

The evolution of large mammal communities: beyond biochronology

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Evolution is commonly studied at different levels, from genes to species. It has been questioned whether all these levels are actually real, although it now seems accepted by most scientific investigators that more than one level is actually targeted by selection. Intriguingly, despite the importance of biological interaction is relevant to the course of evolution (and to the level to which selection applies) the obvious locus for biological interaction, the community, has received little evolutionary attention by mammal paleontologists. Herein, we investigate the concept of a biochron, which is the approximation closest to a real community in the paleontological world, and its applications. Then, we offer some clues as to how to use biochrons for investigating community evolution, and explain why paleontological community evolution is a partly novel, highly promising field of research within the realm of paleobiology.

Introduction

Charles Lyell is known for his clear definition of the Eocene, Miocene and Pliocene epochs by counting the number of molluscan genera they contain which survive to the Recent. Biochronologic units thus were concerned with extinction dynamics from the very beginning. This implicitly evolutionary aspect of biochrons, an essential side that Lyell himself obviously had clear in his mind (Rudwick 1978), has been underestimated and partly unused since his time. However, another and possibly more explicit value of biochronologic intervals rose to prominence, to the advantage of everyday geological and paleontological practice. Biochrons are chronologic units of relative age. They have been con-

ceived, understood, and used as such for decades by most paleontologists, prominently including mammal paleontologists.

Although mammal paleontologists have a long tradition of placing vertebrate evolution in stratigraphic and biochronologic contexts, the term biochronology was rarely used prior to the 1970s when the application of radiometric dating became widespread and the distinction was made between radiochronology and biochronology as different aspects of geochronology (cf. Berggren & Van Couvering 1974). According to the original definition by Williams (1901), a biochron is “a time unit whose measure is the endurance of an organic character”. Based on this definition, Berggren and Van Couvering (1974) suggested the application of the term biochron for units of

geologic time that are based on paleontological data without reference to lithostratigraphy or rock units. Thus, in principle, the emphasis on mammal occurrences *in time rather than in rocks* distinguishes biochronology from other chronologic systems (Lindsay & Tedford 1990). Biochronology is an important concept for geochronology, but its use has been compromised by a history of diverse meanings assumed by different researchers, and by the fact that it has never been discussed in any stratigraphic code because of that “loose and ambiguous” application. Furthermore, biochronology is important to vertebrate chronology because the primary temporal units developed and applied by vertebrate paleontologists for correlation in terrestrial deposits are all biochronologic entities. These timescales are built in terms of conventional mammal biostratigraphic zones or land mammal ages (LMAs), as defined by Lindsay (2003: 222) “relatively short interval[s] of geological time that can be recognized and distinguished from earlier and later such units (in a given region or province) by a characterizing assemblage of mammals”.

Well before Williams’ definition, early attempts to define (and more importantly to use) land mammal biochrons trace back to Pareto (1865) who collapsed under the name Villafranchian, a group of Late Pliocene fossil mammal assemblages coming from the neighborhood of Villafranca d’Asti (northern Italy). The geographically and temporally limited attempt of Pareto was later greatly expanded upon. Locally, Azzaroli (1983) and Azzaroli *et al.* (1988) established a full biochronologic scheme for Pliocene and Early Pleistocene Italian mammal faunas by formalizing the Villafranchian mammal age (Rook & Martinez-Navarro 2010). On a larger scale, the crucial advance over early, locally-defined land mammalian biochrons *à la* Pareto was Mein’s (1975) introduction of continental-level biochrons for the Neogene of Europe, the so-called Mammal Neogene (MN) zones (which are often colloquially referred to as Mein zones). Since Mein’s monumental work in the 1970s, MNs have been reworked, expanded, and better defined (Bernor *et al.* 1996, Rössner & Heisig 1999, Agusti *et al.* 2001). In addition, the European Land Mammal Mega Zones (a later

development inclusive of the MN scheme) now go back to the Paleocene. Even more fundamental is the geographical expansion of the European example to North America (the NALMA system, Woodburne 1977, 1987, Woodburne & Swisher 1995), South America (Marshall *et al.* 1983, Flynn & Swisher 1995), Asia (Tong *et al.* 1995), and even Australia (Woodburne *et al.* 1985, Megirian *et al.* 2010), although the land mammal-based timescale on each continental landmass has its own history of development, reflecting the uniqueness of the records and the extent to which faunal succession has been resolved. A related term of choronofauna is different from biochrons. Whereas the former looks at the taxonomic composition of the fauna (and its change) as a whole, the difference between successive biochrons is delineated by the appearance/disappearance of specific taxa. Whereas this methodological difference is clear, the concepts of choronofaunas and biochrons are used interchangeably and often confounded, since they serve the same goal.

From the huge amount of work that led to the establishment of these timescales comes the intrinsic promise to one day create a global correlational scheme of mammal-bearing outcrops. Beyond pure biochronology, such a super-scheme would allow the study of the multifaceted, complex and partly independent evolution of mammalian clades, the history of their distribution, the fate of individual groups, the way they responded to environmental crises and to major tectonic events, and to the ongoing competition between ecologically similar lineages, or between predators and prey. These questions go far beyond the biochronologic schemes themselves, and the (practical) reason they were created to begin with. For instance, teasing apart the effects of abiotic and biotic factors on species temporal turnover is a classic of evolutionary biology, and one of the battlefields where gradualists and punctuationists meet (Van Valen 1973, Barnosky 2001, Raia *et al.* 2005, Benton 2009). Ironically, the better the biochronologic schemes become, the more Lyell’s original, evolutionary vein is relevant. Biochrons can be, and in fact increasingly are, used to understand the evolution of mammal communities (and hence of biodiversity itself [Fritz *et al.* 2013, Diniz-Filho *et*

al. 2013]), bridging the gaps between the many professions mammalian paleontologists happen to practice.

How many professions are there?

We are not aware of any raw data on this, nor have we set up an experiment, yet we are convinced that most vertebrate paleontologists perceive the existence of different disciplines within their own field. A dense fossil record and literally thousands of living relatives to draw upon is a commodity that a paleontologist working on either dinosaurs, birds, squamates, acanthodians or any other group besides mammals simply does not have access to. Most vertebrate paleontologists are in fact systematists, and others (a minority) are paleobiologists. The good news is that these two broad categories cut across the vertebrate classes. Yet, it takes mammals to be a biochronologist in vertebrate paleontology. Sadly though, although mammalian biochronologists are well aware of (and some in fact are) systematists as well, few of them are paleobiologists *tout court*. The reason for this is quite obvious: biochronology requires a good deal of purely sedimentological knowledge, and the latter comes with geology classes. In fact, whereas many paleontological systematists and paleobiologists have a zoological background (e.g. Alfred Romer and Elizabeth Vrba) most mammalian biochronologists have a degree in geology or are otherwise keen on sedimentology (a few notable exceptions are geology-trained paleobiologists with an inordinate fondness for narrative writing, consider Björn Kurtén for mammals, and also of George G. Simpson and Stephen J. Gould as broader based paleontologists). In this regard, it is not surprising that many mammalian biochronologists are, in a sense, more closely connected to other, non-vertebrate paleontologists, such as paleontological stratigraphers, than most fellow vertebrate paleontologists are. Although presented in a simplistic fashion and therefore limited in scope, we believe this complex situation in part explains why mammalian biochrons parted ways with Lyell's original evolutionary connection, and mammalian paleobiology, although vivid

and productive over the years to the extent of locating paleontology within the Modern Evolutionary Synthesis via Simpson's *magnus opere* in the 1940s and 1950s (Simpson 1944, 1949, 1953) usually has little to do with biochrons. We believe the quest for this missing link can now be embraced, that this is timely, and that we have a lot to gain from bridging the gap.

Evolution above the species level, and at the community level

Richard Dawkin's selfish gene theory (Dawkins 1976) exacerbated the clash between the adaptationist, gene-centered view of evolution and the importance of selection at the level of species (and above; Gould 2002) with which paleobiologists generally feel more comfortable. After early collisions, it now seems accepted that species selection is real, and empirical observations bear out this conclusion (Jablonski 2008). Regardless of whether species selection has much to do with the dynamics of diversification, it is important to community evolution (where "community" for a mammalian paleontologist can be equated with the species in a biochron).

To an ecologist, the evolutionary effects of biological interactions (where the field of interaction is the community) are obvious. For instance, species body sizes may adapt to the presence of similarly-sized competitors, leading to a pattern of evenly spaced body sizes within a subset (guild) of the community, restricted to species competing for the same resources. This pattern, known as community wide character displacement, is an active research field in ecology (Dayan & Simberloff 2005, Meiri *et al.* 2011). Adaptation in the presence of strong competition is not always possible, though, and the poorer competitor often goes locally extinct (Grinnell 1904, Clayton & Bush 2006). Extinction via competitive exclusion is, in fact, one of the multiple forms of species-level selection (or species sorting, that is the term many use). Unfortunately, though, evolutionary time is usually longer than ecological time. That is, since the effects of species selection (e.g. on diversification dynamics) are evolutionary in principle, it takes the study of communities at an evolu-

tionary scale to fully understand how biological interactions affect diversification dynamics. As David Jablonski clearly put it (Jablonski 2008): “The fields of paleontology, comparative phylogenetic analysis, macroecology, and conservation biology are rich in examples of species sorting, but relatively few instances have been well documented, so the extent and efficacy of the specific processes remain poorly known. A general formalization of these processes remains challenging, but approaches drawing on hierarchical covariance models appear promising. Analyses integrating paleontological and neontological data for a single set of clades would be especially powerful.”

In our view, biochrons (defined as a distinctive assemblage of potentially interacting species with a demarcated temporal and geographical extent) provide the study of community evolution with a profitable reference unit. Surprisingly, though, as we have pointed out above, this possibility has been little explored in the past.

Jablonski claimed that macroecology (i.e. the study of major patterns in trait and geographical distribution of species within clades; Brown 1989, Gaston & Blackburn 2000) rightfully stands within the discipline, providing examples for species selection. We attach special importance to macroecology in the present context for one specific reason (which is operationally and philosophically relevant to the use of paleontological data to understand species selection processes, and ultimately, diversity dynamics) that is: macroecology has the geographical dimension. We argue that this dimension has usually been given little attention by paleobiologists, and that this partial ignorance has impeded rethinking and reusing biochrons in an evolutionarily-oriented context. Why does geography matter? Because when a species disperses (on a paleontological time scale), either to track its preferred habitat in the wake of climate change, or to profit from an ecologically vacant space left by a vanished competitor, it will encounter other species, will interact with them, and both the movement itself and the outcome of these interactions will determine its fate, i.e., its survival, and ultimately the timing of its extinction. From a phylogenetic perspective, the fact that phylogenetically related species possess similar traits,

share key innovations for the most part, and have ecologically similar requirements, means that the geographic dimension will affect the fate not just of single species, but of entire clades, their survival, and their likelihood of diversifying. Ultimately, the geographic dimension interacts with community level processes to determine the evolution of traits, and diversification parameters for entire clades. Whereas this has received little attention in the paleobiological field, community ecologists are well aware of these effects, which they started to study at least a decade ago (Webb *et al.* 2002, Kraft *et al.* 2007). Community phylogenetics provides fundamental insights into the phylogenetic diversity of communities and its evolution (Faith 1992, Cavender-Bares & Wilczek 2003). Crucial to the field of paleobiology, community phylogenetics expands the classic question of species temporal turnover (which is a description of a pattern) towards the phylogenetic dimension, showing which clades thrived and where, and through which traits, which is a description of the process of turnover in addition to the pattern itself (Raia 2010).

The PCOM experience

We aspire here to explain why community evolution matters to paleobiology in the broadest sense. We contend that biochrons (once their geographic dimension is recognized) are the fundamental unit of reference: they are the community for a mammalian paleontologist. But which biochrons (or which definition thereof) are the most appropriate? To a paleobiologist, what matters is a coherent assemblage of species that conceivably interacted to an extent, over a defined time span (Tedford 1970, Lindsay 2003, Palombo & Sardella 2007). This may be linked to stratigraphic intervals (Salvador 1994, Ivany & Schopf 1996), yet it clearly calls for biochrons that are not defined by the appearance/disappearance of specific taxa, but on whole-(taxonomic) list comparisons of different time/geographic intervals. In the latter context, paleontological communities have been shown to possess some of the properties of extant communities, such as ecosystem resilience (the ability to resist intermediate levels of disturbance), which in the pale-

ontological literature is known as coordinated stasis (Ivany & Schopf 1996, Brett *et al.* 2009, but *see* Alroy 1996). To a mammalian paleobiologist, biochrons may serve this same purpose.

In theory, the geographical limits of a biochron are one of its components (Tedford 1970). On practical grounds, though, these geographic boundaries are vague, and biochrons are often given temporally non-overlapping distributions, which means that they rarely diverge geographically in contiguous areas (e.g. a continent) although they should in principle do so. This makes biochrons very like stratigraphic biozones (assemblage zones, cf. De Giuli *et al.* 1988) or chronofaunas, and thus less likely to be used in an evolutionary sense. This is possibly linked to the geological background of biochronology as a discipline. As we noted above, it is likely that most biochronologists are simply satisfied with temporally non-overlapping biochrons. Is there any way to break this fourth wall? To do this it takes some specific metric to identify taxonomically distinct assemblages, geographic references for the fossil sites under scrutiny, and, perhaps more importantly, numerical dating of the sites. The reason for the latter is not intuitive and requires comment. Without numerical dating, fossil sites are clustered on the basis of their taxonomic resemblance and nothing else. If taxonomic composition changes over a specific geographic extent (which is obvious as soon as one thinks of living communities), biochrons will include the distribution of species from one extreme to the other of their geographic distribution. This means that biochrons without numerical dating of the fossil sites can be strongly diachronous (Alroy 1998), which negates the geographic dimension of taxonomic turnover (akin to beta diversity in ecology). To remedy this problem absolute dating is necessary. Absolute age estimates are notoriously rare in paleontology. Fortunately, this limitation can now be overcome by at least two different statistical approaches: Alroy's ML AEO (Alroy 2000), and spectral ordering (Fortelius *et al.* 2006, Puolamäki *et al.* 2006).

We took all of the above into account to attempt a potential solution in producing the paleocommunity (PCOM) and Eurasian paleocommunity (EA PCOM) systems (Raia *et al.* 2005, 2006b, 2009). PCOM is a group of fossil

sites which form a statistically distinctive group in terms of its taxonomic component. Once fossil sites are numerically dated via ordination (Alroy 2000, Fortelius *et al.* 2006, Puolamäki *et al.* 2006), PCOM (which equates to a biochron in our evolutionary-oriented definition) has a temporal limit (defined by the youngest and oldest site it includes) and a geographic distribution (defined by the geographical coordinates of the sites it includes). The good news with PCOMs is that they are statistically similar to living communities in terms of species body size frequency distribution and abundance distribution (Raia *et al.* 2006a, Carotenuto *et al.* 2010), and were proved to be very successful in terms of studying the evolution of mammalian communities from the Pliocene to the Recent (Meloro *et al.* 2007, 2008), suggesting that once biochrons are conceptualized in evolutionary terms they will help bridge the gap between paleontological and neontological theories and data in understanding the evolution of biodiversity in the broad sense. The bad news is that since PCOMs do have a temporal distribution, they are essentially different from living communities. This means that although the study of community evolution could be approached by using PCOMs, community evolution is already present *within* PCOMs. This is potentially problematic and must be kept in mind while PCOM, units of coordinate stasis or any other ecological-evolutionary concept of biochron is used.

Communities and climate change

The world is living a moment of dramatic change, if not the sixth mass extinction itself (Barnosky *et al.* 2011, 2012). While humans are at least partially to blame for this havoc, the current biodiversity crisis is mostly about climate change, and what happens to species in the wake of change. Mammalian paleontologists are the established experts on long-term effects of climatic change on species distribution and evolution. And they have provided a wealth of consistent information on the subject matter. Individual lineages and communities of mammals can now be used to understand the evolution of terrestrial biomes, and their fates (Fortelius *et al.* 2002,

Fortelius & Zhang 2006, Damuth & Fortelius 2001, Eronen *et al.* 2009, Liu *et al.* 2009, Passey *et al.* 2009, Eronen *et al.* 2010a, 2010b).

Interest of mammalian paleontologists in the relationship between climate change and mammalian evolution is not new. What is new, and we feel most promising, is the richness of information and theories that mammalian paleobiologists have realized from joining their interests with conservation biologists, in the attempt to understand the causes biodiversity loss. As the world's biota are responding to the harmful effects of biotic homogenization (Olden 2008), habitat loss and degeneration (Novacek 2001), and human overexploitation of resources, having first-hand information on what effects these phenomena (or some of them) produced in the past is crucial to the proposal of possible remedies for the current biodiversity crisis. On the one hand, humans have been shown to be the fiercest over-killers of them all (Alroy 2001), and prey species were little equipped to deal with our technological advancements (Gittleman & Gomper 2001). Further back in the past, the history of mammalian faunas can now be correlated with human dispersal and evolution itself, in order to gain understanding of human/large mammal interaction dynamics (Turner 1984, Arsuaga *et al.* 1993, Fernández-Jalvo *et al.* 1999, Eronen & Rook 2004, Lordkipanidze *et al.* 2007, O'Regan 2008, Rodríguez-Gómez *et al.* 2013). Having this information on hand means understanding what the tempo and mode of species survival were in the past. It is clear to conservationists that acting to save threatened species in isolation is often bound to fail, because species are part of the community they live in and interact with (Nicholson & Possingham 2006). Conservation biologists are relying more and more on the fossil record (e.g. McCallum 2007, Diniz-Filho *et al.* 2013), and we feel that mammalian paleontologists should be scientifically keen and morally obliged to work alongside conservation biologists in the attempt to ameliorate the current biodiversity crisis.

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