THE APPLICATION OF GEOGRAPHIC INFORMATION SYSTEMS TO PALEOBIOGEOGRAPHY: IMPLICATIONS FOR THE STUDY OF INVASIONS AND MASS EXTINCTIONS

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ABSTRACT—Mapping geographic ranges of species and higher taxa using Geographic Information Systems (GIS) produces quantitative data on spatial and temporal changes in geographic ranges. The primary advantage of GIS analysis is that it has the capacity to utilize large amounts of occurrence data of species to produce quantitatively constrained geographic range reconstructions that are amenable to statistical analysis. The basic steps in GIS range reconstruction are database assembly (including taxonomic, geographic, and stratigraphic information for each specimen), mapping of localities of species on modern continental configuration, rotation of occurrence data of species onto paleocontinental reconstructions, and reconstructions of geographic ranges. GIS analysis of ranges of species has been used to assess faunal dynamics of the Late Devonian Biodiversity Crisis, and three case studies are presented here. In these case studies, GIS-derived ranges of species are used to assess the relationship of biogeography with sea level, speciation and extinction rates, mass extinction survival, speciation mode, and invasive history of taxa. These case studies represent a subset of the potential for GIS analyses to examine paleontological patterns and contribute to improving understanding of the interaction between paleobiogeography, paleoecology, and evolution in the fossil record.

GEOGRAPHIC RANGE is intimately related to the biology of a species and its interaction with its environment. Quantifying changes in ranges of species during key bioevents in the history of life can provide insight into faunal dynamics of critical periods in Earth history. Geographic Information System (GIS) methods allow geographic change to be correlated with environmental and evolutionary changes and provide a powerful tool for assessing underlying causes of biotic turnover during intervals of mass extinction. Quantifying changes in geographic range and determining the factors driving 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 (e.g., Peterson and Vieglas, 2001; Johnson et al., 2004; Rushton et al., 2004; Thomas et al., 2004; Wilson et al., 2004).

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. Paleobiogeographic studies have typically examined shifts in geographic range over large time scales (stages or periods), mainly of higher taxa (e.g., Boucot, 1975). Range reconstruction methods using GIS, however, provide promising new opportunities to quantify ranges of individual fossil species in addition to higher taxa across fine temporal intervals (approximating conodont zones) (Rode and Lieberman, 2004, 2005; Stigall Rode and Lieberman, in press). Pioneering work in the use of GIS in paleontology included the development of geospatial databases of occurrences of species (Graham et al., 1996; Juliusson and Graham, 1999; Graham, 2000, this volume; Fergueson et al., 2001). Recent advances in GIS work, including reconstructing the ranges of species of Paleozoic invertebrates through multiple temporal intervals (e.g., Rode and Lieberman,

2000, 2004, 2005), have begun to surpass cataloging occurrences of species and produce data to test paleoecological and paleobiogeographic hypotheses.

GIS METHODS IN PALEOBIOGEOGRAPHY

Advantages of GIS Methods

The reconstruction of geographic ranges of taxa has historically been a key feature of biogeography. Numerous studies have examined the geographic areas occupied by higher taxa, such as families and orders, resulting in significant advances in the delineation of biogeographic realms and provinces (e.g., Boucot et al., 1969; Boucot, 1975; Oliver, 1976; Webby, 1992). Typically, these studies have examined changing geographic ranges at the temporal scale of substages or greater (e.g., Boucot, 1975). These types of analyses continue to produce crucial insight into biogeographic patterns operating at ecosystem and biosphere hierarchical scales. This level of analysis, however, lacks the resolving power to address processes operating at lower hierarchical levels, such as the community and species level. The application of GIS methods in addition to traditional biogeographic methods represents an exciting advance in paleobiogeography in its ability to quantify ranges of species.

The use of GIS has many advantages over traditional mapping of ranges of species, because GIS range maps are constructed dynamically and can be designed to illustrate both temporal and spatial variability (Berry, 1995; Chou, 1997; Burrough and McDonnell, 1998). One of the most significant advantages is the ability to accurately map the ranges of species. Since species are the entities through which the macroevolutionary phenomena of speciation and extinction occur, quantification of ranges of species provides key information for assessing evolutionary patterns. Another key benefit of GIS analysis is that range reconstructions can be based on large data sets and

produce quantitative results. The types of occurrence data of species required for GIS analysis can be both extracted from and donated to large database projects, such as the Paleobiology Database (http://paleodb.org), which ensures further utility of this data to other researchers. Furthermore, repeatable methodologies can be utilized, and data produced are amenable to statistical analyses. The combination of these features indicates that GIS analysis of ranges of species can result in the creation of hypotheses that are testable using statistical methods based on large data sets, a fundamentally useful advance for paleobiogeography.

Outline of GIS Method

Database assembly.-The primary data required to reconstruct a range of a species are the geographic location and the stratigraphic unit from which individuals of that species have been collected. GIS mapping methods, described more fully below, require only taxonomic, geographic, and temporal (stratigraphic) information for each specimen. The occurrence data of species, acquired from museum or field collections, are incorporated into a database. Although the minimal data requirement is three fields, each species' occurrence should include the maximum amount of information available for a specimen. Since correct taxonomic identification is critical to the accurate reconstruction of ranges of species, investigators should verify museum and literature identifications personally whenever possible. Suggested data fields to include are: locality information (geo-referenced latitude and longitude, city, county, state, country), stratigraphic information (group, formation, member, bed or zone), temporal information (stage, correlative biostratigraphic zone, sequence stratigraphic unit), taxonomic information (phylum, class, order, family, genus, species), and environmental information (matrix, substrate type).

Geographic range reconstruction.- Following database construction, geographic data are imported into ArcView 3.2 (ESRI, 1999) and
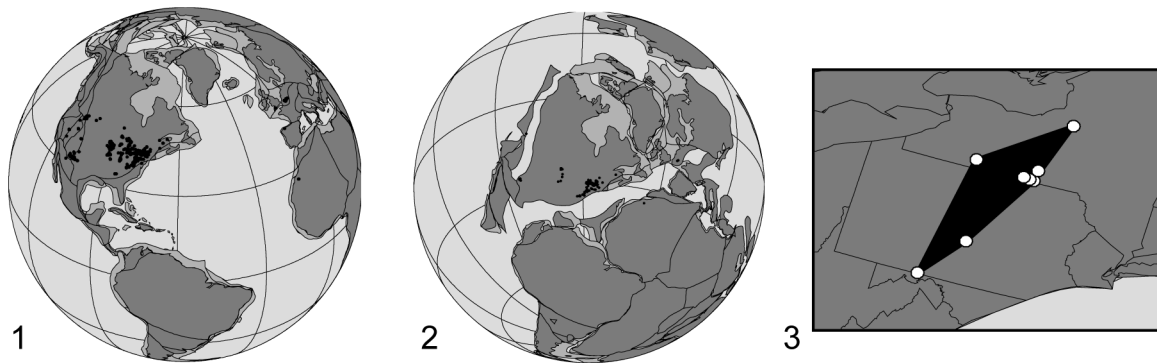
FIGURE 1—Steps in GIS range reconstruction. 1) Distribution of all data points plotted onto a modern continental configuration. 2) Reconstruction of all data points present for a single biozone. 3) Reconstruction of the geographic range of a single species, range is 30.0 x 103 km2. Figure modified from Rode and Lieberman (2004).

distribution ranges estimated for species and clades. There are four basic steps in this process: (1) translate the locality data into latitude and longitude values, (2) rotate the data points onto paleocontinental positions, (3) create range maps from the rotated data points, and (4) calculate paleogeographic ranges. Locality data must be converted into latitude and longitude values by geo-referencing. Once the locality data are translated into latitude and longitude values, they are mapped as an event theme onto a modern continental configuration using ArcView GIS 3.2 (ESRI, 1999) (Fig. 1.1). This coverage is then imported into PaleoGIS/ArcView 3.5 (Ross and Scotese, 2000) and rotated onto paleocontinental positions for each specified time slice (Fig. 1.2). The PaleoGIS program filters the data points so that only species extant during the specified time slice are mapped in each reconstruction. Reconstructions derived from Ross and Scotese (2000) are based on the data assembled through the PaleoMap project of Scotese (1998) and are reconstructed using several data sources including paleomagnetism, paleobiogeography, paleoclimatology, and tectonic and geologic history. The variety of underlying data produces maps that are more robust to anomalies that can occur when paleocontinental reconstructions are based on only a single data source, such as paleomagnetism or paleoclimatology (Scotese and McKerrow, 1990).

Once the data are rotated onto the paleocontinental positions, the reconstructions should be exported into ArcView 3.2 or ArcGIS 8.x for manipulation. Range maps can then be constructed for each species during each time slice in which it was extant. This is accomplished by digitizing a polygon to enclose the distribution data for each species as illustrated in Figure 3. Once range maps have been produced, the area of each polygon can be calculated. From these maps, expansions in geographic range can be quantified and correlated with appropriate geologic events, such as two regions coming into contact during a time interval. Analysis of temporal changes in the range of a single species can be conducted, as well as statistical analyses of numerous species or clades (e.g., Rode and Lieberman, 2004, 2005). More advanced GIS-based methods of range reconstruction are also available; for an example of GIS-based genetic algorithm modeling methods, see Stigall Rode and Lieberman (in press).

CASE STUDIES USING GIS DURING THE LATE DEVONIAN BIODIVERSITY CRISIS

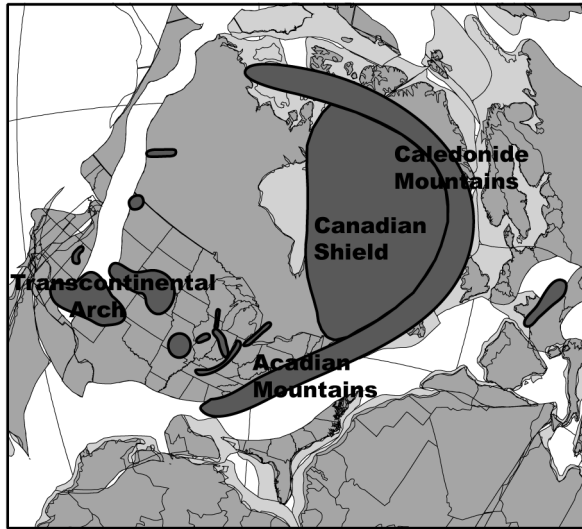The Late Devonian (Fig. 2) was a time of profound evolutionary and environmental change

FIGURE 2—Late Devonian paleogeography of Laurentia after Dineley (1984) and Ross and Scotese (2000) with major tectonic barriers indicated in dark gray.

associated with the Frasnian-Famennian Biodiversity Crisis including reduction in speciation rates, increased extinction rates, rampant invasions of species, 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. 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 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).

Prior to the mass extinction interval, a dramatic biogeographic change occurred from a highly endemic Middle Devonian fauna to a cosmopolitan biota by the late Frasnian (Oliver, 1976, 1990; McGhee, 1996). The expansion of geographic ranges and the transition to a Late Devonian cosmopolitan biota have been documented in many taxa including rugose corals (Oliver, 1976, 1990; Oliver and Pedder, 1994), brachiopods (Boucot, 1975; McGhee, 1981, 1996), foraminifera (Kalvoda, 1990), fishes (Young, 1987), conodonts (Klapper and Johnson, 1980; Klapper, 1995), trilobites (Feist, 1991), and land plants (Raymond and Mertz, 1995). This changing pattern of geographic range, particularly range expansion events analogous to invasions of species during the Middle to Late Devonian transition, has been implicated in survival of species during the biodiversity crisis interval (Rode and Lieberman, 2004).

The combination of biotic overturn, geographic expansion, and extensive 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 three case studies presented below use GIS range reconstuctions to address specific aspects of the Late Devonian Biodiversity Crisis.

Documenting relationships between invasions of species and extinction survival.-GIS analysis of brachiopod and bivalve species from the Middle to Late Devonian in Laurentia by Rode and Lieberman (2004) investigated the relationship between biogeography, relative sea level, and environmental changes. For this analysis a database, including over 8,400 occurrence points of species spanning 19 conodont zones from the Givetian to early Fammenian, was assembled based on museum collections. This database was used to reconstruct 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). The reconstruction of ranges of species both spatially and temporally (at the level of conodont zones) using GIS facilitated quantifying the timing and extent of events such as invasions of species into new tectonic basins and

the importance of geographic range in determining the survival of species through the crisis interval.

This analysis uncovered statistically significant relationships between ranges of species, sea level, and survival of species through the mass extinction interval (Rode and Lieberman, 2004). At least three episodes of elevated rates of invasion of species between tectonic basins were determined from GIS analysis during the Late Devonian (Fig. 3). These correspond to the beginning of the Frasnian, mid-Frasnian, and the late Frasnian, the final two of which relate to the onset and final stage of the biodiversity crisis. These three pulses of invasion also coincide with the onset of transgressive-regressive (T-R) cycles IIb through IId of Johnson et al. (1985). The invasion into new areas and the concomitant expansion in geographic ranges may also to confer an advantage in the survival of species through the crisis interval. Species that persisted into the Famennian have significantly larger geographic ranges than species that became extinct by the end of the Frasnian (t-test, p-value << 0.001). In addition, species that previously underwent interbasinal invasion also preferentially survived the mass extinction event (t-test, p-value <0.001).

The connection between geographic range size and extinction survival has been further examined using niche modeling methods, a more sophisticated computer-learning-based GIS modeling approach (Stigall Rode and Lieberman, in press). The GARP (Genetic Algorithm for Rule-Set Prediction) modeling system used in this study estimates ranges of species by using environmental variables to predict the fundamental niche of a species (Stockwell and Peters, 1999; Stigall Rode and Lieberman, in press). The use of GARP models permits both a comparison in range prediction with the GIS method detailed above and an independent statistical examination of the relationship of geographic range size with the survival of species during the Late Devonian. GARP and GIS range reconstructions agree closely (Fig. 4), and similar statistical patterns emerge. Large geographic range is statistically associated with survivorship of species across the crisis interval for species

FIGURE 3—Paleobiogeographic range reconstruction for *P. devoniana* Webster illustrating an invasion event between two tectonic basins. 1) Reconstructed geographic range in the *transitans* zone (early Frasnian), 18.1 x 10³ km2; 2) reconstructed geographic range in the *punctata* zone (late Frasnian), 31.0 x 10³ km2; this invasion into the Iowa basin is coincident with the onset of cycle IIc of Johnson et al. (1985).

examined in the linguiformis Zone (terminal Frasnian conodont zone) (ANOVA, p = 0.002) (Stigall Rode and Lieberman, in press). The relationship of large geographic range and invasion history of species with survival through the Late Devonian Biodiversity Crisis is again substantiated by detailed mapping of ranges of species and statistical evaluation of patterns recovered.

Inferring ecological interactions and speciation mode.-The spatial relationships between taxa that are reconstructed in GIS analyses can also provide insight about ecological and evolutionary relationships between taxa. Geographic ranges of phyllocarid crustacean species reconstructed at the
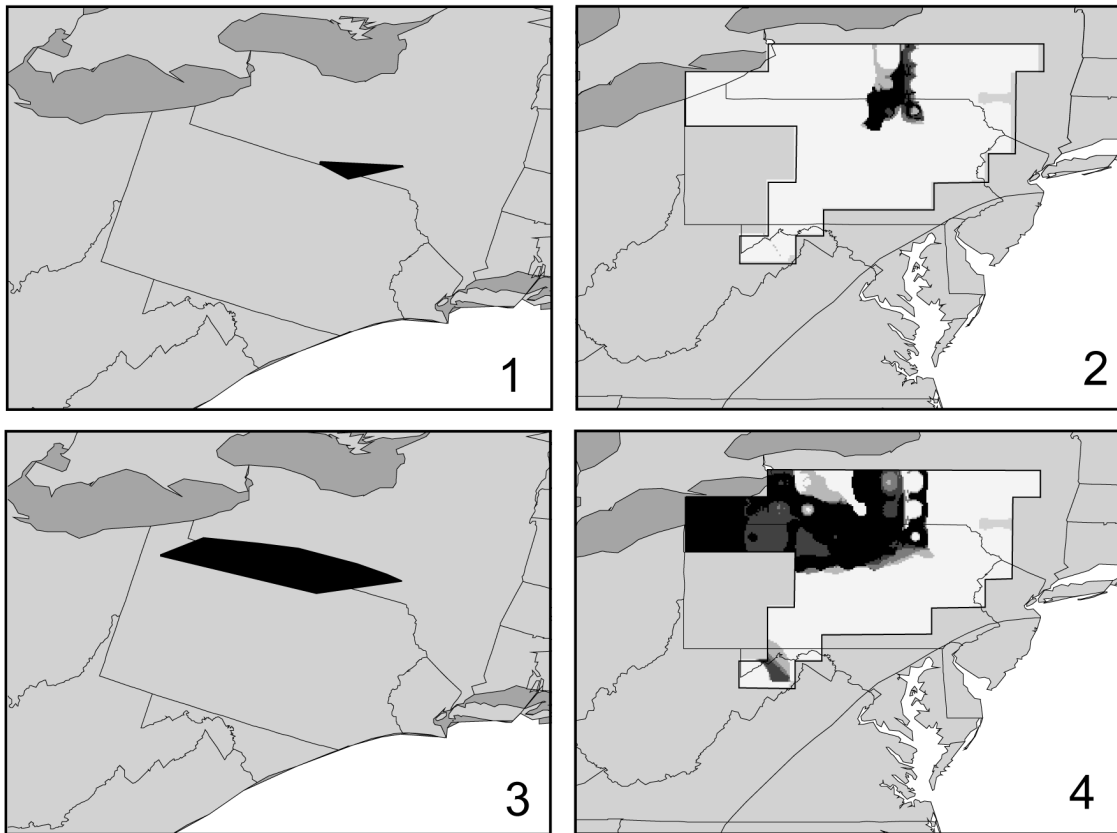
FIGURE 4—Comparison of GIS polygon enclosure range reconstructions and GARP distribution predictions. 1) GIS polygon enclosure range and 2) GARP prediction range for *Cyrtospirifer chemungensis* (Hall) during the linguiformis Zone; 3) GIS polygon enclosure range and 4) GARP prediction range for *Praewaagenoconcha speciosa* (Hall) during the linguiformis Zone.

stage level can be examined to assess the ecological interactions between species and mode of speciation within tectonic basins (Rode, 2001).

A number of phyllocarid species examined by Rode and Lieberman (2005) in eastern North America have overlapping ranges (Rode, 2001). Such spatial overlap may be due to several causes including shared environmental tolerances or common ancestry (Wiley and Mayden, 1985; Brooks and McLennan, 1991). Middle to Late Devonian phyllocarids of eastern North American provide examples of both types of spatial overlap. For example, we can conclude that there are several cases where two or more species of phyllocarids inhabited the same area due to shared environmental tolerances without common ancestry; based on phylogenetic analysis (Rode and Lieberman, 2002) these species are not closely related and are derived from species that had disparate ranges. For example, *Herbertocaris wideneri* and *Rhinocaris ehlersi* occur together in the Silica Shale of northwestern Ohio (Stumm and Chilman, 1969). Although both of these species belong to the family Rhinocarididae, the species are not closely related (Rode and Lieberman, 2002). Since the species are very different in size (*H. wideneri* individuals reach 60 cm, while *R. ehlersi* individuals only reach 20 cm), their

common presence in the same stratigraphic unit and locality may indicate a shared affinity for the depositional environment with possible ecological partitioning (Brooks and McLennan, 1991). Another pair of species that co-occur due to shared environmental tolerance rather than close common ancestry is *Echinocaris multispinosis* and *E. sublaevis* (Figs. 5.1 and 5.2). Although these species belong within the same genus, they are not sister species (Rode and Lieberman, 2002). Unlike *H. wideneri* and *R. ehlersi, E. multispinosis* and *E. sublaevi*s are very similar morphologically and may have either directly competed or have been ecological specialists that preyed on different food items.

Patterns of spatial overlap can also be used to evaluate the mode of speciation when closely related species are considered (Wiley and Mayden, 1985), especially when considered in conjunction with a well-constrained species-level phylogeny, such as that presented for phyllocarids in Rode and Lieberman (2002). Speciation by vicariance can be recognized by the splitting of an ancestral range to produce daughter species within the boundaries of the ancestral range due to emergence of a barrier (Wiley and Mayden, 1985). Vicariance is inferred when sister species have adjacent but nonoverlapping ranges. A possible example of vicariant speciation can be observed among species of *Echinocaris* within the *E. socialis* clade of Rode and Lieberman (2002). For example, *E. sublaevis* occurs in northeastern Ohio in Famennian strata (Fig. 5.2), while its sister species *E. socialis* occurs in adjacent western Pennsylvania in rocks of the same age (Fig. 5.3). *Echinocaris clarkii*, a species more distantly related to *E. socialis* and *E. sublaevis*, also occurs in western Pennsylvania (Fig. 5.4). This suggests that their common ancestor may have also inhabited the Ohio/
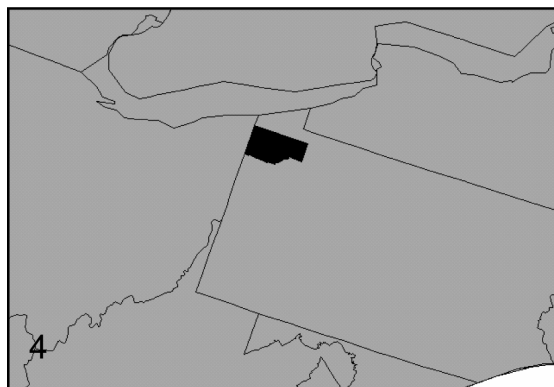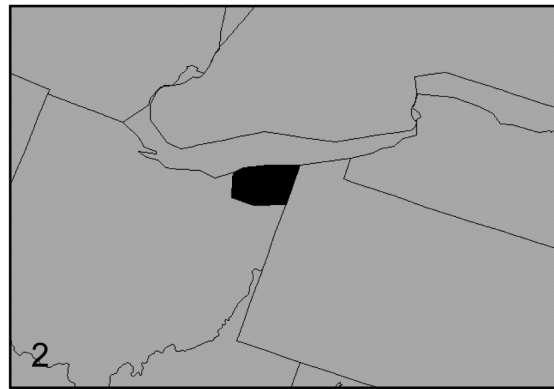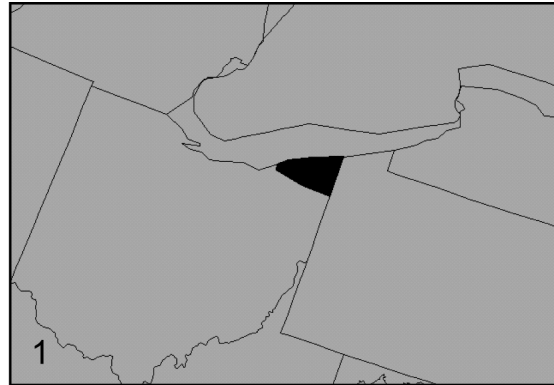
FIGURE 5—Famennian distribution species within the *Echinocaris socialis* clade. 1) Geographic range of *E. multispinosis*; 2) Geographic range of *E. sublaevis*; 3) Geographic range of *E. socialis*; 4) Geographic range of *E. clarkii*.

Speciation rate vs. geographic range
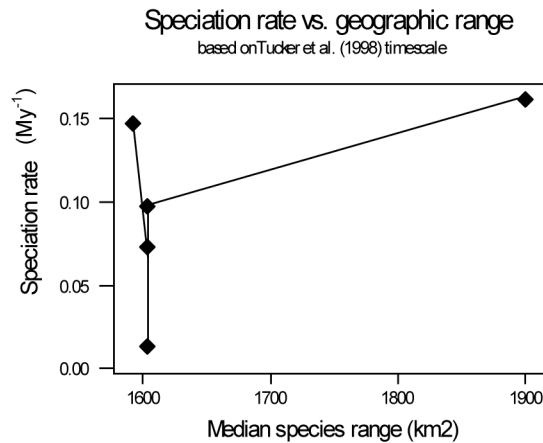based on Tucker et al. (1998) timescale

FIGURE 6—Plot of speciation rate versus median geographic range of phyllocarid species. Speciation rate calculated using the deterministic method based on the time scale of Tucker et al. (1998). Numerical data from Rode and Lieberman (2005).

Pennsylvania/New York tristate area and provides additional support for vicariant speciation. Evidence for speciation by dispersal occurs when a daughter species occupies a geographic range outside of the ancestral range. For example, speciation by dispersal might be inferred if another species of *Echinocaris* within the same cluster of species occupied an unrelated area, such as the Iowa basin.

These potential small-scale dispersal and vicariance events occur on a finer scale than those retrieved by the phylogenetic biogeographic analysis described in Lieberman and Eldredge (1996) and Lieberman (2000), which suggests that a more accurate picture of biogeographic events may be obtained by combining cladistic biogeography of regions with GIS-derived small-scale biogeographic patterns at the county scale.

Relationship of geographic range to speciation/extinction rates.-In addition to examining patterns of spatial overlap between species, Rode and Lieberman (2005) determined mean range of species and extinction and speciation rates for phyllocarids during the Givetian to Famennian stages. GIS analysis provided quantitative estimates of geographic range that were shown to be significantly correlated with both speciation and extinction rate (Rode and Lieberman, 2005).

Several interesting anecdotal patterns emerge from the graph of speciation rate vs. geographic range (Fig. 6). Speciation rate increases as geographic range both increases and decreases from around 1.6 x 103 km2. The increase in speciation rate at small geographic ranges most likely reflects the increased ability of small populations to speciate by vicariance (Mayr, 1942). Conversely, as geographic range increases, the periphery increases at a greater rate than the area, assuming most topologies. This potentially encourages speciation by peripheral isolates and subsequent dispersal (Mayr, 1942). By contrast, the lowest rates of speciation prevail in species of intermediate size, which are more likely to be panmictic and consequently less likely to speciate. It is also interesting to note that the rate of speciation rate increase in Figure 6 is much higher for small, vicariant species than for larger, dispersive species. This pattern suggests that the relative increase in dispersal vs. vicariance observed in the phyllocarids from the Early to Late Devonian using cladistic biogeography (Rode and Lieberman, 2002) should result in a reduction in overall speciation rate. In this case, GIS analysis led to the creation of a hypothesis that should be tested further in taxa with more complete fossil records to determine the generality of the observed pattern to explain speciation reduction. An overall reduction in speciation rate has been documented as one of the primary causes of biodiversity loss during the Late Devonian (McGhee, 1996). Subsequent analysis of speciation rate style in both brachiopod and bivalve clades has, in fact, substantiated the overall reduction in speciation by vicariance during the Late Devonian Biodiversity Crisis (Rode, 2004; Stigall Rode, 2005).

DISCUSSION

The use of GIS in paleontology has been relatively limited to date. Case studies presented above (Rode, 2001; Rode and Lieberman, 2002, 2004, 2005; Stigall Rode and Lieberman, in press) illustrate several ways in which GIS range reconstructions can be used to quantitatively examine the relationship between ranges of species and faunal dynamics during the Late Devonian Biodiversity Crisis. In particular, these analyses illustrated that creation of a very 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, in press). Analyses based on smaller numbers of phyllocarid crustacean species provided evidence for potential ecological interactions between species and had the ability to resolve vicariance and dispersal events within tectonic basins (Rode, 2001). In addition, analyses of phyllocarid ranges of species confirmed statistical relationships between geographic range size and speciation and extinction rates (Rode and Lieberman, 2005). The pattern exhibited by these rates as well as the general reduction in vicariant speciation retrieved from phylogenetic biogeography of this clade (Rode and Lieberman, 2002) support a relationship between speciation mode and size of geographic range. 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 containing later episodes of interbasinal invasion are successful species that survive the biodiversity crisis interval, while stenotopic species with narrow geographic ranges become extinct and do not produce successful daughter species due to 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 ranges of species over short temporal intervals.

CONCLUSIONS

The application of GIS methods in paleobiogeography offers a powerful, quantitative technique for the reconstruction of the geographic ranges of species and higher taxa. Testable hypotheses of relationships between biogeographic patterns with evolutionary and ecological processes can be developed. The quantitative data derived from GIS reconstructions can produce data sets amenable to statistical analyses and hypothesis testing. Results from analyses of Late Devonian ranges of species have uncovered relationships between invasions of species, geographic range, speciation, and extinction during this interval. The case studies presented above represent the first analytical work accomplished through GIS mapping of the marine invertebrate record. 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 have excellent potential to contribute significantly to our understanding of the coevolution of the Earth and its biota.

ACKNOWLEDGMENTS

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