

TRACKING SPECIES IN SPACE AND TIME: ASSESSING THE RELATIONSHIPS BETWEEN PALEOBIOGEOGRAPHY, PALEOECOLOGY, AND MACROEVOLUTION

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Abstract—In all species, geographic range is constrained by a combination of ecological and historical factors. Ecological factors relate to the species' niche, its environmental or biotic limits in multidimensional space, while historical factors pertain to a species' ancestry, specifically the location at which a species evolved. Historical limitations are primary during speciation, while ecological factors control the subsequent expansion and contraction of species range. By assessing biogeographic changes during the lifespan of individual species, we can assess the relationship between paleobiogeography, paleoecology, and macroevolution. Quantitative paleobiogeographic analyses, especially those using GIS-based and phylogenetic methods, provide a framework to rigorously test hypotheses about the relationship between species ranges, biotic turnover, and paleoecology. These new tools provide a way to assess key questions about the co-evolution of life and earth. Changes in biogeographic patterns, reconstructed at the species level, can provide key information for interpreting macroevolutionary dynamics—particularly speciation mode (vicariance vs. dispersal) and speciation rate during key intervals of macroevolutionary change (biodiversity crises, widespread invasion events, and adaptive radiations). Furthermore, species ranges can be reconstructed using ecological niche modeling methods to examine the effects of environmental controls on geographic range shifts. Particularly fruitful areas of investigation in future paleobiogeographic analysis include (1) the relationship between species ranges and speciation events/mode, (2) relationship between shifting ecological regimes and range expansion and contraction, (3) the impact of interbasinal species invasions on both community structure and macroevolutionary dynamics, (4) the mechanics of transitions between endemic to cosmopolitan faunas and local, regional, and global scales, (5) how ecology and geographic range impacts species extinction during both background and crisis intervals.

Three case studies are presented to illustrate both the methods and utility of this theoretical approach of using paleobiogeographic patterns to assess macroevolutionary dynamics. The first case study examines paleobiogeographic patterns in shallow marine invertebrates during the Late Devonian Biodiversity Crisis. During this interval, speciation by vicariance declined precipitously and only species exhibiting expanding geographic ranges survived the crisis interval. Patterns of biogeographic change during the Late Ordovician Richmondian invasion (Cincinnati Arch region) reveal similar patterns; speciation rate declines during invasion intervals and widely distributed endemic species are best able to survive in the new invasive regime. Phylogenetic biogeographic patterns during the Miocene radiation of North American horses suggest climatic parameters were important determinants of speciation and dispersal patterns.

INTRODUCTION

All species, modern or ancient, occupy(ied) a restricted geographic range. The subdisciplines of biogeography and paleobiogeography focus on discerning the factors controlling species distributions both at a single time and how geographic distributions may

change through time. Among modern biogeographers, the field is subdivided into two disciplines: *historical biogeography* assesses the phylogenetic and Earth history constraints on distribution, whereas *ecological biogeography* emphasizes the role of the environment in determining the limits of geographic ranges (Lomolino et al., 2005). While the approach taken by

researchers in these two traditions can be complementary, typically biogeographic studies of modern organisms examine either historical or ecological factors, not both. In the fossil record, we are fortunate to have species preserved within both historical (stratigraphic) and environmental (sedimentologic) contexts. Consequently both historical and ecological biogeographic approaches, and particularly a combination of these, can be used to examine paleobiogeographic patterns, their causes, and the influence of biogeography on evolutionary dynamics.

The relative influence of historical versus ecological factors on geographic distribution shifts during the “lifespan” of a species. During speciation, biogeographic ranges are controlled largely by historical factors. For example, the location where speciation occurs is inexorably tied to the range of the ancestral species. Most speciation events occur through development of allopatry between subpopulations of the ancestral species (Mayr, 1942); following geographic separation, one (or more) of these isolated populations may diverge from the ancestral condition to form a new species. Allopatric speciation proceeds by two primary mechanisms: (1) *vicariance*, in which the ancestral population is passively divided by the formation of a barrier into two or more large subpopulations, all of which diverge to form new species, and (2) *dispersal*, in which a sub-population actively moves away from the ancestral population and establishes a geographically isolated population that subsequently diverges from the ancestral population (Wiley and Mayden, 1985). By examining species geographic ranges within a phylogenetic context, it is possible to identify the style of speciation at individual cladogenetic events (Wiley and Mayden, 1985; Lieberman, 2000, 2003; Wojcicki and Brooks, 2005). Barrier development and episodes of dispersal are contingent events that are historical in nature and highly dependent on the geographic location of the ancestral range.

Following speciation, population increase and subsequent range expansion (dispersion) away from the initial speciation site are controlled by a species’ niche, the set of environmental or biotic limits in multidimensional space that controls where a species is able to maintain reproductive populations (Hutchinson, 1957). While the species’ niche itself may be conservative through time (Peterson et al., 1999), ecological factors such as habitat availability, effects

of predation and competition (Stanley, 2007), and influence of interbasinal species invasions (Rode and Lieberman, 2004) will almost certainly fluctuate during a species’ duration (Vrba, 1992). These ecological changes alter the geographic limits of a species’ niche (Peterson et al. 1999; Stigall Rode and Lieberman, 2005), which may promote habitat tracking (e.g., Vrba, 1992; Brett et al., 2007) and the waxing and waning of geographic range size during a species’ existence (Foote et al., 2007). Since species durations typically persist for hundreds of thousands to several million years, ecological factors influence geographic patterns during a much longer proportion of the species’ “lifespan” than do the historical events controlling speciation. All dispersion, however, is ultimately related to the original location of speciation. For example, penguins (Sphenisciformes) are restricted to the Southern Hemisphere due to a Gondwanan ancestry whereas bears (Ursidae) are largely restricted to the Northern Hemisphere due to evolution in Laurasia.

By quantitatively analyzing biogeographic patterns during the history of species at multiple time slices from speciation through extinction, it is possible to characterize the impacts of both ecological and evolutionary processes. The fossil record provides a rich source of biogeographic data coupled with a temporal framework; consequently paleobiogeographers are able to employ the full spectrum of tools developed by modern biogeography as well as methods specifically derived to examine paleontological data (e.g., Lieberman and Eldredge, 1996; Rode and Lieberman, 2004). Evolutionary processes, in particular speciation, may be assessed using historical biogeographic methods, such as phylogenetic biogeography, coupled with estimation of speciation rates (Stigall 2008). Ecological influences can be examined by mapping parameters onto a phylogenetic biogeographic hypothesis, using GIS to quantify geographic range shifts through multiple time slices (Rode and Lieberman, 2004), and also through environmental niche modeling (Stigall Rode and Lieberman, 2005).

In this paper, I will outline a theoretical approach to integrate paleobiogeography with paleoecology and macroevolutionary patterns and present three cases studies using these methods from Paleozoic marine invertebrates and Cenozoic mammals. These case studies are chosen for their ability to demonstrate ways in which quantitative paleobiogeographic analy-

ses can address key questions about the relationship between species' range, ecology, and macroevolution. Specifically, these case studies model ways which future paleobiogeographic analyses can assess (1) the relationship between species ranges and speciation events/mode, (2) relationship between shifting ecological/climatic/oceanographic regimes and range expansion and contraction, (3) the impact of interbasinal species invasions on both community structure and macroevolutionary dynamics, (4) the mechanics of transitions between endemic to cosmopolitan faunas and local, regional, and global scales, (5) how ecology and geographic range impacts species extinction during both background and crisis intervals.

THEORETICAL AND METHODOLOGICAL FRAMEWORK

Biogeographic Range and Macroevolution

Recent advances in biogeographic methods by both neontologists and paleontologists provide mechanisms to develop quantitative frameworks in which to analyze biogeographic patterns (see Upchurch et al., 2008). The most powerful quantitative methods for addressing issues related to historical biogeography center on analyzing biogeographic patterns within a phylogenetic framework, although methods based on similarity measures and Parsimony Analysis of Endemicity (Rosen and Smith, 1988) are useful when no phylogenetic hypotheses exist for the taxa of interest. Utilizing methods constrained by phylogenetic hypotheses allows the biogeographic patterns exhibited at individual cladogenetic nodes to be analyzed, the evolution of a clade to be placed in a biogeographic framework, and primary biogeographic processes producing congruent patterns across several clades within biogeographic regions to be examined.

Biogeographic analyses based on phylogenetic relationships begin by replacing taxon names on the cladogram with areas of endemism in which each taxon occurs to create a taxon-area cladogram (compare Figs. 1 and 2.1). Relationships between the areas as indicated by the branch topology of the taxon-area cladogram form the basis for further interpretation. Depending on the biogeographic method employed, the internal nodes may or may not be coded and incorporated into the analysis. A number of phylogenetic

biogeographic methods have been proposed in the literature. Some of these methods, particularly cladistic biogeography or components analysis (e.g., Nelson and Platnick, 1981; Humphries and Parenti, 1986; Page, 1988), produce theoretically flawed analyses unless the only biogeographic process operating on the fauna is vicariance. Reasons for this methodological limitation of components analyses are reviewed elsewhere (Lieberman, 2000). Methods which can identify both vicariance and dispersal patterns include LBPA (Lieberman-modified BPA: Lieberman and Eldredge, 1996; Lieberman, 2000), Secondary BPA (Brooks et al., 2001), PACT (Parsimony Analysis for Tree Comparison: Wojcicki and Brooks, 2005), and DIVA (Dispersal-Vicariance analysis: Ronquist, 1997). Both LBPA and PACT assess speciation mode at cladogenetic events by optimizing ancestral nodes through Fitch Parsimony (Fitch, 1971). Fitch Parsimony follows a two step procedure (detailed in Lieberman 2000) for optimizing ancestral nodes and allows multiple reversals and multi-state characters (Fitch, 1971). Of these methods, LBPA incorporates an additional unique feature that provides a way to determine whether cyclical (such as sea level or climatic oscillations) or singular events (such as tectonic events) are more important drivers of biogeographic pattern in the clades examined, which is particularly useful in paleobiogeographic analyses.

As described above, one of the key parameters required for most speciation events is geographic isolation, which can occur through either vicariance or dispersal. When species-level phylogenetic hypotheses are examined, speciation mode may be determined by optimizing biogeographic states onto the ancestral nodes of a taxon-area cladogram using Fitch Parsimony (Fitch, 1971) as outlined in Lieberman (2000) (see Fig. 2.1). Speciation by vicariance is inferred when a descendant species occupies a subset of the ancestral range, whereas speciation by dispersal is inferred when the descendant species range occupies an area additional to or different from the ancestor (see Figs. 2.1 and 3) (Lieberman and Eldredge, 1996). If the descendant and ancestral species have identical ranges, speciation must have occurred within the region in question. This pattern does not imply sympatric speciation per se, but simply that the scale of the analysis is too coarse to resolve speciation mode at that node. Speciation mode can also be compared to phylogenetic

ically constrained speciation for the clade to further constrain the relationship between quantitative estimates of speciation and biogeographic processes. By examining speciation in terms of both rate and mode, a more complete picture of macroevolutionary processes can be developed as will be demonstrated in the first case study.

While assessing the biogeographic history of individual clades can provide key insight into speciation dynamics, these patterns can be highly idiosyncratic for specific taxa. For example, vicariance would be expected to occur at higher rates in clades with sessile larval and/or adult stages compared to clades with planktonic larvae or a vagile, migrating adult life habit. Consequently, the primary goal of many biogeographic analyses is to examine the evolution of biogeographic regions to determine general area patterns, rather than the biogeographic histories of individual

clades. In this context, cladogram topology is used as evidence of relationship between biogeographic areas rather than taxa (Lomolino et al., 2005). The dichotomous backbone of the cladogram provides information about the timing of regions splitting (vicariance of areas), whereas shifts in distribution coded as dispersal above provide information about joining of areas (geo-dispersal). Using parsimony (in Secondary BPA, LBPA, and PACT) or Bayesian methods (DIVA), it is possible to determine the best supported set of vicariance and geo-dispersal relationships present in the underlying data (e.g., Figs. 2.2-2.3). Processes that drive area vicariance and geo-dispersal are geological or environmental in nature and include climatic and sea-level changes and tectonic events. By analyzing area relationships, it is possible to tie Earth history events into the macroevolutionary processes during specific time intervals. In other words, these methods provide

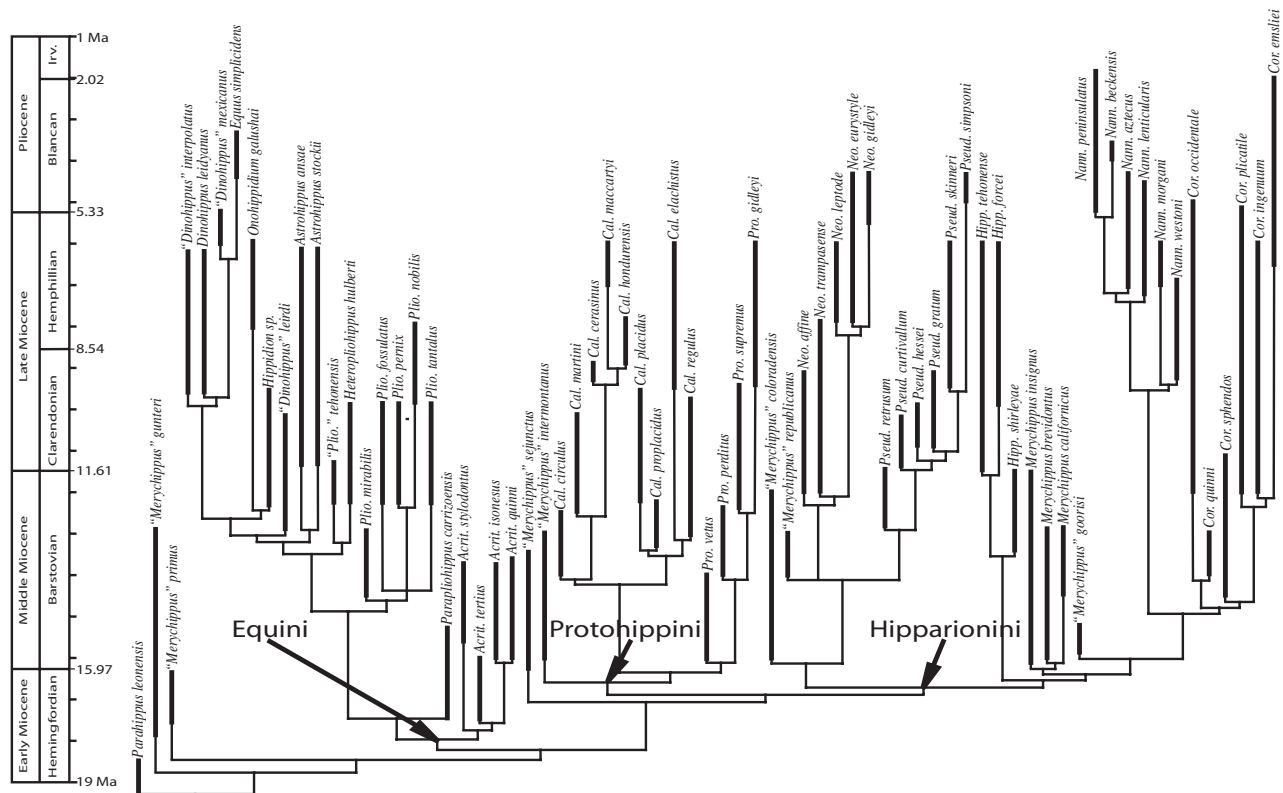


Figure 1—Strato-cladogram of the subfamily Equinae. Phylogenetic relationships adapted from Hulbert (1993); time scale from Gradstein et al. (2004). Bold vertical lines indicate recorded range while narrow lines indicate ghost lineages. Taxa abbreviations: *Plio* = *Pliohippus*, *Acrit* = *Acritohippus*, *Cal.* = *Calippus*, *Pro.* = *Protohippus*, *Neo.* = *Neohipparion*, *Pseud.* = *Pseudhipparion*, *Hipp.* = *Hipparion*, *Nann.* = *Nannippus*, *Cor.* = *Cormohipparion*. Modified from Maguire and Stigall (in press).

a way to quantify how “Earth and life evolve together” (Croizat, 1964).

Biogeographic Range and Paleocology/Extinction

Whereas historical biogeographic methods based on phylogenetic relationships provide insight into cladogenesis and the evolution of regional faunas, quantifying range changes during the duration of a species provides insight into the effect of ecological factors (both abiotic and biotic) on species distribution. The relationship between geographic range and extinction can also be assessed. Although extinction is frequently coupled with speciation in discussions of biodiversity, extinction is effectively an ecological rather than evolutionary process. Extinction is simply the termination

of a lineage when population size equals zero, which could be due to any number of environmental factors, both biotic and abiotic. Studying the relationship between species’ distributions and ecological parameters has long been an active area of inquiry in paleontology (e.g., Boucot et al., 1969; McGhee and Sutton, 1981; Hallam, 1994); however, recently developed methods for using geographic information systems (GIS) in paleobiogeographic analyses provide a level of quantitative rigor not previously attainable in the fossil record (Rode and Lieberman, 2000, 2004, 2005; Stigall Rode and Lieberman, 2005). A more complete discussion of advantages and data requirements of GIS methods is provided in Stigall Rode (2005a) and Stigall (2008). GIS-based range maps can be constructed following

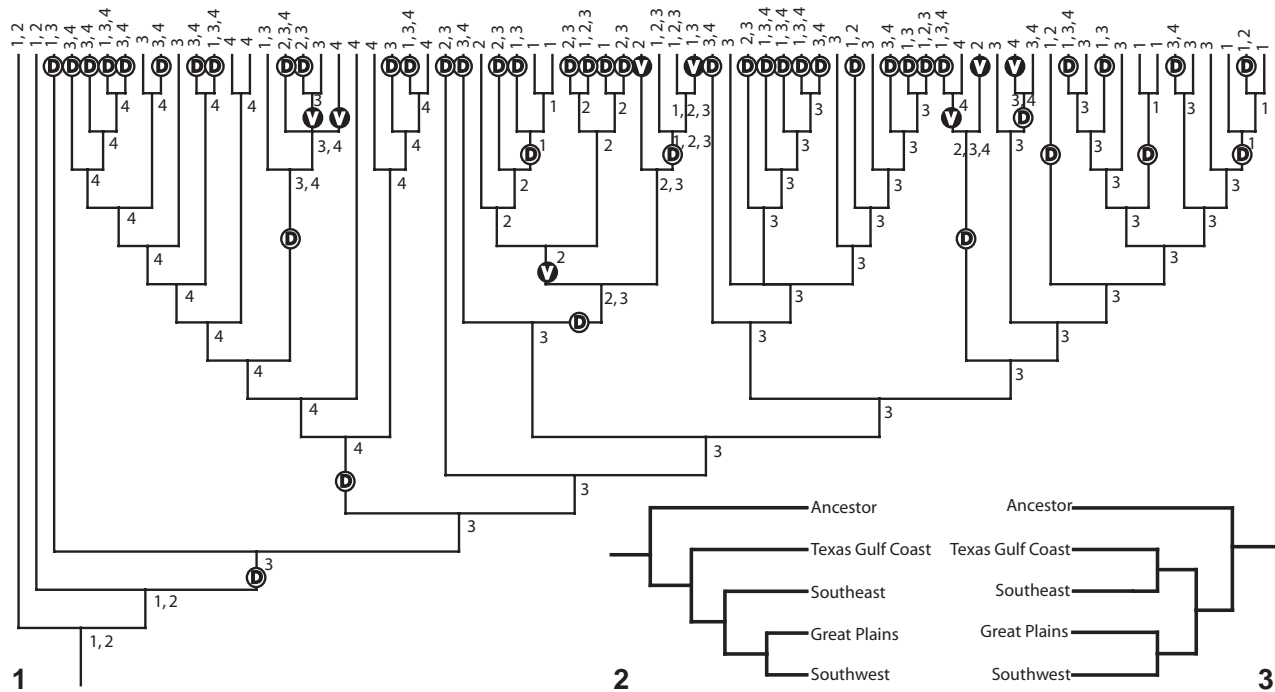


Figure 2—Phylogenetic biogeography of the subfamily Equinae. (1) Taxon-area cladogram of the subfamily Equinae based on phylogenetic topology in Figure 5. First, terminal taxon names are replaced with the areas of endemism in which each taxon occurs. Then areas of endemism are coded for internal nodes using Fitch Parsimony as detailed in Lieberman (2000). Areas of endemism indicate regions of North America; 1: Southeast, 2: Gulf Coast, 3: Great Plains, 4: Southwest. Specification (cladogenetic) events marked by changes in biogeographic states between ancestor-descendent nodes/terminals are coded as resulting from vicariance (V) or dispersal (D) on the branch leading to the cladogenetic split. For example, this taxon-area cladogram indicates that the Equinae ancestrally occupied areas 1 and 2 (the Southeast and Gulf Coast), but underwent speciation by dispersal into area 3 (the Great Plains) at the node where “*Merychippus*” *primus* separated from the ancestral equids. (2) Vicariance and (3) geo-dispersal area cladograms derived from Lieberman-modified Brooks Parsimony Analysis. Modified from Maguire and Stigall (in press).

two methods, polygon enclosure reconstructions and ecological niche models (ENM) (Fig. 4). These are two end-members of a potential continuum of methods that couple species occurrence data with varying amounts of sedimentological data (from none to very detailed data) to model species distributions.

Polygon enclosure reconstructions employ the minimal amount of data: species occurrences denoted by latitude and longitude of collection site and stratigraphic unit of occurrence (Rode and Lieberman, 2004). The occurrence data are mapped and the geographic range is reconstructed as the polygon enclosing the points with the fewest possible sides (known as a convex hull) (Fig. 4.1-4.3). Polygon enclosure mapping has the advantage of being simple to imple-

ment. Data can be extracted from museum collections or online databases with a temporal resolution as fine as the stratigraphic information of those sources will allow. The disadvantage of this method is that the paleogeographic reconstructions necessarily are oversimplified from the true geographic ranges occupied by these species. Some convex hulls will over-estimate and some will under-estimate true range; when large sample sizes are used, these effects are random and should not introduce directed error into the dataset (Stigall Rode, 2005a). Areas of geographic ranges are calculated in the GIS (ex., ArcGIS 9.x; ESRI, 2007) and spatial overlap between the reconstructed range of species between time slices or between contemporaneous species can be assessed using spatial statistics,

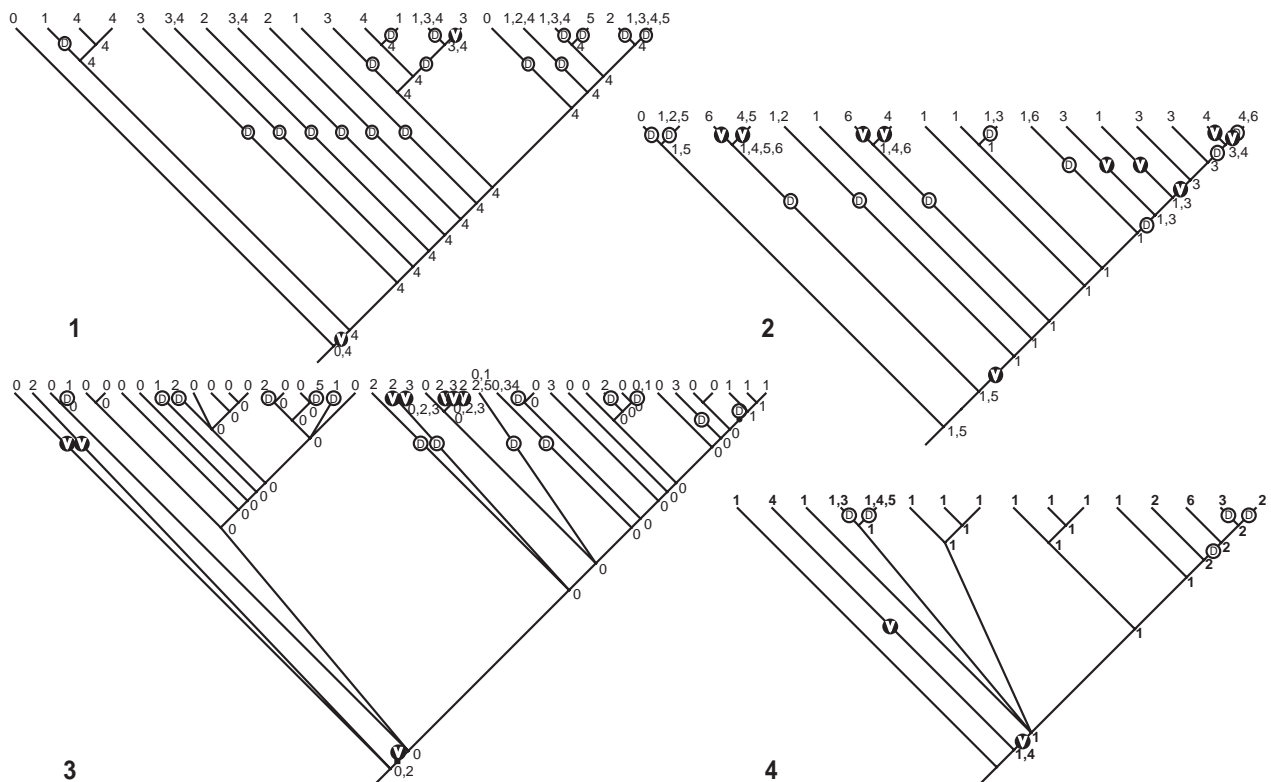


Figure 3—Taxon-area cladograms for the brachiopod clades (1) *Schizophoria* (*Schizophoria*) and (2) *Floweria*, (3) the crustacean suborder Archaeostraca, and (4) the bivalve clade *Leptodesma* (*Leiopteria*). Taxon-area cladograms are constructed from species-level phylogenetic hypotheses as outlined in Figure 2. V indicates speciation by variance, D indicates speciation by dispersal. For (1) and (2), areas of endemism are coded as: 0: Europe, 1: Appalachian Basin, 2: Michigan Basin, 3: Central United States, 4: Western United States, 5: Western Canada. For (3), areas of endemism are coded as: 0: Appalachian Basin, 1: Michigan Basin, 2: Rhenish Massif and Bohemia, 3: Southern England, 4: Massif Armoricain, France, 5: Western Canada, 6: China, 7: Bolivia, 8: Australia, 9: India. For (4), areas of endemism are coded as: 1: Northern Appalachian Basin, 2: Southern Appalachian Basin, 3: Michigan Basin, 4: Midcontinent Basins, 5: Western United States, 6: Northern Africa. Taxon-area cladograms modified from Stigall Rode (2005b), Rode and Lieberman (2002), and Rode (2004).

such as spatial autoregression and spatial auto correlation. These quantitative values for estimated range size can be used to examine the relationship between range size and environmental parameters or extinction rates as illustrated in the case studies below.

In order to address the issues related to oversimplification of polygon enclosure mapping, more sophisticated range models can be constructed by modeling the environmental niche of a species using ecological niche modeling (ENM) (Stigall Rode and Lieberman, 2005). ENM uses sedimentary parameters as proxies for environmental conditions to estimate the ecological niche for a species and then models the species range as the geographic area where the set of environmental conditions in the reconstructed niche occurs (Fig. 4.4) (Stockwell and Peters, 1999; Peterson and Vieglais, 2001). Because ENM range models use multiple environmental variables in addition to species geographic and stratigraphic occurrence data, reconstructed ranges are more complex and provide more accurate estimates of a species' true niche than polygon enclosure mapping. The data set required to conduct ENM, however, is much more substantial and requires detailed sedimentological information from locations distributed throughout the study region. This level of information is often not preserved within museum collections or online databases and requires either new field work or a dense literature source on sedimentological parameters from theses, field guides, and journal articles, or both. Consequently, although ENM methods provide more accurate range reconstructions, for some appli-

cations, such as determining the relationship between average range size and extinction risk for an entire fauna, the cost of this additional accuracy may outweigh the benefits. However, the high level of detail provided by ENM provides a framework to test hypotheses that cannot be addressed easily with polygon enclosure models. For example, ENM is particularly useful for conducting spatial analyses of the percent overlap or spatial correction between the range of a species and a specific environmental variable, such as water depth (Stigall Rode and Lieberman, 2005). A powerful application of ENM is testing for niche conservatism in a species. A null hypothesis of niche conservatism, that is, constancy of environmental preferences in a species through time, can be assessed by modeling the ecological niche of a species in one time slice, projecting the same niche model onto the environmental layers of a second time slice, and then using spatial statistics to analyze whether the species range for the second time slice matches that predicted from its earlier niche. ENM methods have only been applied in a limited way so far to the fossil record, but the first uses (Stigall Rode and Lieberman, 2005; Maguire and Stigall, in review) indicate great potential for future uses as discussed in the case study below.

Synthesizing Biogeography, Evolution, and Ecology

While both approaches outlined above produce robust, quantitative analyses of evolutionary and ecological patterns, respectively, the combination of both meth-

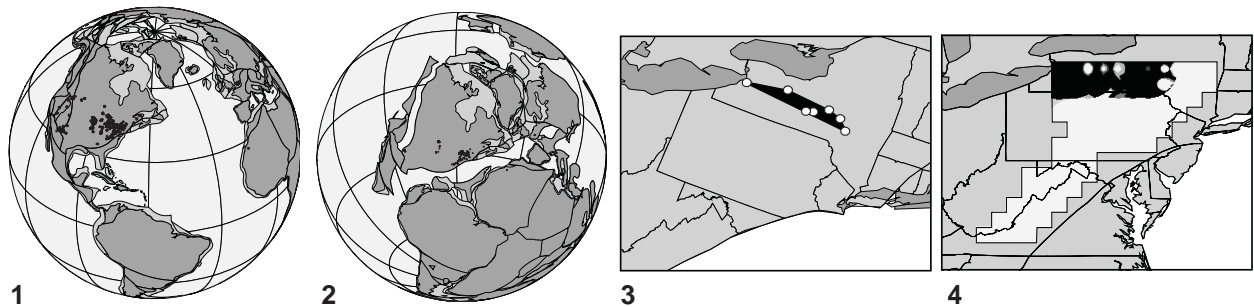


Figure 4—Basic steps and outputs of GIS-based paleobiogeographic range reconstruction of polygon enclosure method and ecological niche modeling (ENM) from Late Devonian case study. (1) Plot of species occurrence data for all taxa on a modern continental configuration. (2) Using PaleoGIS (Ross and Scotese, 2000) data points were rotated onto paleocontinental reconstruction; this reconstruction of all data points present for the *linguiformis* Zone (uppermost Frasnian). (3-4) Output of range reconstructions from the brachiopod species *Cariniferella carinata* Hall during the *varcus* Zone (uppermost Givetian) using (3) polygon enclosure method and (4) ENM range reconstruction. Modified from Stigall Rode and Lieberman (2005).

ods to analyze hypotheses related to biotic turnover is even more powerful. By focusing on species, the fundamental unit of evolution, it is possible to tie the biogeographic controls on speciation mode, speciation rate, range expansion and contraction, and extinction into a comprehensive analysis that can elucidate key controls on the history of life during critical intervals. This synthesis will be explored more fully in the case studies below.

CASE STUDIES

The examples presented below illustrate the use of phylogenetic biogeography and GIS range reconstructions to address specific aspects of the Late Devonian Biodiversity Crisis, Late Ordovician Richmondian Invasion, and Miocene radiation of the Equinae. These case studies illustrate the potential for paleobiogeographic analyses to examine paleontological patterns and contribute to improving understanding of the interaction between paleobiogeography, paleoecology, and evolution in the fossil record.

Late Devonian Biodiversity Crisis: Shallow Marine Invertebrates

A combination of phylogenetic biogeography and GIS-based range reconstructions for individual species was used to assess the relationship of biogeography with sea level, speciation and extinction rates, mass extinction survival, speciation mode, and invasive history of brachiopods, bivalves, and phyllocarid crustacean species during the Late Devonian (approx 340-350 Ma). During the Middle and Late Devonian, repeated transgressive events (Johnson et al., 1985) and pulses of global cooling altered the global oceanic and climatic dynamics (van Geldern et al., 2006). The Late Devonian was an interval of rapid biotic turnover and reorganization which included profound evolutionary and environmental change, including reduction in speciation rates, increased extinction rates, rampant species invasions, and ecosystem restructuring (McGhee, 1996; Sepkoski, 1996; Droser et al., 2000). Although the Late Devonian (Frasnian-Famennian) Biodiversity Crisis is often regarded as one of the “Big Five” mass extinctions, recent statistical analyses have demonstrated that extinction rate does not necessarily exceed background levels (Bambach et al., 2004); reduced

speciation rate, however, resulted in significant biodiversity decline (McGhee, 1996; Stigall, in review). 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) (McGhee, 1996). This changing pattern of geographic range, particularly species invasions, during the Middle to Late Devonian transition, have been implicated in species extinction and speciation reduction during the biodiversity crisis interval (Rode and Lieberman, 2004; Stigall and Lieberman, 2006). 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 combination of biotic turnover, geographic expansion, and extensive fossil and sedimentary record make the Late Devonian of eastern North America an excellent interval in which to implement phylogenetic biogeography and GIS methods to decipher the faunal dynamics of a key event in Earth’s history.

Speciation and biogeography.—Although a decline in speciation during the Devonian has previously been recognized (McGhee, 1996), the reason for this decline has been unknown. To assess speciation within a biogeographic framework, species level phylogenies of four clades of Middle to Late Devonian taxa (two brachiopod genera, one bivalve genus, and an order of crustaceans) were subjected to phylogenetic biogeography, including assessing speciation mode as described above (Fig. 3). Within these clades, the majority of speciation events for which speciation mode could be determined were due to dispersal while vicariance was comparatively rare (Fig. 3; 72% dispersal versus 28% vicariance) (Stigall and Lieberman, 2006). This level of vicariance is greatly reduced compared to that observed in modern clades. In analyses of speciation mode in the modern biota (e.g., Wiley and Mayden, 1985; Brooks and McLennan, 1991), the vast majority of allopatric speciation occurs via vicariance (72% vicariance, 28% dispersal). Comparisons of speciation rate versus geographic range in Late Devonian phyllocarids indicate that speciation occurs at higher rates in taxa with smaller geographic ranges than those with higher geographic range (Rode and Lieberman, 2005). This pattern is consistent with a decline in speciation by vicariance during the Frasnian Age, during which range expansion and interbasinal invasion

events resulted in the development of a cosmopolitan biota. Consequently, the potential reduction in vicariance and preponderance of dispersal during the Late Devonian likely contributed to the reduced speciation rate noted (e.g., McGhee [1996]) during this interval.

To further test the relationship between speciation rate and mode, species-level phylogenetic hypotheses from Rode (2004) and Stigall Rode (2005b) were converted to strato-cladograms, similar to that illustrated in Fig. 1. Strato-cladograms were constructed as described in Stigall (2008) by assuming that sister taxa evolved by simultaneous speciation events and constructing ghost lineages to extend the observed stratigraphic ranges of taxa backward to the interpreted time of cladogenesis. Rates of biodiversity change, speciation, and extinction were calculated from these data using a pure birth process model, a deterministic exponential model of taxon growth used for calculating instantaneous rates of biodiversity change within a phylogenetic framework (detailed in Fig. 5). Results of rate calculations indicate several basic patterns. Net biodiversity loss during the Late Devonian biodiversity crisis occurred during the crisis interval (late Frasnian). This loss was driven partly by extinction (Fig. 5.3), but not entirely. In fact, extinction rates for all clades were higher during preceding intervals, particularly the early and late Eifelian, than during the late Frasnian. Speciation rates, however, declined from moderate rates during the Middle Devonian to near zero in the Frasnian (Fig. 5.2). Thus, it is probable that speciation decline was the key determinant of net biodiversity loss. The relative paucity of vicariant speciation discussed above may have contributed significantly to the overall pattern of speciation decline because all but two documented vicariance events preceded the Late Devonian (Stigall, 2008).

Ecology and biogeography.—The relationship between biogeography, relative sea level, environmental change, and extinction were analyzed for brachiopod and bivalve species from the Middle to Late Devonian of North America by Rode and Lieberman (2004) using polygon enclosure reconstructions (Fig. 4.1-4.3). To reconstruct species ranges, a database of species occurrence points, including over 8,400 species occurrence points spanning 19 conodont zones from the Givetian to early Famennian, was assembled from museum collections. This database was then used to

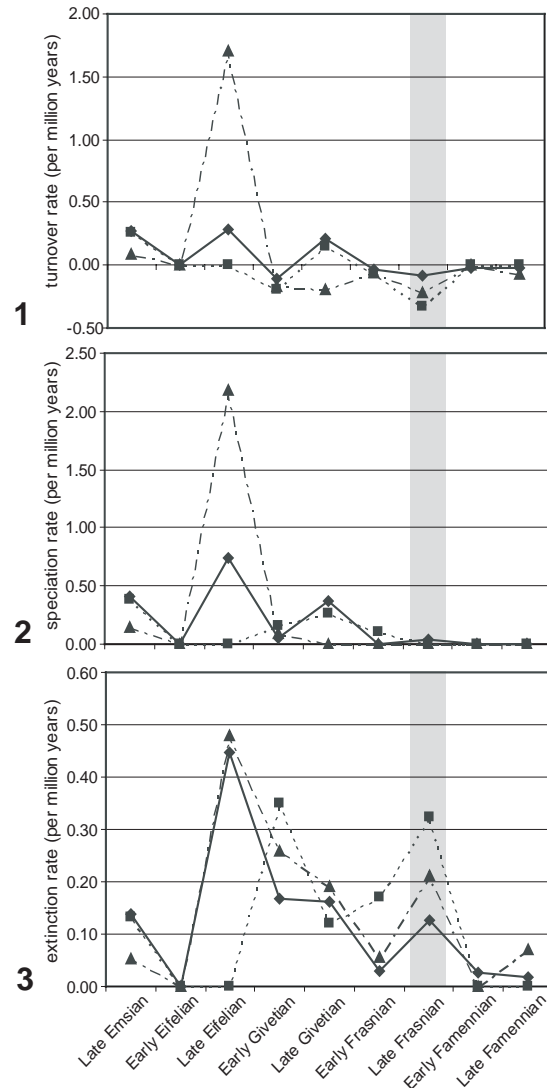


Figure 5—Rates of biodiversity turnover in the brachiopod clades *Schizophoria* (*Schizophoria*) and *Floweria* and the bivalve clade *Leptodesma* (*Leiopteria*) during the Middle and Late Devonian. (1) Rate of net biodiversity change calculated from equation: $R = (\ln N_1 - \ln N_0) / \Delta t$; (2) Speciation rate calculated from equation: $S = (\ln (N_0 + o_0) - \ln N_0) / \Delta t$; (3) Extinction rate calculated from equation: $E = (\ln (N_0 + o_0) - \ln N_1) / \Delta t$. 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 , Δt represents the duration of the interval $t_1 - t_0$, and o_0 is the number of speciation events during interval $t_1 - t_0$. Taxon symbols: solid line, *Schizophoria* (*Schizophoria*); short dash, *Floweria*; long-short dash, *Leptodesma* (*Leiopteria*). Shaded area indicates crisis interval. Modified from Stigall (2008).

reconstruct the ranges of 341 species of the 28 most common brachiopod and bivalve genera in North America during the Middle to Late Devonian following the procedure outlined above (Rode and Lieberman, 2004). Because species ranges were reconstructed both spatially and temporally, the timing and extent of events such as species invasions into new tectonic basins and the importance of geographic range in determining species survival through the crisis interval could be assessed quantitatively.

This analysis uncovered statistically significant relationships between species ranges, sea level, and species survival through the mass extinction interval (Rode and Lieberman, 2004). Four pulses of elevated rates of species invasions into new tectonic basins (i.e., basins other than the one in which the species originated) were identified from GIS analysis during the Late Devonian: the beginning of the Frasnian, mid Frasnian, and two pulses in the late Frasnian, which relate to the onset and final stage of the biodiversity crisis. These invasion pulses also coincided with rapid sea level rise (Johnson et al., 1985). The invasion into new areas, and the concomitant expansion in geographic range, appears to confer an advantage in species survival 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 $\ll 0.001$) (Rode and Lieberman, 2004); the relationship between species longevity and range size has been documented previously in other clades (Vrba, 1987; Jablonski and Raup, 1995; Stanley, 2007; Hendricks et al. 2008). In addition, species exhibiting episodes of interbasinal invasion also preferentially survived the biodiversity crisis event (t-test, p-value < 0.001) (Rode and Lieberman, 2004).

The connection between geographic range size and extinction survival was further examined using ENM based on sedimentological parameters such as substrate type, inferred water depth, and depositional setting (Stigall Rode and Lieberman, 2005). ENM and polygon enclosure reconstructions agree closely (Figs. 4.3 and 4.4), and similar statistical patterns emerge from analyses of geographic ranges reconstructed using both methods. 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, 2005). The relationship of large geographic range and species invasion history with survival through the Late Devonian Biodiversity Crisis is again substantiated by detailed mapping of species ranges and statistical evaluation of patterns recovered.

Synthesis: Biogeography of the Late Devonian Biodiversity Crisis.—Integrating the results of the biogeographic analyses of evolutionary and ecological patterns indicates that episodes of dispersal and species invasions played a fundamental role in mediating biodiversity dynamics during the Late Devonian crisis interval. Species with invasive histories preferentially survived the biodiversity crisis interval compared to non-invasive species, resulting in a depauperate post-crisis fauna. The survival advantage conferred to invasive (or dispersing) species resulted in reduced opportunities for speciation via vicariance and also a dramatic decline in overall speciation rate during the Late Devonian. Only by characterizing changing biogeographic patterns during this interval both temporally and spatially using GIS within a phylogenetic framework could the increased frequency of species invasions be correlated with mass extinction survival, reduction of speciation by vicariance, and dramatic decline in speciation rates. 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.

Late Ordovician Richmondian Invasion: Brachiopod Biogeography

The second case study focuses on the biogeography of brachiopod species from the Late Ordovician (Cincinnatian) strata of the Cincinnati Arch. Cincinnatian strata are subdivided into three stages: the Edenian, Maysvillian, and Richmondian. The Maysvillian-Richmondian boundary coincides with an invasion of species from the Midcontinent into the Cincinnati region; Holland and Patzkowsky (1996) have termed this episode the Richmondian invasion and related it to changes in paleoceanographic circulation mediated by global cooling. Gradient ecology and biofacies analyses indicate a fundamental breakdown and

restructuring of community structure immediately following the invasions followed by reestablishment of defined communities after the early Richmondian, but communities that differ significantly from those of the Maysvillian due to the ecological dominance of many invader taxa (Holland and Patzkowsky, 2007). While the taxonomic turnover and ecology of this invasion have been well constrained, no previous studies have specifically addressed biogeographic patterns in species across the invasion interval.

Biogeographic analyses.—As with the Late Devonian case study, species geographic ranges were reconstructed using polygon enclosure ranges (Stigall, 2007). Brachiopod species distribution data were collected for all stratigraphic sequences in the Maysvillian and Richmondian Stages to incorporate the interval prior to and following the Richmondian invasion. Over 1200 data points for 45 species were assembled for 5 time slices, each representing a depositional sequence of Holland and Patzkowsky (1996). A polygon enclosure reconstruction was created for each species in each time slice in which it was extant. Brachiopod species preserved in Cincinnati strata during this in-

terval were categorized into four groups: species that were native to the Cincinnati region but became extinct by the end of the Maysvillian, Cincinnati natives that carried over into the Richmondian, species that evolved in the Richmondian from Cincinnati natives, and extrabasinal invaders that arrived during the Richmondian invasion. Interestingly, no speciation events are recorded during the first depositional sequence of the invasion; this observation is consistent with the Devonian data indicating decline in speciation rate and lack of vicariance during invasive regimes (Stigall, 2007). When the geographic areas of species ranges are compared against group membership, several statistical patterns emerge (Fig. 6). When the geographic range size of all native species is compared to that of extrabasinal invaders, no statistical difference emerges (t-test, $p = 0.998$), although it is apparent that native species have a higher variance in range values (Fig. 6.1). When native species that survived into the Richmondian (carryover species) are compared with those that became extinct by the end the Maysvillian, however, the ranges are significantly different (t-test, $p = 0.0005$; Fig. 6.2). Specifically, carryover species

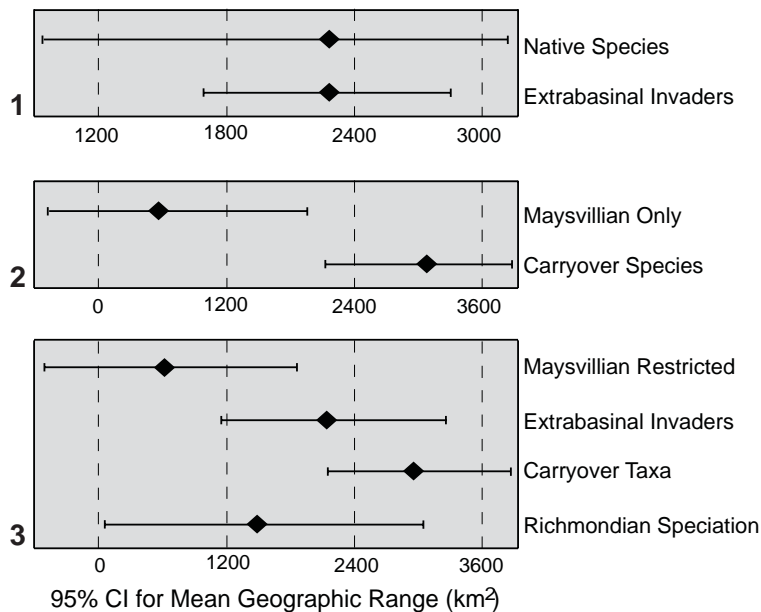


Figure 6—Statistical comparison of Cincinnati brachiopod species’ ranges versus group membership. (1) Comparison of the geographic range of native vs. invasive species (T-test, $p = .998$, $N = 59$); (2) Comparison of survival status of native species vs. geographic range (T-test, $p < .0005$, $N = 39$); (3) Comparison of species groups vs. geographic range (ANOVA, $p = .025$, $N = 59$).

are broadly distributed whereas narrowly distributed species became extinct.

Range size is a function of ecological tolerance (Hutchinson, 1957); consequently species with larger ranges were potentially more broadly adapted and better able to persist through the changing environmental conditions (Vrba, 1992). This result is consistent with the Devonian pattern in which generalist species preferentially survive intervals of biotic overturn compared to ecological specialists. Furthermore, the average geographic range for all four species groups are significantly different (ANOVA, $p = 0.025$; Fig. 6.3). Extrabasinal invaders are intermediate in geographic range between the Richmondian carryover and Maysvillian restricted taxa. New species that evolved in the Richmondian from Cincinnati natives are also intermediate, suggesting radiation into empty ecological niches, including the specialist niches vacated by the extinction of the Maysvillian taxa. Finally, a phylogenetic hypothesis currently exists for only one genus of Cincinnati brachiopod, *Hebertella* (Stigall, 2007); however, it is apparent that speciation by dispersal is much more common than vicariant speciation in this clade, a pattern congruent with the lack of vicariance observed in the Late Devonian taxa.

GIS-based and phylogenetic biogeography of Late Ordovician brachiopod species in the Cincinnati Arch indicates that the impacts of Late Devonian invasive taxa, reduced speciation by vicariance and extinction resistance of species with larger ranges (presumably of generalist ecology) during invasive regimes, may be a common feature of intervals of intense interbasinal invasion pressure in Earth's history.

Phylogenetic Biogeography of the Miocene Radiation of the Equinae

The third case study provides a contrast from the previous two by emphasizing phylogenetic biogeography during a radiation, rather than a crisis interval, and by focusing on a terrestrial mammal clade rather than on marine invertebrates. In particular, this case study focuses on the Miocene radiation of horses in North America. This radiation has been linked to climatic and vegetation changes that occurred in North America during this time (MacFadden, 1984; Hulbert, 1993). This taxonomic pattern of the radiation is well known from a morphological perspective (e.g., Simpson, 1951; Hulbert, 1993) and equid phylogeny is well

constrained; however, prior to the work of Maguire and Stigall (2008) the relationship between climate change and speciation has not previously been studied quantitatively using phylogenetic biogeography. Due to the well-constrained phylogenetic hypotheses and the extensive collection of fossil horse material in North America, this radiation can be studied to determine the evolution of the subfamily, including the effect of climate and geological events on biogeographic patterns using phylogenetic biogeography. Specifically, the relative roles of geo-dispersal and vicariance in the evolution and distribution of the subfamily can be constrained.

Species occurrence data were collected for all Miocene species within eighteen equinid genera through a literature review and online databases (Miocene Mammal Mapping Project [MIOMAP; Carrasco et al. 2005] and the Paleobiology Database [www.paleodb.org]) (Fig. 1); Maguire and Stigall, 2008). Ancestral nodes were optimized using Fitch Parsimony, and speciation via dispersal and vicariance were identified (Fig. 2). Speciation by dispersal occurred in these areas more frequently than did vicariant speciation in the evolution of this clade (83% dispersal vs. 17% vicariance); frequent dispersal events are congruent with the ecology of horses, which are vagile herbivores (MacFadden, 1994). Furthermore, nodal analysis indicates that each of the three tribes of horses diversified ancestrally in a distinct region (Equini in the Southwest, Protohippini in the Gulf Coast, and Hipparionini in the Great Plains), and subsequent dispersal events led to the late Miocene overlap of ranges between these clades (Fig. 2, Maguire and Stigall, 2008).

LBPA analysis resulted in recovery of a single most parsimonious area cladogram for both vicariance patterns (Fig. 2.2) and geo-dispersal patterns (Fig. 2.3). The vicariance tree (Fig. 2.2) indicates that a division between the Great Plains and Southwest occurred most recently. Before then, a barrier rose between these two areas and Florida and ancestrally, a barrier rose between these regions and the Gulf Coast. The geo-dispersal tree (Fig. 2.3) indicates dispersal occurred within two major areas of North America: (1) between the Great Plains and Southwest and (2) between the Gulf Coast and Florida. Congruence between the geo-dispersal and vicariance trees indicates that fluctuating climatic conditions repeatedly joined and divided taxa inhabiting the four areas. Consequently, the gen-

eral pattern of biogeographic relationships of the clade as a whole appears to be more strongly affected by climatic rather than tectonic events (Maguire and Stigall, 2008). During the Neogene in North America, the fluctuating climate resulted in a variety of fragmented habitats as woodlands slowly shifted to open grasslands (Webb, 1983). Speciation by geo-dispersal was a result of biogeographic shifts in response to environmental alteration caused by climate change.

SUMMARY

Quantitative paleobiogeographic methods are now available to assess speciation mode, biogeographic evolution of clades, and geo-dispersal and vicariance relationships between regions as well as GIS-based methods for reconstructing species' geographic ranges and assessing ecological biogeographic patterns. By combining approaches typically divided between the subdisciplines of historical and ecological biogeography, new insights into the interplay between biogeography, evolution, and ecology can be developed. At present, these methods are under-utilized in paleontology. This failing is likely due to a combination of factors, including the limited number of species-level phylogenetic hypotheses for invertebrate clades or the limited amount of sedimentological data available for continental fossils. Phylogenetic biogeographic methods are relatively straightforward to apply if a hypothesis of phylogenetic relationships is available, and the explanatory power of these methods greatly exceeds narrative approaches to paleobiogeography. GIS-based methods, while methodologically simple to implement, require large data sets that can be much more cumbersome to acquire for some taxa or depositional environments than others. When these methods are employed in concert, however, new insights can be derived that could not be explored using a single method.

The case studies presented herein provide a brief survey of some of the ways in which phylogenetic and ecological paleobiogeography can be employed to address speciation during both biodiversity crises and adaptive radiations. In the case of the Late Devonian and Late Ordovician, the impact of invasive species can be constrained by identifying a reduction in speciation rate overall and speciation by vicariance

specifically. This factor combined with the extinction resistance conferred on invasive or broadly distributed taxa to result in a widespread loss of ecological specialists within the ecosystem during both invasive regimes. Because the modern biodiversity crisis exhibits strong similarities to these intervals in frequency of dispersals of non-native taxa, it is possible a similar depression of speciation may be operating at present or in the next several hundreds to thousands of years in the modern ecosystem. The equinid Miocene radiation presents a different view of dispersal and speciation. During this time, climatic changes in North America resulted in frequent speciation by dispersal, but horses retained high speciation rates during this time. This pattern may suggest that speciation via dispersal (i.e., speciation within a new environment after active geographic isolation) does not impact negatively the ecosystem in the same way as interbasinal invasions involving dispersal without new speciation events (i.e., dispersal and colonization of a new environment without concomitant speciation).

One of the greatest strengths of phylogenetic and GIS-based paleobiogeographic methods is the ability to test hypotheses quantitatively and generate new hypotheses from analyses. As implementation of some of these methods is relatively novel, I look forward to new studies and analyses in the coming years in which these and other creative, quantitative methods are implemented and developed to explore the relationship of biogeography, speciation, ecology, and Earth history events. As the Paleontological Society moves forward into our second century, we have a tremendous opportunity to combine the previous data collected on species occurrences, phylogenetic relationships, environmental conditions, climatic and oceanographic changes, and tectonic events with new theoretical approaches in paleobiogeography. As we move forward as a discipline, there are many promising avenues for paleobiogeographic research, many of which are under-explored or under-utilized, some of which are entirely novel that will allow integration of biogeographic, macroevolutionary, and paleoecologic patterns. Some of the most immediately productive avenues of paleobiogeographic research include investigating (1) the relationship between species ranges and speciation events/mode, (2) the relationship between shifting ecological regimes and range expansion and contraction, (3) the impact of interbasinal species invasions on both

community structure and macroevolutionary dynamics, (4) the mechanics of transitions between endemic to cosmopolitan faunas and local, regional, and global scales, (5) how ecology and geographic range impacts species extinction during both background and crisis intervals. These questions are of interest, not only to paleontologists, but to our colleagues in neontology and conservation biology as well. Understanding the impact of biogeographic changes in the past will help to better constrain the long term impacts of modern human-induced species invasions and habitat fragmentation.

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