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GEOGRAPHY AND EVOLUTION

The Geography of Evolution and the Evolution of Geography

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Abstract Insights into the geography of life have played a fundamental role in motivating major developments in evolutionary biology. The focus here is on outlining some of these major developments, specifically in the context of paleontology, by emphasizing the significance of geographic isolation and allopatric speciation, punctuated equilibria, and the Turnover Pulse Hypothesis to evolutionary theory. One of the major debates in evolution concerns the relative contributions of abiotic and biotic factors to macroevolution, and each one of these developments increasingly suggested that it was climatic and geologic factors, rather than competition, that played the primary role in motivating macroevolution. New technical developments, including in the area of Geographic Information Systems, allow continued detailed testing of the relative roles that biotic as opposed to abiotic factors play in causing evolution, and some of the work in this area will also be described.

Keywords Macroevolution · Biogeography · Punctuated equilibria · Turnover pulse · GIS

Introduction

It was Charles Lyell (1832) who argued for the relevance of organismic distributional information to the fields of biology and geology, and he invoked the famous dictum "As in space, so in time." Here, arguments for expanding that dictum to encompass both biogeography and paleontology, "Space and time," are presented. Biogeography is the discipline that focuses on reconstructing the history of biotas, and by biotas what is meant are groups of species that occur in particular regions. The discipline has a long and extensive history that extends well back into the eighteenth century and biogeographic research played a pivotal role in the development of evolution, particularly in the works of Wallace and Darwin (Brooks and McLennan 1991; Lieberman 2000; Morrone 2008; Wiley and Lieberman 2011). This research was particularly relevant because it considered how species' differentiation across geographic space became translated into evolutionary differentiation through time. Darwin himself in the introduction to the *Origin of Species* argues that it was biogeographic patterns and patterns in the fossil record that convinced him that evolution had happened, and the role of geography and paleontology in the development of Darwin's ideas has been considered in detail in the pages of this journal (e.g., Eldredge 2009a, b) so that will not be the principal focus here. Instead, the focus will be on some of the key developments in evolutionary theory post-Darwin (1859), especially in the area of macroevolution, and further how these involved more thoroughly and properly integrating geography into evolution through analysis of patterns preserved in the fossil record (Lieberman 2008). However, some brief background on the role of biogeographic patterns in convincing Darwin that evolution had happened is worthwhile. In particular, during Darwin's voyage aboard HMS *Beagle*, he recognized the existence of closely similar species separated by geographic barriers. For instance, in South America, there are two species of large flightless birds or Rheas. One occurs north of a large river in Argentina, the Rio Negro, whereas the other species occurs south of the river. Darwin came to learn of more examples on the Galapagos Islands including mockingbirds and also tortoises. Although he did not assert the evolutionary significance of this in his book *The Voyage of the Beagle* (Darwin 1839), he did in the

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Darwinian notebooks (Sulloway 1979; Barrett et al. 1987), where he argued that geographic barriers could serve to isolate populations of species, leading to differentiation.

Today, we refer to this style of speciation as geographic or allopatric speciation. This style of speciation is especially significant to evolutionary theory because if speciation is primarily allopatric, then the forces that produce geographic barriers play a big role in causing evolution. These forces principally involve episodes of geologic and climatic change. Notably, phenomena akin to allopatric speciation were described before Darwin's voyage on the *Beagle*; for instance, by Leopold von Buch in 1825, based on his work in the Canary Islands. Still, Darwin, along with Wallace, was one of the first to synthesize this pattern and recognize its significance (Lieberman 2000). It is somewhat interesting then that although this pattern helped convince Darwin that evolution had happened, he later came to de-emphasize allopatric speciation, particularly in Darwin (1859). There he held that rather than geographic isolation, it was primarily competition that led to the formation of new species. His emphasis shifted to a reliance on what is today called sympatric speciation to explain diversification and thus on a view that evolution is driven by competition rather than by climate change and geology (Lieberman 2008).

Reinstating Geography into Evolution

Following the publication of Darwin (1859), for a long time, most scientists tended to de-emphasize the role of allopatric speciation, although some including Gulick (1872), Wagner (1873), and Jordan (1908) did continue to assert its significance, such that climatic and geologic factors were not typically viewed as the primary factors motivating speciation. It was not until Ernst Mayr's documentation of the omnipresence of allopatric speciation, e.g., Mayr (1942, 1963) that allopatric speciation returned to the fore. Now, most neontological and paleontological studies continue to reiterate the notion that speciation is transcendentally allopatric (e.g., Eldredge 1971; Eldredge and Gould 1972; Wiley and Mayden 1985; Eldredge 1989; Brooks and McLennan 1991; Lieberman 2000; Coyne and Orr 2004; Rode and Lieberman 2005; Morrone 2008; Stigall 2010). Although Mayr did grasp the centrality of allopatric speciation, it took a while before the full macroevolutionary significance of it was recognized.

Punctuated Equilibria

Eldredge (1971) and then Eldredge and Gould (1972) conducted the research and made the theoretical insights that led to the recognition of the significance of allopatric speciation for paleontology and macroevolutionary theory. In a sense, it was reintegrating the proper role of geography into evolutionary theory in general, and speciation in particular, that allowed them to make key predictions about the nature of species and speciation in the fossil record. They recognized that most species throughout their history, often many millions of years, were stable and displayed what they termed stasis (Eldredge 1985). This stasis need not be obdurate, there could be subtle oscillations in morphology (Lieberman et al. 1995; Eldredge et al. 2005), but overall net stability prevailed. Further, evolutionary change was concentrated in geologically relatively short intervals that might represent 5,000 to 50,000 years. Based on applying the allopatric model, they recognized that change would appear relatively sudden in the fossil record and further would typically occur in narrow, peripheral environments along the margins of the species range. As such, usually it would be difficult to capture speciation in action in the fossil record. Instead, the appearance of a new species in the fossil record would usually represent migration of a population that evolved in allopatry. By contrast, widespread, abundant species, the species most likely to be preserved in the fossil record, should show little concerted change. The pattern of punctuated equilibria not only characterized the bulk of species preserved in the fossil record, but also very much went against the Darwinian notion that species should be changing slowly and gradually over millions of years across their entire range (Eldredge and Gould 1972; Eldredge 1985). On the one hand, the development of punctuated equilibria certainly did very much rely on correctly incorporating geography into evolution, but of course it did also rely on a more literal reading of the fossil record than Darwin promulgated. One of the main points in Darwin (1859) is that the fossil record is too incomplete to study evolution in detail. Simpson (1944) and Eldredge and Gould (1972) rightly rejected this view.

The Turnover Pulse Hypothesis

Another major innovation in macroevolutionary theory was Elisabeth Vrba's development of the Turnover Pulse Hypothesis (Vrba 1980, 1985, 1992). Eldredge (1971) and Eldredge and Gould (1972) in their formulation of punctuated equilibria did rely on allopatric speciation, but they specifically focused on Mayr's (1942, 1963) discussion of the concept whereby geographic isolation occurred when a population of a species dispersed over a preexisting geographic barrier. This is clearly an important mode of allopatric speciation (e.g., Wiley and Mayden 1985; Brooks and McLennan 1991; Lieberman 2000; Stigall 2010; Wiley and Lieberman 2011). However, when allopatric speciation transpires in this manner, it usually will involve only a single species at a time; and further, whether or not speciation happens depends to a major extent on the individual ecological characteristics of the organisms in the species. Vrba's (1980, 1985, 1992) innovation with the Turnover Pulse Hypothesis was that she recognized the significance of the fact that during intervals of climate change, the geographic ranges of many species would be affected simultaneously. She specifically focused on Neogene tropical mammal species that during times of warmth might have broad geographic ranges. As temperatures cooled, ranges would become more narrowly circumscribed and populations of many species would get isolated in small refugia. Some of these species would experience such profound range reductions that they would go extinct (the Turnover phase of her hypothesis). However, for those populations that persisted and stayed isolated in these refugia for long enough, they would diverge and eventually speciate (Vrba 1980, 1985, 1992) (the Pulse phase of her hypothesis). In this manner, several new species in the same region would evolve at roughly the same time. Further, these speciation events would be triggered directly by climatic change. The Turnover Pulse Hypothesis provided a means of extending punctuated equilibria from the single species case to the multiple species case.

There is an important connection in Vrba's work to developments in the area of vicariance biogeography. In vicariance biogeography, the emphasis is on using phylogenies to see if groups of species show similar or "congruent" patterns of evolution across geographic space (Wiley 1981; Brooks and McLennan 1991; Lieberman 2000; Morrone 2008; Wiley and Lieberman 2011). The value of this approach is that it emphasized developing techniques to rigorously analyze biogeographic patterns using phylogenies. Then, if similar patterns of evolution are found across geographic space, it suggests that changes in geology or climate motivated the macroevolutionary patterns in the group. If, by contrast, various groups of species that occur in the same region show different patterns of evolution across geographic space, it suggests that the individual ecological characteristics of species played the primary role in motivating diversification. Thus, vicariance biogeography provides a means of directly considering and testing the relative roles that geology and climate play as processes that motivate macroevolution. Vrba (1980, 1985, 1992) essentially extended vicariance biogeography directly into the realm of evolutionary theory by focusing on the significant role that climate change plays in causing evolution via the mechanisms of geographic isolation and allopatric speciation.

Quantifying Geographic Range to Make Macroevolutionary Insights

New insights into macroevolution focusing on the analysis of biogeographic patterns preserved in the fossil record have also been enabled through the application of Geographic Information Systems (GIS). These techniques make it possible to precisely and repeatably calculate the geographic range of individual species using locality information. This approach can be applied to modern species but also to fossil species as well. In the case of fossil species, first fossil distributions from various localities are plotted on a modern map in GIS. Then, through the use of the program PaleoGIS (Ross and Scotese 2000), the continents can be rotated back into the position they once were in when those fossil taxa were actually living (Fig. 1). One instance where such techniques have proven valuable is in showing the role that invasive species played in causing the Late Devonian biodiversity crisis (Rode and Lieberman 2004, 2005; Stigall 2010). Another instance where GIS has proven valuable in the analysis of geographic data from fossils is in studies looking at the role competition plays in macroevolution (Myers and Lieberman 2011). Darwin (1859), Dawkins (1976), and many others have argued that competition is a significant evolutionary force, yet evidence from the fossil record has always been limited (Gould and Calloway 1980;

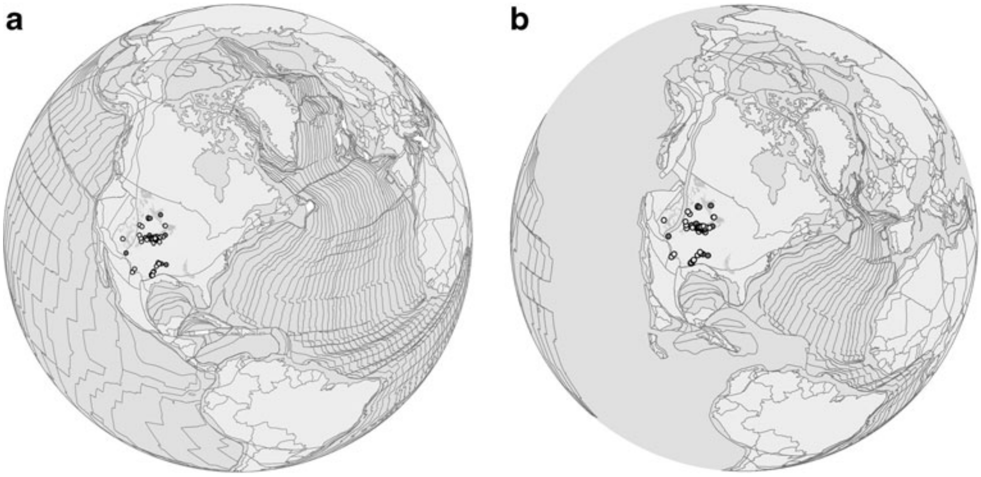

Fig. 1 Occurrence records for some Late Cretaceous marine vertebrates, a shark (*light gray*) and a mosasaur (*dark gray*), shown on a map of the modern world (**a**) and the Cretaceous world (**b**), from Myers and Lieberman (2011), used with permission

Benton 1996). GIS provides an excellent means to consider how the geographic ranges of species interact with one another through time. Myers and Lieberman (2011) used the GIS to consider the geographic ranges of several fossil marine vertebrate species from the Cretaceous Western Interior Seaway, a large, mostly tropical seaway running up through the center of North America (Fig. 1) that is the source of numerous, extensive fossil marine deposits. Myers and Lieberman (2011) specifically focused on whether there was any evidence for competitive replacement: a phenomenon where one species appears within another species' geographic range, its range expands, and it slowly and gradually drives the other species to extinction. They found no statistical evidence for competitive replacement. Instead, in the Cretaceous Western Interior Seaway, it was changes in the physical environment that appear to be the primary factors controlling changes in geographic distribution through time, and also the primary factors that cause species to become extinct (Fig. 2). Here, GIS confirmed the important role that the environment plays in influencing macroevolution and concomitantly the more limited role competition plays in that arena.

Conclusions

Patterns pertaining to the geographic distribution of organisms and patterns in the fossil record played a fundamental role in convincing Darwin and other scientists that evolution had happened, and they still play an important role today in providing insights into the evolutionary process. Prominent advances aiding progress in the field of biogeography since Darwin's day include a deeper understanding of speciation, discoveries in the area of paleontology and macroevolutionary theory, and the development of new methods for analyzing biogeographic data including phylogenetic approaches and approaches using GIS. One GIS-based methodology that figures to be especially important in helping to lead to future biogeographic discoveries in the area of paleontology is ecological niche modeling. This approach can be used to consider a variety of interesting biogeographic questions including ecological changes at speciation (Peterson et al. 1999), what abiotic and biotic factors control species ranges (Stigall and Lieberman 2006; Maguire and Stigall 2009), and also how species niches change through time (Dudei and Stigall 2010). Integrating these new methodological developments with

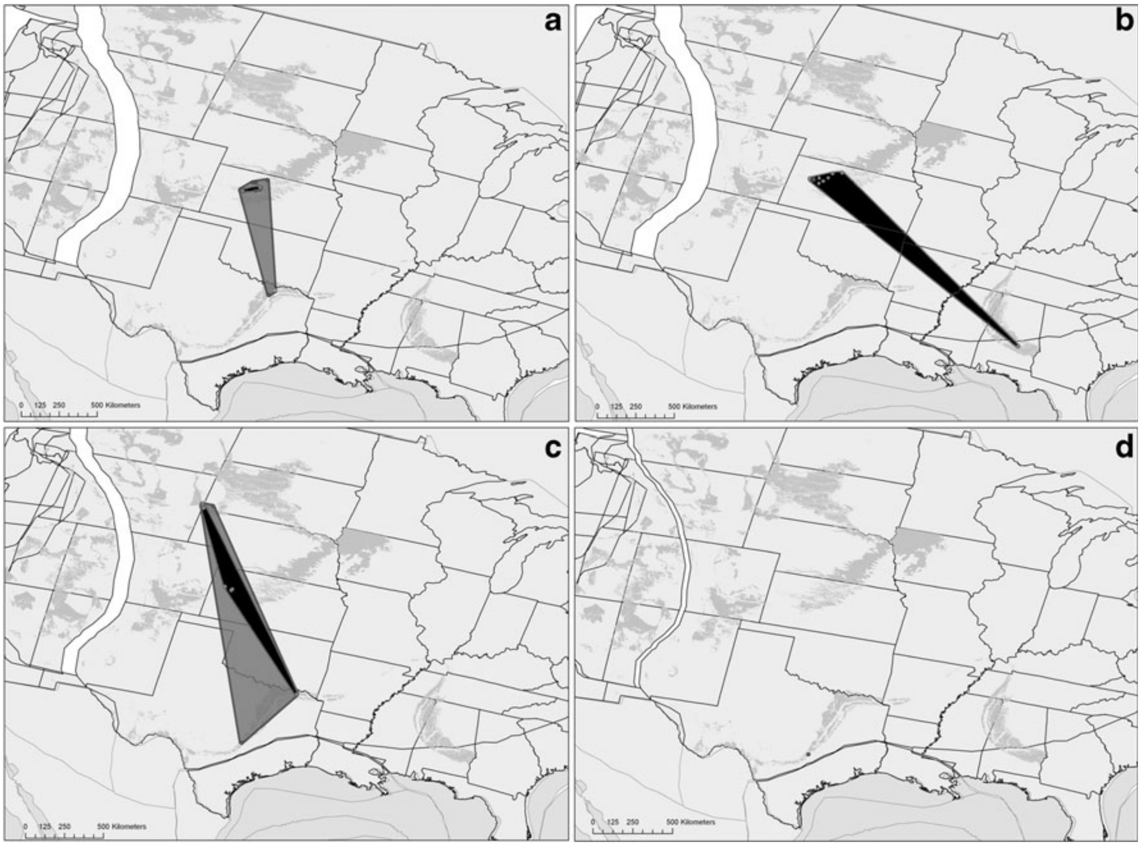

Fig. 2 Range reconstructions for marine vertebrate species from the Late Cretaceous showing how species distributions typically change through time. *Darker polygons* show the ranges of the mosasaur *Platecarpus* for different stages (**a**–**d**) of the Late Cretaceous. *Lighter polygons* show the ranges for the mosasaur *Tylosaur*. These ranges change through time but do not show a statistical association with one another and instead appear to be associated with changes in the environment, from Myers and Lieberman (2011), used with permission

important theoretical insights holds major promise for the future of biogeography and charts a pathway connecting past and future discoveries.

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