



Going south: Latitudinal change in mammalian biodiversity in Miocene Eurasia



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ABSTRACT

For palaeontologists, the challenge is to reconstruct biodiversity patterns of the past. Mammal richness in grids is used to assess the stability of biodiversity hotspots and document changes over time in Europe for Mammal Neogene units 3 to 11 (19.5 to 7.6 Ma), early to late Miocene. The maps clearly show the patchiness of the fossil record. As the Miocene was an eventful epoch with severe environmental changes, Europe slowly became drier, and more seasonal, both in temperature and precipitation. From the early to middle Miocene an area of high biodiversity moved from higher to lower latitudes, culminating in one of the most remarkable hotspots in the history of mammals: the early late Miocene (Vallesian mammal stage) faunas from the Vallès-Penedès (Catalonia, Spain). Remarkably, the surrounding areas did not exhibit similar richness. During the subsequent Vallesian turnover event (~9.7 Ma), the large and small mammal distribution became more equitable and the hotspots less prominent. The richest area was found in the periphery of the humid Miocene ecosystem, which experienced species influx from the drier south. The southward shift was a result of the expansion of the humid area with subsequent closed environments and related mixing of ecosystems, coming to a halt in the late Miocene, when all of Europe became equally open.

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1. Introduction

Biodiversity is not equally distributed in time and space. While some areas contain only a few species, others have a remarkably high number of taxa. The latter are called biodiversity hotspots. These hotspots, however, are not stable (Renema et al., 2008). As the Earth and its climate change, so does the distribution of flora and fauna.

Relating to the current biodiversity crisis (IPCC, 2007; Dirzo et al., 2014), a major goal for many palaeontologists is reconstructing past diversity. Enormous quantities of information about fossil animals and their environments are stored in numerous databases. The challenge is to recognize non-random patterns in these data. Biologists focus on areas with high species diversity, or high richness, and view these hotspots as the prominent places for nature conservation. Historical data can show how hotspots came to be and, more importantly in these days of crisis, how they came to their demise. To study these areas of high richness, they first have to be identified, followed by the reconstruction of dispersal patterns by tracking their movements. For a better understanding of the link between climatological and distributional changes in the Miocene, insight into the processes behind hotspot

formation and termination is needed. In this paper, mammal diversity (genus richness) of the European Miocene is reconstructed.

The Miocene (23.0 to 5.3 Ma) was a turbulent time, marked by major faunal turnovers and climate changes. During this epoch, land masses assumed their present configuration and modern mammal groups were established. The first hyenas, bears and dogs arose, and primitive antelope, deer and giraffe appeared in Eurasia, together with the first modern horses and higher primates (Behrensmeyer et al., 1992). Temperatures were high during the Mid-Miocene Climatic Optimum, with a lower limit of the mean annual temperature (MAT) of 17.4 °C (Zachos et al., 2001; Böhme, 2003; Mosbrugger et al., 2005; Sun and Zhang, 2008; Merceron et al., 2012), followed by the Mid-Miocene Cooling, characterized by a dramatic drop in the MAT of probably more than 7 °C to temperatures around 15 °C. This drop can be attributed predominantly to a decrease of more than 11 °C of the minimum cold months's temperature (Van der Meulen and Daams, 1992; Zachos et al., 2001; Böhme, 2003; Shevenell et al., 2004; Lewis et al., 2008).

Europe was also affected by major tectonic events, such as the uplift of the Alps and other mountain ranges. The uplift of the Tibetan Plateau changed atmospheric circulation, which caused increased seasonality in Eurasia in the later parts of the epoch (Agustí et al., 1997; Broccoli and Manabe, 1997; Van Dam, 2006; Jiménez-Moreno et al., 2010). The closure of the Tethys Ocean in the east, at the end of the early Miocene, provided a migration route to and from Africa, the so-called

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Gomphotherium landbridge (Rögl, 1999; Harzhauser et al., 2007a). The palaeogeography of Europe continued to change, particularly as a result of the developments in the Paratethys (Rögl, 1999; Popov et al., 2006; Harzhauser and Piller, 2007; Harzhauser et al., 2007b). The last dramatic change in the Miocene map of Europe came at the Messinian (7.2 to 5.3 Ma), as most of the Mediterranean Basin disappeared during the salinity crisis (Rögl, 1999; Agustí et al., 2006; Popov et al., 2006; Van der Made et al., 2006; Krijgsman et al., 2010).

Due to changing palaeogeography, Europe experienced, besides the faunal exchange with Africa (e.g., Proboscidea), also exchange with both Asia (including Cricetodontinae, Murinae and Cricetinae) and North America (e.g., *Anchitherium*, *Hippotherium*). It has been long since recognized that Eurasia contains different bioprovinces, with a varying degree of similarity (Bernor, 1984; Bernor et al., 1996; Maridet et al., 2007; Casanovas-Vilar et al., 2010). In addition, a latitudinal gradient influenced the distribution of at least some mammal orders, such as the insectivores (Furió et al., 2011).

The overall trend in the Miocene of Eurasia can be characterized as a long-term shift towards progressively drier, more seasonal conditions and open vegetation (Broccoli and Manabe, 1997; Barry et al., 2002; Van Dam, 2006; Van Dam et al., 2006; Stromberg et al., 2007; Eronen et al., 2012). According to Van Dam et al. (2006), this was the result of a southward extension of the moisture belt, followed by retreat to the north. Body weight distributions of late early to middle Miocene (ca. 17 to 14 Ma) mammalian communities indicate that a strong latitudinal gradient existed during this warm, almost subtropical, period (Costeur and Legendre, 2008). The Iberian Peninsula had an arid climate and open environments at this time, whereas more closed to dense forest and a very humid climate progressively occurred towards the north (Maridet and Costeur, 2010). Other studies have postulated a precipitation latitudinal gradient already present in the late early to early middle Miocene (Jiménez-Moreno and Suc, 2007; Furió et al., 2011). This means that, with the north–south humidity gradient, focusing on only higher or only lower latitudes will not show much change. In southern Europe it mainly continued to stay dry, while in northern Europe the wetness persisted (Böhme et al., 2006). Therefore, the focus of this study is Eurasia through time, to detect the subtle changes in the middle latitudes, which show the effects of changing distribution of the southern dry area.

The New and Old Worlds (NOW) database is the leading repository of information concerning Neogene age fossil mammals and provides a basis for reconstructing biodiversity patterns of the past (Fortelius, 2013). Even though a correlation between the observed richness and the number of localities has been reported by previous studies based on various versions and subsets of the NOW database (Peláez-Campomanes and Van der Meulen, 2009), this resource gives the best coverage to get as close as possible to a true overview of the dispersal patterns of Miocene mammals in Europe.

The analysis of patterns and trends in past diversity always has to deal with the unwanted biases inherent to the nature of the fossil record and methodologies. A common bias is uneven sampling, where richer or more intensively sampled sites or time intervals contain more rare taxa and thus show a higher richness. A peak in data quality could lead to an overestimation of the recorded richness (Casanovas-Vilar et al., 2014). To assess such biases, robust diversity measures are needed, taking into account abundance, sample size and the probability of finding a certain taxon at a specific site (Barry et al., 2002, 2013; Van Dam, 2006; Casanovas-Vilar et al., 2014). The availability of deposits of a certain age also provides a bias, this is however an integral part of the fossil record.

Even though there is a good understanding of the development of mammalian communities in the Eurasian Miocene (Fortelius et al., 1996; Eronen et al., 2009; Ataabadi et al., 2013), less effort has been taken towards the quantification of mammalian faunal developments. With the present availability of better tools and information, now is the time to more precisely explore, quantify, and illustrate these patterns.

Here, the possibilities of presenting richness in grids were explored in order to examine the stability of biodiversity hotspots and document changes over time.

2. Material and methods

2.1. Dataset

In this paper, the terms biodiversity, mammal diversity and richness are defined as genus number. A single locality cannot give a complete overview of the biodiversity in a particular period. Therefore, in order to be able to combine data from an area, rather than from single localities, a large set of fossil mammal data was downloaded from the New and Old Worlds (NOW) database (Fortelius, 2013).

The dataset contains both large and small mammals and consists of over 13,000 specimens (4694 large and 8544 small) from 1219 localities. Small mammals encompass the orders Chiroptera, Chrysochloridea, Eulipotyphla, Hyracoidea, Lagomorpha, Macroscelidea and Rodentia as appearing in the NOW database. The large mammals encompass the orders Artiodactyla, Carnivora, Condylarthra, Creodonta, Embrithopoda, Marsupialia, Perissodactyla, Pholidota, Placentalia, Primates, Proboscidea, Ptolemaiida and Tubulidentata. All were identified to the genus level, with a total of 557 genera (307 large and 250 small).

Even though collection techniques for large and small mammals differ, as does the accuracy of taxonomic identification (Alroy, 2003), they are expected to react to the same signals, for example in response to climatic or tectonic changes. Therefore, micro- and macromammals are analysed both separately and collectively. Compiling the dataset, several choices concerning taxonomic level, time control and (other) biases had to be made.

2.2. Taxonomic level

While ecological interpretations based on genera or higher taxonomical groups are said to be unreliable (Martín-Suárez et al., 2001), and ecological preferences may not have been the same for all species in a genus (Casanovas-Vilar and Agustí, 2007), species level analyses are likely to introduce more noise. Biodiversity estimates based on species, for example, can be inflated because of false or unrecognized synonymies (Alroy, 2002, 2003). Alroy (1996, 2003) compared genus and species level results of his diversity analysis of North American mammalian palaeofaunas, concluding that the genus level data are more taxonomically robust and preserve much of the same signal as the species level data. Genus is the lowest taxonomic level to which specimens are typically identified (Forcino et al., 2012), and genus assignments have more consensus than species determinations (Peláez-Campomanes and Van der Meulen, 2009).

A good indicator of how well the fossil data reflects the actual mammal community is completeness (“the proportion of taxa that have left some fossil record” (Foote and Raup, 1996)) is not only higher for small mammals, but for genera as well (Alba et al., 2001). Alba et al. (2001) stated that the mammalian fossil record from the Neogene of the Iberian Peninsula is very complete, as their calculations showed it captured 77% at the specific, and more than 90% at the generic level. Although the large mammal record of the NOW database seems to be biased by sampling effort at the metacommunity level, as well as at the locality level, the small mammal record is considered to be mostly homogeneous (Peláez-Campomanes and Van der Meulen, 2009). Taking all of the above into account, all analyses were performed on the genus level.

2.3. Biogeography and chronology

Mammal point data at the genus level were divided into grid cells, squares of $1.5 \times 1.5^\circ$ (ca. 150×150 km at the equator) and plotted using both a GIS programme designed by the Naturalis Biodiversity Center, Leiden, namely NaturalisGrid and R (R Core Team, 2014), with

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