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Quantitative palaeobiogeography: GIS, phylogenetic biogeographical analysis, and conservation insights

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ABSTRACT

Aim The utility of GIS-based and phylogenetic biogeographical analysis in palaeobiogeography is reviewed with reference to its ability to elucidate patterns of interest for modern conservation biology, specifically the long-term effects of invasive species.

Location Emphasis is on biogeographical patterns in the Appalachian basin and mid-continent of North America during the Devonian. Global palaeobiogeographical patterns of the Cambrian are also considered.

Methods Palaeobiogeographical patterns are assessed within a GIS framework, including both direct range reconstruction and niche modelling methods, and within phylogenetic biogeographical analysis. Biogeographical patterns are considered within multiple clades of fossil invertebrates, including trilobites, crustaceans, brachiopods, and bivalves.

Results GIS-based analysis (including niche modelling methods) of Devonian invertebrates demonstrates a tightly correlated relationship between sea-level rises and range expansion, dispersal events, and species invasions. The predominance of range expansion and species invasions during the Late Devonian reduced opportunities for vicariant speciation during this interval. Comparison of phylogenetic biogeographical patterns between Cambrian and Devonian trilobites allows discernment of the relative roles of tectonics and eustasy in driving biogeographical patterns.

Main conclusions GIS analysis and phylogenetic biogeography are powerful tools for analysing the coevolution of the Earth and its biota. Analyses can identify episodes of vicariance and geo-dispersal and produce testable hypotheses for further analysis within the fossil record.

Keywords

Conservation biogeography, Devonian, geo-dispersal, GIS, historical biogeography, modified Brooks parsimony analysis, niche modelling, North America, palaeobiogeography, vicariance.

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SIGNIFICANCE OF PALAEOBIOGEOGRAPHY

Palaeobiogeography is the study of biogeography in the fossil record and pursues as an overall goal tracing the coevolution of the Earth and its biota (Lieberman, 2005). Reconstructing the biogeographical ranges and examining the distribution of fossil organisms has long been an important area of palaeontological research. For example, the recognition that fossils of *Mesosaurus*, a freshwater reptile, were deposited in South America and Africa, on opposite sides of what is today an

insurmountable marine barrier, was one of the key pieces of evidence in Alfred Wegener's original formulation of continental drift (Hallam, 1981). Distributions of fossil organisms continue to provide critical information for calibrating modern plate tectonic reconstructions (e.g. Scotese & McKerrow, 1990).

Palaeobiogeographical studies of higher taxa, such as families and orders, contribute important information about the evolutionary history of clades and their coevolution with the Earth. Characterization of the ranges of individual fossil

species, however, provides additional insight into evolutionary processes such as speciation and extinction. In particular, quantifying changes in the spatial distribution of species ranges through time can provide insight into the feedbacks between biogeography, palaeoecology, and macroevolution. The geographic range of a fossil species, as in a modern species, represents the geographic limits of the realized niche of that taxon (Brooks & McLennan, 1991, 2002; Lomolino *et al.*, 2005). Quantifying the spatial shifts in these distributions over geologic time can, therefore, provide information about changing environmental tolerances of species or (more commonly) habitat tracking of a species exhibiting niche conservatism through time (Stigall Rode & Lieberman, 2005b). Moreover, species ranges, when combined with species-level phylogenetic information, can provide insight into either a vicariance or dispersal mode of speciation, and into extinction resistance during intervals of biodiversity crisis (Lieberman & Eldredge, 1996; Rode & Lieberman, 2005; Stigall Rode & Lieberman, 2005a).

Quantification of the interaction between species range expansion and contraction and macroevolution in the fossil record also has the potential to provide insight into the predicted long-term effects of range changes occurring today that are associated with the modern biodiversity crisis. This is because the fossil record provides a rich record of range expansions, and these, which in the marine record often involve interbasinal species invasions, can be studied as analogues of modern invasive events. This allows characterization of the long-term ecological and evolutionary effects of invasive species and may provide a long-term context for understanding the threats to modern ecosystems that invasive species pose.

It is crucial to monitor and understand the reasons for geographic range expansion and contraction when examining the ecological and evolutionary history of both individual species and monophyletic clades (Enserink, 1999; Engler *et al.*, 2004; Gurevitch & Padilla, 2004; Wilson *et al.*, 2004). The importance of maintaining the geographic ranges of modern species is emphasized throughout the modern biological conservation literature (e.g., Peterson & Vieglais, 2001; Johnson *et al.*, 2004; Thomas *et al.*, 2004; Wilson *et al.*, 2004). In addition, determining the effect of invasive species on modern ecosystems is an active area of research (e.g., Lodge, 1993; Williamson, 1996; Mooney & Hobbs, 2000; Mooney & Cleland, 2001; Gurevitch & Padilla, 2004; Hastings *et al.*, 2005). However, modern ecology and conservation biology studies can only address phenomena that occur over time-spans of years to decades. The long-term evolutionary impacts of species invasions (those effects requiring hundreds of thousands of years or longer to manifest themselves) can only be directly assessed by studying similar events in the geologic past.

One of the fundamental divides in biogeography has centred around the distinction between those studies that consider ecological biogeographical patterns and those studies that consider phylogenetic biogeographical patterns (Brooks & McLennan, 1991; Lieberman, 2003). Studies in both areas have contributed greatly to our understanding of biogeographical

patterns and processes. It is advantageous, where possible, to consider phylogenetic information in conjunction with information about species' ranges, quantified through GIS and considered in light of environmental conditions. This approach allows information from each of these partly disparate areas, ecological and phylogenetic biogeography, to be considered in concert, and, when applied to studies of palaeobiogeography, may provide a useful understanding of how ecological and phylogenetic biogeographical patterns and processes are linked over long time-scales. We will outline here how these two methods, phylogenetics and GIS, can be combined in palaeobiogeographical studies to provide a synthetic understanding of biogeographical patterns in the fossil record.

METHODS IN PALAEOBIOGEOGRAPHY

Previous methods of quantification of species ranges

The study of the geographic ranges of extinct taxa has been a key research area in palaeobiogeography. Numerous studies have examined the geographic areas occupied by higher taxa, such as families and orders, resulting in the delineation of biogeographical realms and provinces (e.g. Boucot, 1975; Oliver, 1976; Webby, 1992). Typically, these studies have examined changing geographic ranges at the temporal scale of millions to tens of millions of years (e.g. Boucot, 1975). Palaeobiogeographical analyses of this type commonly involve plotting taxonomic occurrences on continent- or basin-scale maps and using similarity metrics or qualitative comparisons to differentiate biogeographical regions. Examination of the changes in the elevational or latitudinal distribution of species over time (e.g. Heaney, 1986, 2001; Roy *et al.*, 2004) has also provided insight into biogeographical trends in a more quantitative manner and on shorter geological time-scales. These types of analyses continue to produce crucial insight into biogeographical patterns operating at the ecosystem and biosphere levels (e.g. Shen & Shi, 2004).

Quantitative methods in palaeobiogeography

The development of quantitative methods for assessing species ranges in the fossil record and relating them to evolutionary patterns has advanced in recent years. New methods include mapping geographic ranges using GIS and assessing biogeographical patterns and speciation mode using phylogenetic palaeobiogeography. The strength of these methods is that they permit the analysis of ancient biogeographical patterns with increased detail and precision. The implementation of phylogenetic biogeographical methods permits the analytical determination of cross-faunal patterns of vicariance and geo-dispersal (Brooks & McLennan, 1991; Lieberman & Eldredge, 1996). These methods in many ways mirrors the use of phylogenetic biogeography in modern taxa. In addition, these methods provide the potential to discern geo-dispersal patterns and the ability to relate patterns recovered to Earth

history events and to ascertain how particular Earth history events may have shaped the biota over time (Lieberman, 2000). The implementation of GIS methodology in palaeobiogeography provides the opportunity to examine biogeographical patterns quantitatively within and among taxa within both temporal and spatial frameworks (Rode & Lieberman, 2004). GIS analysis represents a potentially useful advance over qualitative approaches for reconstructing ranges of fossil taxa, and can even be modified to create sophisticated species range models (Stigall Rode & Lieberman, 2005b). In particular, examining palaeobiogeographical patterns within a quantitative framework provides the opportunity to examine temporal and spatial patterns in the fossil record in a rigorous manner. Statistical analyses comparable to those used within the modern biota can then be applied to the fossil record, making it possible to compare patterns in fossil taxa with those documented for modern species.

GIS METHODS IN PALAEOBIOGEOGRAPHY

The use of GIS has many advantages over traditional mapping of species ranges because GIS range maps can be constructed dynamically and can be designed to illustrate both temporal and spatial variability (Berry, 1995; Chou, 1997; Burrough & McDonnell, 1998; Stigall Rode, 2005b). The dynamic nature of GIS means that maps can be continuously updated as new data become available or interpretations are revised, a facility that is not available with traditional mapping methods. Data stored and analysed in this manner can therefore be maintained in a way that ensures their continued relevance and utility to future analyses. A further key benefit of GIS analysis is that range reconstructions can be based on large data sets and produce quantitative results. The types of species occurrence data required for GIS analysis can be both extracted from and donated to large data-base projects, which are becoming important in biology and palaeontology. The incorporation of high-quality data within large data-base projects, such as the Palaeobiology Database, ensures future utility of the data to other researchers. Furthermore, repeatable methodologies can be utilized and the data produced are amenable to statistical analyses. Tens to hundreds of species maps can be created efficiently, providing large data sets from which to examine patterns using both traditional and geospatial statistics.

The initial use of GIS methods in palaeontology included the development of geospatial data bases of species occurrences (Graham *et al.*, 1996; Graham, 2000; Ferguson *et al.*, 2001). Recent advances in GIS work, including reconstruction of the species ranges of Palaeozoic invertebrates through multiple temporal intervals (e.g. Rode & Lieberman, 2000, 2004, 2005; Stigall Rode, 2005b), have produced data to test palaeoecological and palaeobiogeographical hypotheses. In addition, the use of computer learning-based genetic algorithms has the potential greatly to enhance our ability to predict and interpret the causes of species range shifts in the fossil record (Stigall Rode & Lieberman, 2005b).

Case studies: GIS-based analyses of Late Devonian biogeographical patterns

The case studies presented herein incorporate GIS-derived species ranges for individual species in order to study a variety of palaeobiogeographical patterns, including the relationship between geographic ranges and: ancient sea levels; speciation and extinction rates; propensity to survive during a mass extinction interval speciation mode; and invasive history of taxa. The Late Devonian included an interval of rapid biotic overturn and reorganization known as the Late Devonian Biodiversity Crisis (c. 374 Ma). During this time there were profound evolutionary and environmental changes, including reductions in speciation rates, increased extinction rates, rampant species invasions, and ecosystem restructuring (McGhee, 1996, 2001; Sepkoski, 1996; Droser *et al.*, 2000). To unravel the faunal dynamics of this complex crisis, it is critical to understand the spatial and temporal patterns associated with biodiversity decline. The extensive fossil and sedimentary records of the Late Devonian of eastern North America provide an excellent geologic setting in which to implement GIS methods to study faunal dynamics during this key episode in the history of life. The examples presented below illustrate the use of GIS range reconstructions to address specific aspects of the Late Devonian biodiversity crisis. These case studies represent a subset of the potential for GIS analyses to examine palaeontological patterns and to improve our understanding of the interaction between palaeobiogeography, palaeoecology, and evolution in the fossil record.

Documenting relationships between species invasions and extinction survival

The GIS analysis of brachiopod and bivalve species from the Middle to Late Devonian of North America by Rode & Lieberman (2004) investigated the relationship between biogeography, relative sea level, and environmental changes. A database including over 8,400 species occurrence points spanning 19 conodont zones from the Givetian (c. 390 Ma) to early Famennian (c. 365 Ma), was assembled based on museum and field collections. This data base was then used to reconstruct the ranges of 341 species of the 28 most common brachiopod and bivalve genera in North America during the Middle to Late Devonian, as illustrated in Fig. 1. Reconstructing species ranges spatially and temporally facilitates assessment of the timing and extent of species invasions into new tectonic basins and of the importance of geographic range in determining species survival through the crisis interval.

This analysis uncovered statistically significant relationships between species ranges, sea level, and species survival through the mass extinction interval (Rode & Lieberman, 2004). At least three episodes of elevated rates of species invasions in the Frasnian Stage (early Late Devonian, leading up to the biodiversity crisis event) were recognized using GIS analysis (Fig. 2). These involved the movement of species into new

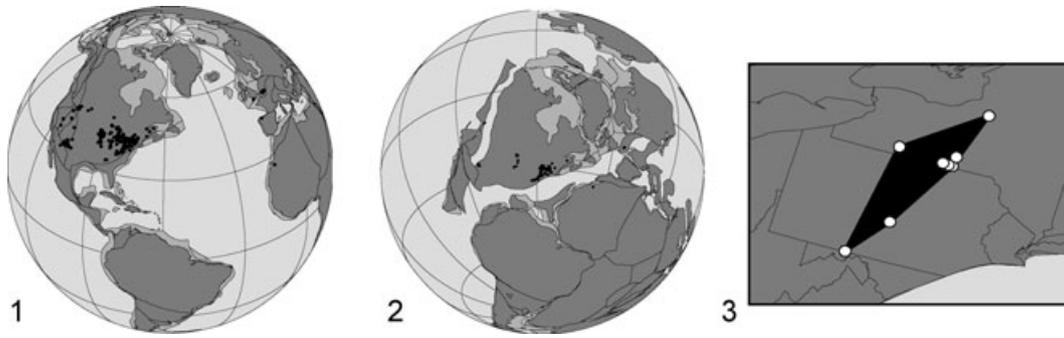


Figure 1 Steps in GIS range reconstruction. (1) Following the assembly of the geographic data set, all data points are plotted onto a modern continental configuration. (2) Data for each time slice are then rotated onto palaeocontinental positions in separate reconstructions. These are the data for the late *rhenana* zone, a single biostratigraphic interval, plotted on the palaeocontinental configuration. (3) Within a biostratigraphic interval, the geographic range of each species is then constructed individually by creating a polygon to enclose the species occurrence points. This is the range of a brachiopod, *Tylothyris mesacostalis*, during the Late *rhenana* Zone. Figure modified from Rode & Lieberman (2004).

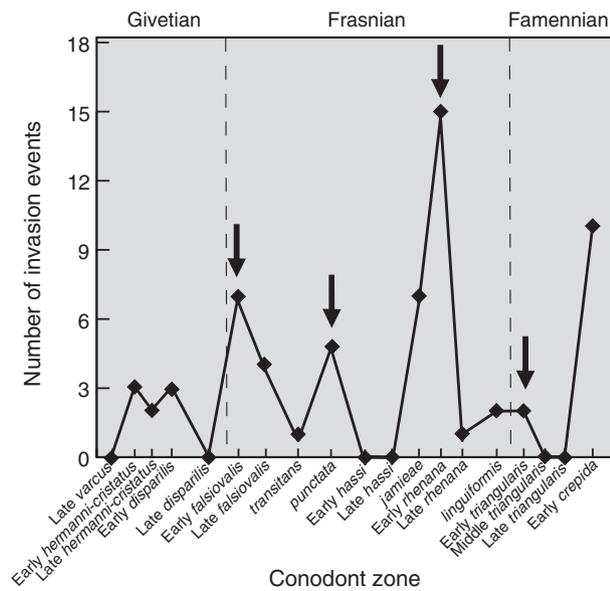


Figure 2 Number of invasion events between tectonic basins per biostratigraphic interval. Vertical arrows indicate episodes of sea-level rise from the Johnson *et al.* (1985) Devonian sea-level curve. Local optima in invasion events during the Frasnian Stage correspond with episodes of sea-level rise. The biodiversity crisis interval extends from the Early *rhenana* Zone to the Early *triangularis* Zone. Figure modified from Rode & Lieberman (2004).

tectonic basins (i.e. into basins other than the one in which the species originated). These pulses occurred at the beginning of the Frasnian, in the mid-Frasnian and in the late Frasnian. The second and third of the pulses correspond to the onset and final stage of the crisis event, respectively. The timing of these invasion pulses also coincides with times of rapid relative sea-level rise (Johnson *et al.*, 1985). The invasions into new areas, and the concomitant expansion in geographic range, appear to confer increased likelihood of species survival during 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 \ll 0.001; Rode & Lieberman, 2004). In addition, species with episodes of interbasinal invasion during their history also preferentially survived the mass extinction event (*t*-test, *P*-value < 0.001; Rode & Lieberman, 2004).

The connection between geographic range size and extinction survival has been further examined using niche modelling methods – a more sophisticated computer-learning-based GIS modelling approach (Stigall Rode & Lieberman, 2005b). The GARP (genetic algorithm for rule-set prediction) system used in this study predicts species range by using environmental variables to estimate the fundamental niche of a species (Stockwell & Peters, 1999; Peterson, 2001; Sánchez-Cordero *et al.*, 2004; Stigall Rode & Lieberman, 2005b). Environmental variables considered within this analysis included parameters related to substrate type, bedding style, water depth, oxygenation, bioturbation, and biotic assemblage (Stigall Rode & Lieberman, 2005b). GARP and simple GIS range reconstructions agree closely (Fig. 3), and similar statistical patterns emerge. A large geographic range is statistically associated with species survivorship across the crisis interval for species examined in the *linguiformis* Zone, the terminal Frasnian conodont zone (ANOVA, *P* = 0.002; Stigall Rode & Lieberman, 2005b). The relationship of large geographic range and species invasion history with survival through the Late Devonian biodiversity crisis is substantiated by detailed mapping of species ranges and statistical evaluation of the patterns recovered.

Relationship between macroevolution and biogeography

Several lines of evidence suggest that the size of species' geographic ranges may be directly related to both the rate and style of speciation within clades. Rode & Lieberman (2005) determined the mean species range and calculated extinction and speciation rates for phyllocarid crustaceans, an abundant macro-arthropod group, during the Givetian to Famennian stages (late Middle to terminal Devonian). GIS range

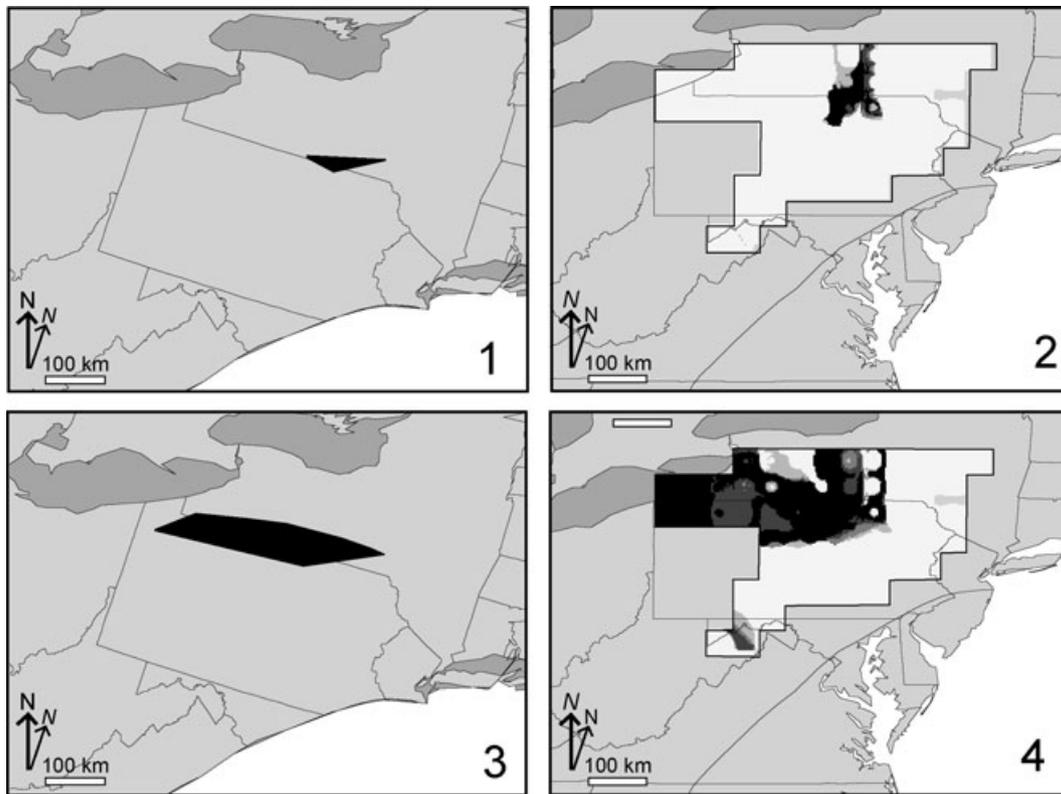


Figure 3 Comparison of GIS reconstructions created by the method outlined in Fig. 1 and GARP (Genetic Algorithm for Rule-set Prediction) distribution predictions. Note that GIS boundary polygons are rotated onto palaeocontinental positions, while GARP predictions are not. The north arrow in roman font indicates present-day north, while that in italics indicates palaeonorth. GARP ranges illustrate increased precision in prediction compared with direct GIS reconstructions. (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. Figure based on data from Stigall Rode & Lieberman (2005b).

reconstructions of phyllocarid species occurrences created using the method described above provided quantitative estimates of species' geographic ranges that were shown to be significantly correlated with both speciation and extinction rates ($r^2 = 0.855$ and $r^2 = 0.833$, respectively, $P < 0.05$ for each; Rode & Lieberman, 2005). The resulting graph of speciation rate vs. geographic range points to a potentially interesting pattern: speciation rate increases as geographic range *both* increases and decreases from the median value (Rode & Lieberman, 2005). The increase in speciation rate at small geographic ranges probably reflects the increased ability of small populations to speciate by allopatry, perhaps related to vicariance. Smaller geographic ranges can be more easily divided by the emergence of geographic barriers. Conversely, large geographic ranges may potentially encourage speciation by promoting peripheral isolates, since the periphery of the species range increases at a rate greater than that of the area of the range (assuming most realistic topologies of species distribution), or episodes of dispersal (either jump dispersal or congruent geo-dispersal). By contrast, the lowest rates of speciation prevail in species with geographic ranges of intermediate size, which are perhaps more likely to be panmictic and are consequently less likely to speciate.

Also of interest is the fact that the speciation rate increases more rapidly in species with smaller ranges, which are more likely to speciate by vicariance, than for species with larger ranges, which are more likely to speciate by dispersal. This pattern suggests that, as opportunities for dispersal increase relative to opportunities for vicariance, there should be an overall reduction in speciation rate. This is in fact precisely the pattern observed in the phyllocarid crustaceans (Rode & Lieberman, 2002). During the Late Devonian the mean geographic ranges of species increased while their net rate of speciation decreased. If the net rate of speciation decreases, even while extinction rates remain constant, the result will be a net biodiversity decline (McGhee, 1996; Rode & Lieberman, 2002).

In this case, GIS analysis leads to the formulation of a hypothesis: on average, increases in dispersal can lead to declines in speciation rate, which can ultimately trigger biodiversity declines. This should be tested further in taxa with more complete fossil records to determine the generality of the observed pattern. An overall reduction in speciation rate has been implicated as one of the primary causes of biodiversity loss during the Late Devonian (McGhee, 1996).

Subsequent analyses of speciation-rate mode in both brachiopod and bivalve clades using phylogenetic

Table 1 Comparison of episodes of speciation by vicariance and dispersal across Late Devonian clades. *Schizophoria* (*Schizophoria*) and *Floweria* are brachiopod clades; data from Stigall Rode (2005a). *Leptodesma* (*Leiopteria*) is a bivalve clade; data from Rode (2004). The suborder Archaeostraca is a phyllocarid crustacean clade; data from Rode & Lieberman (2002)

Clade	Number of vicariance events	Number of dispersal events	Percentage speciation by vicariance	Percentage speciation by dispersal
<i>Schizophoria</i> (<i>Schizophoria</i>)	2	17	11	89
<i>Floweria</i>	7	7	50	50
<i>Leptodesma</i> (<i>Leiopteria</i>)	2	6	25	75
Archaeostraca	6	13	32	68
Overall	17	43	28	72

biogeographical methods have substantiated the fact that there was an overall reduction in speciation by vicariance during the Late Devonian biodiversity crisis (Rode, 2004; Stigall Rode, 2005a). Cladogenetic events within species-level phylogenies of Middle to Late Devonian taxa were characterized as arising from either vicariance or dispersal following the procedure in Lieberman (2000). Within the clades investigated, vicariance events comprised a minority of discernable speciation events (Table 1). This level of vicariance is greatly reduced compared with that observed in modern clades. In analyses of speciation mode in the modern biota (e.g. Wiley & Mayden, 1985; Brooks & McLennan, 2002), it is found that the vast majority of allopatric speciation occurs via vicariance (72% vicariance, 28% dispersal). Results for the Late Devonian, however, indicate the dominance of speciation by dispersal (72% dispersal, 28% vicariance; Table 1 and Rode & Lieberman, 2002; Rode, 2004; Stigall Rode, 2005a). The potential shift in speciation mode from vicariance to dispersal during the Late Devonian may signify something unique or unusual about this key episode in the history of life and probably contributed to the reduced speciation rate noted (e.g. McGhee, 1996) during this interval.

Role of species invasions during the Late Devonian

By combining the analyses discussed above, an overall picture of the role of species invasions during the Late Devonian biodiversity crisis begins to emerge. Invasive species are identified, in this context, as species that evolved within one tectonic basin and secondarily invaded and populated additional tectonic basins previously isolated from the ancestral range. Species identified as invasive migrate into a previously established ecosystem and successfully found and sustain populations that are geographically distinct and previously isolated from their ancestral range. In this context, Late Devonian species invasions may be viewed as analogues for the long-term (hundreds to thousands of years or more) effects of modern invasive species.

During the Late Devonian, species that increased their geographic ranges, particularly by the invasion of additional basins, preferentially survived the Late Devonian biodiversity crisis. In addition, species that inhabited offshore environments preferentially survived compared with near-shore

species (Rode & Lieberman, 2004). These findings suggest that invasive species, particularly those inhabiting deeper waters, were more likely to survive the biodiversity crisis. The reduction in vicariant speciation during this interval may also be linked to the marked expansion in geographic range by many species at this time. Allopatric speciation by vicariance requires the isolation of previously adjacent populations (Mayr, 1942). The numerous range expansion events during this interval would, however, make it difficult to sustain isolation, thereby potentially cutting off the main mechanism of vicariant speciation. Moreover, since 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 the extinction rate, rather than to produce a speciation event, at least during the Late Devonian. A summary of the effects of species invasions during the Late Devonian would therefore be a reduction in speciation rates and an overall eventual homogenization of the fauna. The latter resulted in the cosmopolitan fauna documented for many Late Devonian clades, for example rugose corals (Oliver, 1976, 1990), brachiopods (Boucot, 1975; McGhee, 1981, 1996), foraminifera (Kalvoda, 1990), fishes (Young, 1987), conodonts (Klapper & Johnson, 1980; Klapper, 1995), trilobites (Feist, 1991), and land plants (Raymond & Mertz, 1995).

PHYLOGENETIC PALAEOBIOGEOGRAPHY

Phylogenetic palaeobiogeography provides additional power for deciphering the mode of speciation during cladogenetic events and for resolving the interaction between Earth history events and evolution. A variety of biogeographical methods exist, but those methods based on a modified version of Brooks parsimony analysis (see the discussions in Brooks & McLennan, 1991, 2002; Lieberman & Eldredge, 1996; Lieberman, 2000; Rode & Lieberman, 2005) have been most successfully applied to palaeobiogeographical studies. These methods rely on phylogenetic information and search for congruent patterns of vicariance and geo-dispersal. Geo-dispersal is a biogeographical process, and is described in detail in Lieberman & Eldredge (1996) and Lieberman (2000). This process was defined based on the recognition that sometimes geological or climatic processes can cause several

different lineages to expand their ranges congruently. Although originally defined and codified based on biogeographical patterns present in the fossil record, several scientists studying biogeographical patterns in the extant biota have also recognized geo-dispersal (e.g. Brooks & McLennan, 2002; Conti *et al.*, 2002). It is important to take geo-dispersal into account in biogeographical studies not only because it is a biogeographical process that produces congruence, but also because if it is ignored, and only vicariant patterns are considered, the resultant biogeographical patterns may be inaccurate or difficult to interpret.

Case studies

A comparison of phylogenetic palaeobiogeographical patterns in trilobite clades extant during the Cambrian radiation (these first trilobites lived between *c.* 530 and 510 Ma) with patterns of those extant during the Devonian (clades that lived between *c.* 400 and 380 Ma) shows that differences in the geological events (or Earth history regime) present at any one time are correlated with differences in biogeographical and evolutionary patterns (Lieberman, 1999, 2005; Meert & Lieberman, 2004). In total these analyses, along with many other studies conducted by other authors, illustrate the important control that Earth history has on evolution and provide tangible evidence that Earth-history change is one of the fundamental driving forces of evolution. Palaeobiogeographical patterns in trilobites extant during the Cambrian radiation and during the Devonian were assessed using analytical biogeographical methods based on a modified version of Brooks parsimony analysis (again, see the discussions in Brooks & McLennan, 1991, 2002; Lieberman & Eldredge, 1996; Lieberman, 2000; Rode & Lieberman, 2005). Analyses of trilobites extant during the Cambrian radiation show well-resolved vicariant biogeographical patterns, and relatively poorly resolved patterns of geo-dispersal (Lieberman & Meert, 2004). Moreover, the recovered biogeographical patterns correspond closely to the inferred breakup sequence of a supercontinent shortly before the Cambrian radiation began (Meert & Lieberman, 2004). Furthermore, during the Cambrian radiation, trilobite clades exhibited high levels of speciation (Lieberman, 2001), which might be predicted with the pervasive opportunities for vicariance created by the breakup of a supercontinent. Several palaeontologists have suggested a link between the major geological changes at the end of the Precambrian and the major biological changes at the start of the Cambrian: phylogenetic palaeobiogeographical analysis substantiates this link between Earth-history change and evolution.

In the case of the Devonian, the Earth-history regime is very different. Instead of a supercontinent breaking up, one is being assembled, representing an initial stage in the development of the supercontinent Pangea (see the discussions in Scotese & McKerrow, 1990; Lieberman & Eldredge, 1996; Rode & Lieberman, 2002). The palaeobiogeographical patterns in Devonian trilobites, again based on the modified version of Brooks parsimony analysis, show prominent differences from

the patterns in trilobites extant during the Cambrian radiation. In particular, during this time period the patterns of geo-dispersal are well resolved (Lieberman & Eldredge, 1996), and concomitantly the rates of speciation are lower in these trilobites than in their Cambrian kin (Lieberman, 1999), as would be predicted as opportunities for geo-dispersal increased while potentially opportunities for vicariance declined. Again, the evolutionary and biogeographical patterns are consistent with the Earth-history regime during this time period. One of the fundamental patterns emerging from these phylogenetic palaeobiogeographical patterns is that a changing Earth-history regime is reflected in a changing evolutionary pattern.

More generally, the pattern of increased geo-dispersal and declining speciation rates observed in Devonian trilobites is probably related to the patterns described above from other Late Devonian lineages. Thus, these palaeontological results also suggest a cautionary tale when we consider the modern biota. It is well known that a major cause of the current biodiversity crisis is human-induced species invasions (either accidental or purposeful) (see fuller discussion below). If Late Devonian species invasions and range expansions contributed to reduced vicariance, as suggested by these results, then the current flux of species invasions that we are mediating may be expected to depress speciation rates in the modern biota, even as they amplify extinction rates. This suggests that our effects may comprise a one-two punch to the Earth's biota: we increase extinction rates while turning off the speciation motor that would otherwise eventually allow for recovery from these extinctions. Thus our current effects on the modern biota may even be more profoundly negative than once thought.

IMPLICATIONS FOR CONSERVATION BIOLOGY

Palaeobiogeographical analysis has much to offer the field of conservation biology. Since the fossil record is our only record of the history of changes in biodiversity, an understanding of the nature of ancient biodiversity changes is essential for making future projections regarding the present biodiversity crisis. As detailed above, biological and ecological research is of fundamental importance but is temporally restricted to manipulating systems over several years to decades. Thus, the long-term history preserved within the fossil record is an essential source of information on evolutionary, ecological, and biogeographical changes during longer periods of time.

The Devonian case studies presented above focused on how an examination of the ranges of fossil species can provide information about the potential long-term effects of invasive species. The modern spread of invasive species, attributable primarily to humans, is one of the primary causes of the current biodiversity crisis (Enserink, 1999). Modern species invasions have negative repercussions on biodiversity, causing extinctions that spread throughout the entire ecosystem (e.g. Lodge, 1993; Mooney & Hobbs, 2000; Gurevitch & Padilla, 2004; Hastings *et al.*, 2005). Determining the effect of invasive species on modern ecosystems is a very active area of research;

likewise, the study of the long-term effects of invasive species is becoming an active research area, and one to which palaeobiogeography can contribute in important ways. As noted above, the fossil record contains a rich history of range expansions and interbasinal species invasions that can be studied as analogues of modern events in order to characterize the long-term effects of species invasions.

The effect of species invasions on Late Devonian biodiversity appears to have had at least two aspects. Species with invasive histories preferentially survived the biodiversity crisis interval compared with non-invasive species, resulting in a depauperate post-crisis fauna. In addition, species invasions during the Late Devonian (c. 364 Ma) have been shown to correlate with a change in speciation mode from vicariance (dominant in the modern biota) to dispersal (dominant in the Late Devonian), resulting in a reduction in the overall speciation rate. Characterizing biogeographical patterns during this interval both temporally and spatially using GIS and a phylogenetic framework allowed the interplay between species invasions, mass extinction survival, and change in speciation mode to be determined. If the Late Devonian is an accurate analogue, we should expect modern species invasions to result in a similar long-term diversity decline as a result of the preferential survival of broadly adapted invasive species and the suppression of vicariant speciation of new species.

CONCLUSIONS

The application of quantitative methods originally applied to the extant biota to studies of the fossil record is becoming more widespread. GIS methods provide useful quantitative techniques for reconstructing the geographic ranges of species and higher taxa. Testable hypotheses of relationships between biogeographical patterns and 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 species ranges uncovered relationships between species invasions, geographic range, speciation, and extinction. Phylogenetic palaeobiogeography offers the means of relating specific episodes of Earth-history change to specific evolutionary patterns. The results retrieved from both types of palaeobiogeographical studies can reorient and change our ideas on the nature of evolution, shifting them away from a deterministic, competition-based framework to one in which opportunities for allopatric speciation mediated by contingent geological and climatic changes become the pacemakers of evolution.

There is much room for palaeobiogeography to grow in the future: one area in which we anticipate growth involves the broader use and continued development of more sophisticated GIS methods and applications; another area involves increasing the number of phylogenetic studies, which can then be integrated into analytical phylogenetic palaeobiogeographical studies. The results from the palaeobiogeographical case studies described suggest that GIS-based and phylogenetic

biogeographical studies have the potential to contribute to our understanding of the coevolution of the Earth and its biota through time and to our understanding of topics relevant to the conservation of the modern biota.

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BIOSKETCHES

Alycia L. Stigall studies the interactions between evolutionary palaeobiology, biogeography, and palaeoecology and their impact on global change. In particular, her work emphasizes the application of quantitative palaeobiogeographical methods to investigate speciation mode and the impact of invasive species during the Late Devonian and Late Ordovician mass extinctions.

Bruce S. Lieberman studies the relationship between biogeography and macroevolution. He is particularly interested in investigating the roles that geological change and biogeographical processes played in motivating key episodes in the history of life such as the diversification of animals during the Cambrian radiation.

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