (Stigall Rode and Lieberman, 2005a). By combining these results, an understanding of faunal dynamics begins to emerge for the Late Devonian Biodiversity Crisis, one in which species originating from dispersal events and participating in later episodes of interbasinal invasion are successful species that survive the biodiversity crisis interval, whereas stenotopic species with narrow geographic ranges become extinct and do not produce successful daughter species because of the general shutdown of vicariant speciation during this interval. This combination of quantitative and spatial analysis could not have been created without the use of GIS to map species ranges over short temporal intervals.

5.7 CONCLUSIONS

The application of GIS methods in palaeobiogeography offers a powerful technique for the reconstruction of the geographic ranges of species and higher taxa. Data derived from GIS reconstructions can produce datasets amenable to statistical analyses and hypothesis testing. The ability to quantify the spatial and temporal extent and variability in the geographic range of taxa further provides a framework in which geographic changes can be compared with environmental or climatic fluctuations or tectonic events. Hypotheses of relationships between biogeographic patterns and evolutionary and ecological processes can be rigorously assessed.

Results from analyses of Late Devonian species ranges have uncovered relationships amongst species invasions, geographic range, speciation, and extinction during this interval. In particular, species with larger ranges and invasive histories were more likely to survive the biodiversity crisis than species with narrow ranges or lacking prior invasions. Species invasion events were facilitated by tectonic activity and events of relative sea level rise. The survival advantage conferred to invasive (or dispersing) species results in reduced opportunities for speciation via vicariance and also a dramatic decline in overall speciation rate during the Late Devonian. The complex relationship between invasive spread of species and decline in overall speciation rate could not have been discerned without a combination of GIS-based species range reconstructions and well-constrained phylogenetic hypotheses. The complex interplay between biogeographic and evolutionary patterns during the Late Devonian is potentially relevant to the modern biodiversity crisis. If the spread of modern invasive species results in a similar feedback loop between speciation and extinction, we may expect a dramatic decline in speciation in the near future.

The case studies reviewed above represent the first analytical work accomplished through GIS mapping of marine invertebrate species. There is much room to grow with broader use and continued development of more sophisticated GIS methods and applications. The results from these case studies suggest that further GIS-based biogeographic studies coupled with phylogenetic methods have excellent potential to contribute significantly to our understanding of the co-evolution of the Earth and its biota.

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LITERATURE CITED


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