

# EMERGING SYNTHESSES BETWEEN PALAEOBIOGEOGRAPHY AND MACROEVOLUTIONARY THEORY

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Macroevolutionary theory is one of the fundamental contributions palaeontology has made to evolutionary biology. One of the key areas macroevolutionary theory has focused on is the role that geographic differentiation, and the factors that govern it, play in producing, or checking, evolutionary divergence. The focus on geographic differentiation provides a direct connection between theories of macroevolution and palaeobiogeographic patterns. In particular, many of the important developments in macroevolutionary theory, including punctuated equilibria and the turnover pulse hypothesis, involved incorporating geographic isolation and differentiation into evolution, and making predictions about how these factors should affect the topology of evolution; in effect, these theories considered the evolutionary impacts of various palaeobiogeographic processes including vicariance and geodispersal. Darwin's early musings on evolution, as expressed in the Darwinian notebooks, suggest that initially he too focused in an important way on what relevance the fossil record and biogeography had for evolutionary theory. Later, however, in '*On the Origin of Species* ...' his emphasis shifted away from biogeographic factors. Given the dynamic nature of climate and geology, and the important affects changes in these have on biological evolution, it suggests that palaeobiogeography is a discipline with important relevance for evolution in general and macroevolution in particular.

*Key words:* Palaeobiogeography, macroevolution, punctuated equilibria, turnover pulse, vicariance, geodispersal.

PALAEOBIOGEOGRAPHY is a field marked by important intellectual insights and developments; recently the field has shown signs of emerging insights and new growth. This positive trajectory can be ascribed to several significant developments. Chief among these is our growing knowledge of the fossil record, involving the publication of more detailed palaeobiogeographic studies (Mawson et al. 1998; Shi & Grunt 2000; Talent et al. 2001; Meyer-Berthaud et al. 2003; Meert & Lieberman 2004; Shi 2006). It is also related to an increasing emphasis on quantification in palaeobiogeography (eg. Shi 1993), expanding the precision and sharpening the interpretation of results. Coupled with this is the growth of phylogenetic approaches to biogeography and palaeobiogeography (Brooks & McLennan 1991; Lieberman 2000) that allow patterns to be related directly to evolutionary diversification. Ultimately, however, aspects of the growth of palaeobiogeography can be tied to the intrinsic nature of palaeobiogeographic data themselves. In particular, these are the geographic distributions of species (or other taxa) in the fossil record, thereby joining the discipline with another important research area, macroevolution.

## THE GEOGRAPHY OF MACROEVOLUTION

### *Punctuated equilibria*

Macroevolutionary theory is a fundamental contribution palaeontology has made to evolutionary biology. For example, punctuated equilibria (Eldredge & Gould 1972), the turnover pulse hypothesis (Vrba 1980, 1985), and species selection (Vrba 1984; Vrba & Eldredge 1984; Lieberman & Vrba 1995) were all developed either directly from analysis of the fossil record or at least benefited from palaeontological insights. One common thread that punctuated equilibria and the turnover pulse hypothesis share is they both posit that evolution in general and speciation in particular occurs in a geographic context. Punctuated equilibria was based on the recognition that speciation is allopatric *sensu* Mayr (1942, 1963). (Research documented in Brooks & McLennan [2002] continues to confirm that speciation typically occurs via allopatry.) Eldredge & Gould (1972) used this recognition to predict the general topology of evolution in the fossil record: the conditions that encourage speciation are small, geographically isolated populations; these populations will diverge relatively rapidly and by their very nature will be less likely to be preserved in the fossil record. Further, in the ab-

sence of geographic isolation, speciation and evolutionary divergence should not be expected.

In effect, geographic isolation becomes the force driving evolution. If geographic isolation is the motive force of evolution, the processes that initiate geographic isolation emerge as significant evolutionary mechanisms, and scientists need look no further than the geological record to find such mechanisms. Included would be tectonic and climatic change, which at times are coupled (eg. Hallam 1981a; Lieberman 2000).

It is interesting, or ironic, depending on your perspective, that geographic factors not only encourage evolutionary divergence at the species level: sometimes they act to promote evolutionary stasis. In particular, the differentiation of species into distinct geographic populations can serve as a mechanism that prevents evolutionary change, leading to net species stasis (Lieberman et al. 1995; Eldredge et al. 2005).

Darwin, in his early notebooks of 1837 and 1838 (Barrett et al. 1987), recognized the important role geographic isolation played in motivating speciation. In at least one place in these early notebooks he even suggested that isolation was more apt to occur in marginal environments, showing some parallelism to ideas on punctuated equilibria (Eldredge 2005: 134). This was partly based on biogeographic patterns Darwin recognized in the Galapagos and on the South American mainland (Grinnell 1974; Kottler 1978; Sulloway 1979; Richardson 1981; Lieberman 2000). Later, however, in *'On the Origin of Species ...'* Darwin (1859) de-emphasized geographic isolation and the geological or climatic processes that might cause it, viewing these mechanisms as subordinate to competition and natural selection. This was partly because he came to see island biotas, like those inhabiting the Galapagos, as depauperate and inferior to biotas living on larger land masses. For example, '(a)lthough I do not doubt that isolation is of considerable importance in the production of new species, on the whole I am inclined to believe that largeness of area is of more importance, more especially in the production of species, which will prove capable of enduring for a long period, and of spreading widely' (Darwin 1859: 105).

The erudite and hugely influential views of Darwin (1859, 1872) meant that the role of geographic isolation as an important evolutionary mechanism was downplayed and ignored by generations of evolutionary biologists. In effect, what the early authors who argued for the important role of geographic isolation in evolution, like Wagner (1873), Gulick

(1872), and Mayr (1942) ultimately accomplished was to keep Darwin's early, private views alive while reinstating them into the mainstream of evolutionary theory. Punctuated equilibria accomplished this, showing that Darwin's predicted pattern of evolutionary gradualism did not square with the actual details of the fossil record. Instead, the evolutionary motor – geographic isolation of small populations in marginal environments – would produce long periods of stasis in species punctuated by relatively rapid periods of change. A clear connection can be traced from Wagner (1873) to Mayr (1942, 1963) to Eldredge & Gould (1972), and ultimately this intellectual evolution generated a more accurate picture and better understanding of the way macroevolution happens: a view that corresponds better, in some respects, to Darwin's private musings of 1837–1838 than the views he developed in Darwin (1859, 1872). Punctuated equilibria, perhaps modern palaeontology's most significant macroevolutionary theory, was developed by squaring geography and evolution with patterns in the fossil record.

#### *Turnover pulse*

Eldredge & Gould (1972) did not explicitly dignify geological and climatic change as the primary processes that cause geographic isolation leading to speciation because this was not the focus of their paper. The emphasis on the control of climate and geology reached its macroevolutionary specification and fruition in Vrba's (1980, 1985) turnover pulse hypothesis which considers how the various components of biotas may evolve or go extinct in concert.

Vrba (1980, 1985, 1992) argued, based on examples from the Neogene of Africa, that numerous representatives of regional biotas (her focus was on tropical mammals) showed concerted pulses of extinction and speciation; these pulses were associated with climatic change. Deteriorating climatic conditions (relative to the preferences of tropical mammals) caused population size to decline and populations to fragment as they tracked smaller and smaller stretches of their preferred environment. The small isolated populations became more susceptible to extinction; also, because they were geographically isolated, they become subject to the very conditions that encourage speciation. In cases where geographic isolation is mediated by climatic or geological change, and leads to differentiation and speciation, the term 'vicariance' is used (eg. Brooks 1985; Wiley

& Mayden 1985; Brooks & McLennan 1991). (The usage of the term vicariance has a long and interesting history [see Croizat 1982 for discussion].)

Vrba's turnover pulse extends the single species emphasis of punctuated equilibria to a regional, biogeographic context; this regional approach came under Darwin's purview in his early writings (Darwin 1909) when he considered the evolutionarily distinct nature of a hypothetical fauna similar to the Galapagos and further speculated how the diversification of this fauna might have been driven by changes of sea-level (Lieberman 2000).

The turnover pulse is an important contribution to macroevolutionary theory and also is fundamentally linked to palaeobiogeography through the touchstone of vicariance. Patterns equivalent to those described using the original example of the turnover pulse have sometimes been referred to under the rubric of 'coordinated stasis' based on studies of the Palaeozoic of North America by Brett & Baird (1995) and others.

#### GEODISPERSAL, MACROEVOLUTION, AND THE FOSSIL RECORD

##### *Geodispersal, its significance, including an historical perspective*

Vicariance is not the only biogeographic process relevant to macroevolutionary theory. Just as geological and climatic changes can cause geographic barriers to form, leading to geographic isolation and vicariant speciation, sometimes geological and climatic changes cause geographic barriers to fall, allowing several taxa to congruently expand their ranges. Lieberman & Eldredge (1996) and Lieberman (2000, 2003) termed this process geodispersal. Recently, Halas et al. (2004) have used the term 'taxon pulse', after Erwin (1979) to refer to this same process. The potential problem with Halas et al.'s (2004) usage is that what Erwin (1979, 1981) had in mind when he used the term 'taxon pulse' was a taxon's adaptive shift from one habitat into another along an adaptive pathway (eg. Erwin, 1981: 175). Such changes could be caused by tectonic or climatic processes, but they could also be mediated by ecological mutualisms or coevolutionary dynamics (Erwin 1981). By contrast, the term geodispersal of Lieberman & Eldredge (1996) requires no assumptions about the adaptive basis for any change in geographic range, and considering such are often untestable in the palaeontological record, it may be apt to use a more theory neutral term.

Lieberman (2000, 2003) provided a long list of authors extending back to Lyell (1832) who had described phenomena similar to geodispersal. One important example of geodispersal missed by Lieberman (2000, 2003) that deserves amplification here is Hallam (1981a, b). Hallam was a pioneer in the rigorous analysis of palaeobiogeographic data and its application to study plate tectonics (see Lieberman 2003). He also was an important early proponent of a process akin to geodispersal. Hallam (1981b: 340) regarded vicariance and geodispersal (term not used) 'as equally important phenomena and two sides of the same coin. Thus, the creation of the Central American Isthmus and the Middle Eastern closure of Tethys promoted vicariance among marine organisms and (geo)dispersal among terrestrial organisms.' Also, one of the important themes considered in Hallam (1981a) was how the primary locus of biogeographic change can oscillate through time, shifting between plate tectonics and sea-level rise and fall, depending on the prevalent earth history regime. As the locus shifts it causes differences in the relative amounts of vicariance or geodispersal through geological time (Lieberman 2005). Rull (2004) and Hembree (2006) are other recent studies that emphasise the importance of considering both vicariance and geodispersal in palaeobiogeographic studies.

##### *Geodispersal and punctuated equilibria*

Punctuated equilibria posits that typically the appearance of a new species in the fossil record does not mark the species' evolutionary origin but rather its movement from a geographically restricted small population to a widespread, common species (Eldredge & Gould 1972). This expansion could occur by traditional dispersal (see Lieberman 2000) over a pre-existing geographic barrier or it could be mediated by a climatic or geologic change that effaced a pre-existing geographic barrier. A way of testing these alternative hypotheses would be to search for biogeographic congruence and investigate whether several other taxa concurrently expanded their geographic ranges.

##### *Geodispersal and the turnover pulse*

The turnover pulse was first developed by Vrba (1980, 1985, 1992) to explain evolutionary dynamics in Tropical Africa during the Neogene: a time of oscillating climate. It not only invoked a series of

congruent vicariance events in African mammals driven by climatic cooling; it also posits that because of periods of subsequent climatic amelioration these episodes will be followed by instances of geodispersal; multiple taxa will expand their ranges after geographic barriers to their free movement (including the absence of appropriate intervening habitat) fall.

It is noteworthy that these coupled episodes of vicariance and geodispersal will not always lead to speciation and extinction. Sometimes, particularly if climate is changing rapidly enough that vicariance and geodispersal follow closely on the heels of one another, habitat loss and geographic isolation does not persist for long enough to spark evolutionary divergence or extinction (Vrba 1995). In this case actually, the quickly coupled episodes of vicariance and geodispersal may produce a shuffling selective regime that acts to cancel out accrued divergence, leading to net evolutionary stasis in species (see Bennett 1990). It was described above for the case of punctuated equilibria how geographic factors can mediate both species divergence and stability: here we see evidence at a broader hierarchical scale that the biogeographic patterns mediating evolutionary stability and change of multi-species assemblies are conjoined. Thus, an understanding of biogeographic mechanisms can help explain what pushes forward, or holds back, evolutionary change.

*The possible connection between geodispersal, species invasions, and extinctions*

One additional area where geodispersal may be relevant to macroevolutionary theory is the extent to which episodes of geodispersal, when they bring new species into contact with one another, may trigger wholesale extinction. The answer to this question will partly devolve to the role of competition in macroevolution (see discussion in Gould & Calloway 1980; Vrba 1992; Benton 1996 and refs. therein). The Great American Interchange was long thought of as one such example (eg. Darwin 1859; Matthew 1915), although now the dynamics of the interchange seem more explicable as the result of the vagaries of changing climate (Vrba 1992). Still, it is also clear that today's biodiversity crisis is caused in no small part by invasive species, whose range expansions are mediated by our own species; these bring novel and naïve species into contact with one another, sometimes creating ecological interactions that cause dramatic population declines and extinctions. Similar dynamics may have occurred in other examples pre-

served in the Neogene marine fossil record (Vermeij 1978). At this point it remains an open ended question as to whether or not geodispersal may prove an important factor that precipitated extinctions preserved in the geological record. If ultimately such episodes prove to be important, it would provide another connection between macroevolution and palaeobiogeography.

CONCLUSIONS: PALAEOBIOGEOGRAPHY AND EVOLUTIONARY DYNAMICS

It is clear that important connections exist between several aspects of macroevolutionary theory and biogeography; one other fundamental palaeobiogeographic topic with macroevolutionary implications is the extent to which species modify their ranges through time. Coope (1979) has demonstrated that throughout the Pleistocene many species of still extant beetles underwent prodigious shifts in geographic range (see also discussion in Hallam 2004); the same is true of many other Pleistocene taxa (eg. Davis 1986; Huntley & Webb 1989). Species seem capable of profound modifications in their geographic range throughout their evolutionary history; this fact powerfully confronts studies of extant taxa and speaks to the importance of having the temporal context for changing geographic range that only the fossil record can provide. As Hooker (1853: xix) recognised '(t)he distribution of species has been effected by natural causes, but these are not necessarily the same as those to which they are now exposed.'

Because of the incompleteness of the fossil record it is of course true that for some cases, and for certain types of taxa, it is not always possible to determine how the geographic range of an extinct species changed through time, from its evolutionary origin to its extinction. However, there are a wealth of data preserved in the fossil record illustrating among species patterns of biogeography and macroevolution; in cases it may even be possible, especially in the Pleistocene, to discover patterns of palaeobiogeographic and evolutionary differentiation within individual species (eg. Polly 2003).

One thing that seems clear is there is a dynamism in the biological realm that is directly related to the dynamic nature of our planet's climate and geology (Lieberman 2005). At times this dynamism sparks diversification, at other times it prevents it; ultimately this reflects the important mechanistic coupling between macroevolution and palaeobiogeography.

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