



Going south: Latitudinal change in mammalian biodiversity in Miocene Eurasia

P.A. (Anneke) Madern ^{a,b,*}, Lars W. van den Hoek Ostende ^a

^a Naturalis Biodiversity Center, Room C01.10, P.O. Box 9517, 2300 RA, Leiden, The Netherlands

^b Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Barcelona, Spain



ARTICLE INFO

Article history:

Received 11 August 2014

Received in revised form 4 February 2015

Accepted 11 February 2015

Available online 18 February 2015

Keywords:

Neogene

Miocene

Vallesian

Mammals

Europe

Biodiversity

Biogeography

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.

© 2015 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

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

* Corresponding author at: Naturalis Biodiversity Center, Room C01.10, P.O. Box 9517, 2300 RA, Leiden, The Netherlands. Tel.: +31 71 751 9642; fax: +31 71 568 76 66.

E-mail address: anneke.madern@naturalis.nl (P.A.(A.) Madern).

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, Chrysocloridea, Eulipotyphla, Hyracoidea, Lagomorpha, Macroscelidea and Rodentia as appearing in the NOW database. The large mammals encompass the orders Artiodactyla, Carnivora, Condylarthra, Creodonta, Embriopoda, Marsupialia, Perissodactyla, Pholidota, Placentalia, Primates, Proboscidea, Ptolemaida 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

packages 'raster' (Hijmans and van Etten, 2012) and 'maptools' (Lewin-Koh and Bivand, 2012). Grouping in this manner makes the analysis more conservative, since multiple-locality complexes may otherwise bias the results (Jernvall and Fortelius, 2002).

Since western Europe is one of the most intensively studied areas in mammalian palaeontology, this area was chosen and extended for a better overview of longitudinal (between 10° W and 50° E) and latitudinal (between 15° to 55° N) distribution changes (Fortelius et al., 1996, 2002, 2006).

This study encompasses eight successive biochronological units; Mammal Neogene units 3 to 11 (19.5 to 7.6 Ma) (Mein, 1975). These MN units span the interval early to late Miocene, a period which has been sampled homogeneously and is well-studied (Peláez-Campomanes and Van der Meulen, 2009). Mammal Neogene units represent varying time spans. The definition is based on (1) faunal associations, (2) first appearances and (3) last appearances of both large and small mammals (De Bruijn et al., 1992; Steininger et al., 1996; Mein, 1999; Steininger, 1999; Agustí et al., 2001).

2.4. MN system

The definition of the time intervals and therefore varying lengths is a complicating factor. The criteria for defining MN units are mainly based on the first or last appearance of certain taxa, which leads to higher origination and extinction rates at MN boundaries (Agustí et al., 2001; Casanovas-Vilar et al., 2010). The MN system contains 17 units of different lengths, varying between 0.5 and 3.0 Myr (e.g., MN 3 is more than twice as long as MN 4). The different unit durations pose a problem for analyses of diversity because longer units are expected to contain more species than shorter units. However, MN 6, 7 + 8, 9 and 10 have similar lengths and obviously non-similar diversities. Differences between bioprovinces, relating the MN units to the marine record and spatial diachrony across Europe, further complicate matters (Van Dam et al., 2001; Gómez Cano et al., 2011; Van der Meulen et al., 2011, 2012; Ataabadi et al., 2013).

There is need for a revision of the biochronological framework for the European Miocene (Costeur et al., 2007) or even for an independent chronology, excluding biochronology altogether (Domingo et al., 2007; Ataabadi et al., 2013). Unfortunately, this is not yet possible. A new (bio)chronology asks for better dated records in order to use absolute dating instead of a relative scale such as the MN system (Domingo et al., 2014).

A number of criteria for undertaking the analyses were applied. Localities were excluded when they (1) could not be assigned to the temporal span of a single MN unit or (2) lacked geographic positional data (such as coordinates). For the entry/exit events, that is, first or last occurrence of a taxon, the maximum or respectively minimum age was used. In addition, all age assignments were converted to their corresponding MN unit, i.e. Mammal Neogene Equivalents (MNEQs), which are based on MN unit correlation scheme of the NOW database (Steininger et al., 1996; Ataabadi et al., 2013). Uncertain genus determinations were omitted from the study. No exclusions based on the number of taxa per locality were made, as, according to Ataabadi et al. (2013), the number of taxa used does not affect the spatial geographic patterns.

2.5. Bias

A common problem with palaeontological data is the unevenness of the fossil record. According to Alroy (2010), most counting methods have severe biases that can only be resolved using occurrence data rather than presence/absence data. However, data on relative abundances of taxa are only scarcely available for localities, as they have either not been recorded or are not comparable due to different sampling methods. Sampling biases could result in artificial hotspots. One can attempt to remove some of the bias by subsampling records. This has,

however, a few disadvantages. Subsampling reduces the number of records and cannot correct for unsampled areas. Also, locally dense records might be a true reflection of the relative suitability of the habitat.

To assess the bias in the data, the correlation between diversity and sample size was computed for small and large mammals, both separately and combined. Barry et al. (2002) investigated the relationship between the number of specimens and the number of events, by calculating the correlation between sample size per interval and the number of events, that is, first (FO) and last (LO) occurrences. They found that a correlation between interval sample size and number of events indicates a bias, casting doubts on the truth of turnover events (Badgley and Gingerich, 1988). To eliminate or at least minimize the bias' effects, the number of specimens should be taken into account. As the NOW provides presence-absence data, this is not exactly possible, consequently the number of genus records is taken as sample size. Relationships between the number of events, the sample size and the richness were calculated.

3. Results

3.1. Biogeography and biodiversity

The maps (Fig. 1a–h) show the patchiness of the fossil record during the Miocene. However, despite this irregularity, a pattern appears of an area of high richness moving from high to lower latitudes through time.

The shifting hotspot is best visible from the early to middle Miocene (MNEQ 3 to 7 + 8, Fig. 1a–e). Starting in the northern parts of Europe, it slowly travelled southwards. During MNEQ 3, the highest numbers per grid cell were in Germany and the Czech Republic, but maximum numbers did not exceed 65 genera. In MNEQs 4, 5 and 6, the biodiversity rose through Europe, in Germany, as well as France, but was still concentrated around Germany and Austria. After reaching a climax of 120 genera in MNEQ 7 + 8 in France, MNEQ 9 had the most southern hotspot in Catalonia, Spain, with 95 genera (Fig. 1f).

Following the middle to late Miocene faunal turnover that marks the beginning of the Vallesian mammal stage (Steininger et al., 1996), the diversity in the Vallès-Penedès basin increased. The biodiversity peak was relatively short-lived as the species number decreased dramatically halfway through the Vallesian. This drop in diversity is referred to as the Vallesian Crisis (Agustí, 1981; Agustí et al., 2013). Richness of inland basins of the Iberian Peninsula was far lower than of the coastal basins. Moreover, apart from being brief in duration, the high richness appears to be rather local, which is consistent with Casanovas-Vilar et al. (2014) questioning the wide range and extent of the Crisis.

Furthermore, there was a southward shift of the richest latitude for the entire period (Fig. 2). While in early to middle Miocene (MNEQ 3 to 7 + 8; Fig. 2a–e) the maximum number of genera per grid cell was located in the higher latitudes with around 80 genera, the concentration of genus richness changed in the early late Miocene. The change from MNEQ 7 + 8 to MNEQ 9 is a clear example of an area of high richness shifting from high (Fig. 2a–e) to low latitudes (Fig. 2f–g). In the late Miocene, MNEQs 10 and 11 (Fig. 2g–h), mammal biodiversity was more homogeneously spread over Europe. The maximum numbers are much lower, not even reaching 70 genera per grid cell. Here, hotspots are less clearly identified and peaks in genus counts less pronounced.

3.2. Large vs. small mammals

Despite the differences in dispersal abilities and other dynamics (Casanovas-Vilar et al., 2010; Maridet and Costeur, 2010), the general pattern visible in both micro- and macromammals was expected to be the same, based on their similarities in the NOW database (Peláez-Campomanes and Van der Meulen, 2009). Even though Heikinheimo et al. (2007) stated that macromammal biodiversity is more related to environmental changes, the micromammals are expected to be more sensitive to changes, because of their smaller geographic ranges

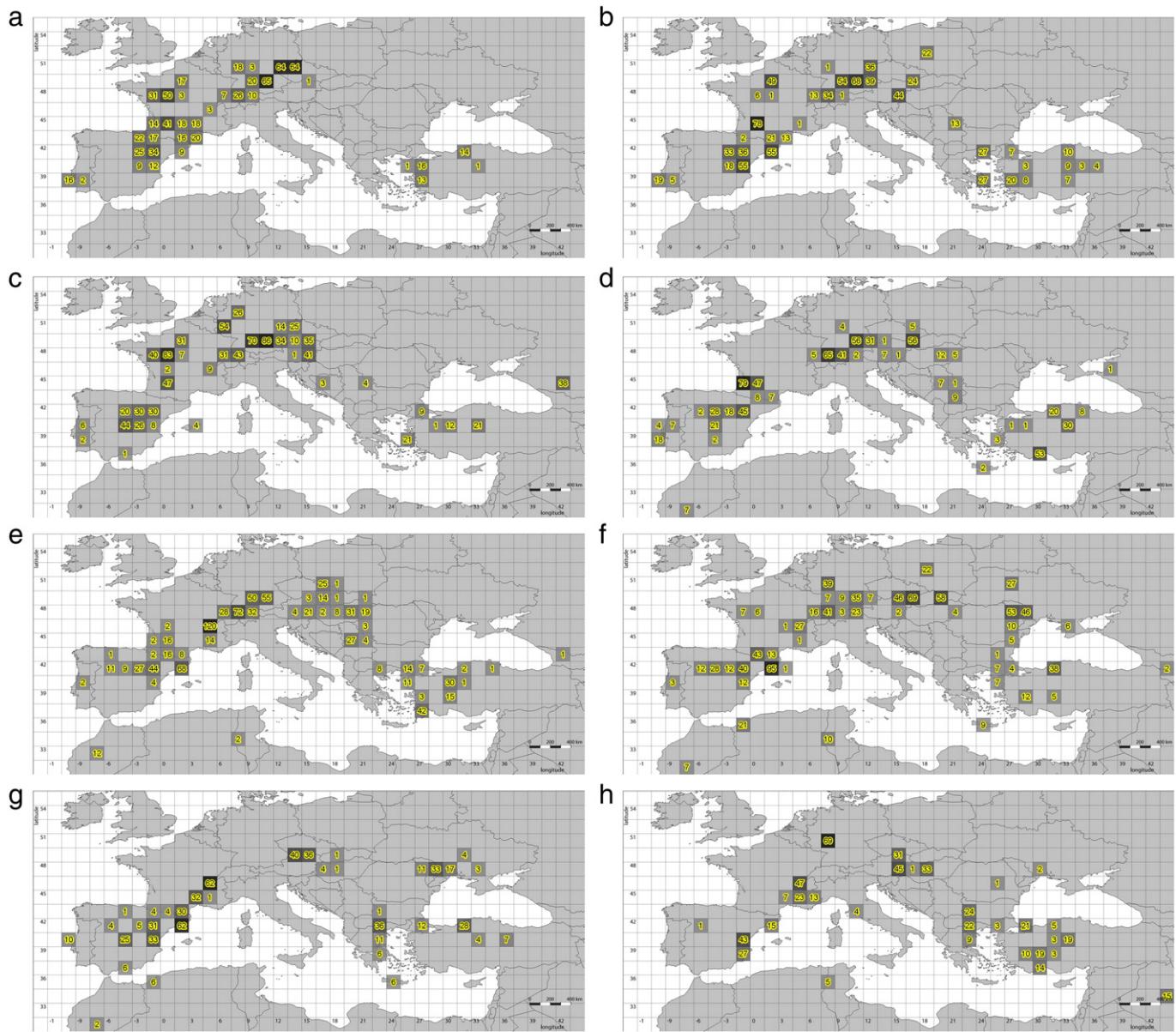


Fig. 1. a–h. Biodiversity per $1.5 \times 1.5^\circ$ grid cell for large and small mammals together, plotted per MNEQ.

(Marinet et al., 2007). The large and small mammals indeed behaved in a comparable manner during the study interval, although the pattern of shifting hotspots was more pronounced in the small mammals (Fig. 2).

3.3. Bias

The correlation between diversity (Fig. 3a) and sample size was calculated (Fig. 3b) to test for bias in the data. Spearman rank correlation analysis per MNEQ unit showed that there is no significant correlation, as all have low rho-values and non-significant p-values (combined: $\rho^2 = 0.09$, $p = 0.47$; large: $\rho^2 = 0.10$, $p = 0.46$; small: $\rho^2 = 0.15$, $p = 0.35$). (Note that 'sample size' here is actually the matrix of recorded sites and species, for lack of abundance data.)

Following Barry et al. (2002), relationships between the number of events (first and last occurrences, that is, FOs and LOs), the sample size and the richness were calculated. After an initial decrease during MNEQ 6, there was an increase in entries in MNEQs 7 + 8 and 9

(Fig. 3c). However, there also was a high number of exits at the same time, indicating a period of faunal turnover. After MNEQ 9, the number of exits did not radically increase. In MNEQ 10 the number was lower than in MNEQ 7 + 8 and during MNEQ 11 it even declined further. While the number of events and sample size are not significantly correlated (combined: $\rho^2 = 0.07$, $p = 0.53$; large: $\rho^2 = 0.15$, $p = 0.35$; small: $\rho^2 = 0.00$, $p = 0.91$), the relationship between the number of events and the richness, the number of genera present per MNEQ, is highly significant for both large and small mammals (combined: $\rho^2 = 0.81$, $p = 0.0024$; large: $\rho^2 = 0.66$, $p = 0.0149$; small: $\rho^2 = 0.51$, $p = 0.0465$) (Fig. 3d).

As there is no significant relationship between the sheer number of finds (e.g., sample size) and the richness (e.g., number of genera), it is possible to distinguish between peaks in diversity that are artifacts and real diversity fluctuation. Hence, the richness signal here is not a direct function of sampling. An example is the hotspot in MNEQ 9, which still exists when the richest site, Can Llobateres 1, is excluded (Casanovas-Vilar et al., 2014).

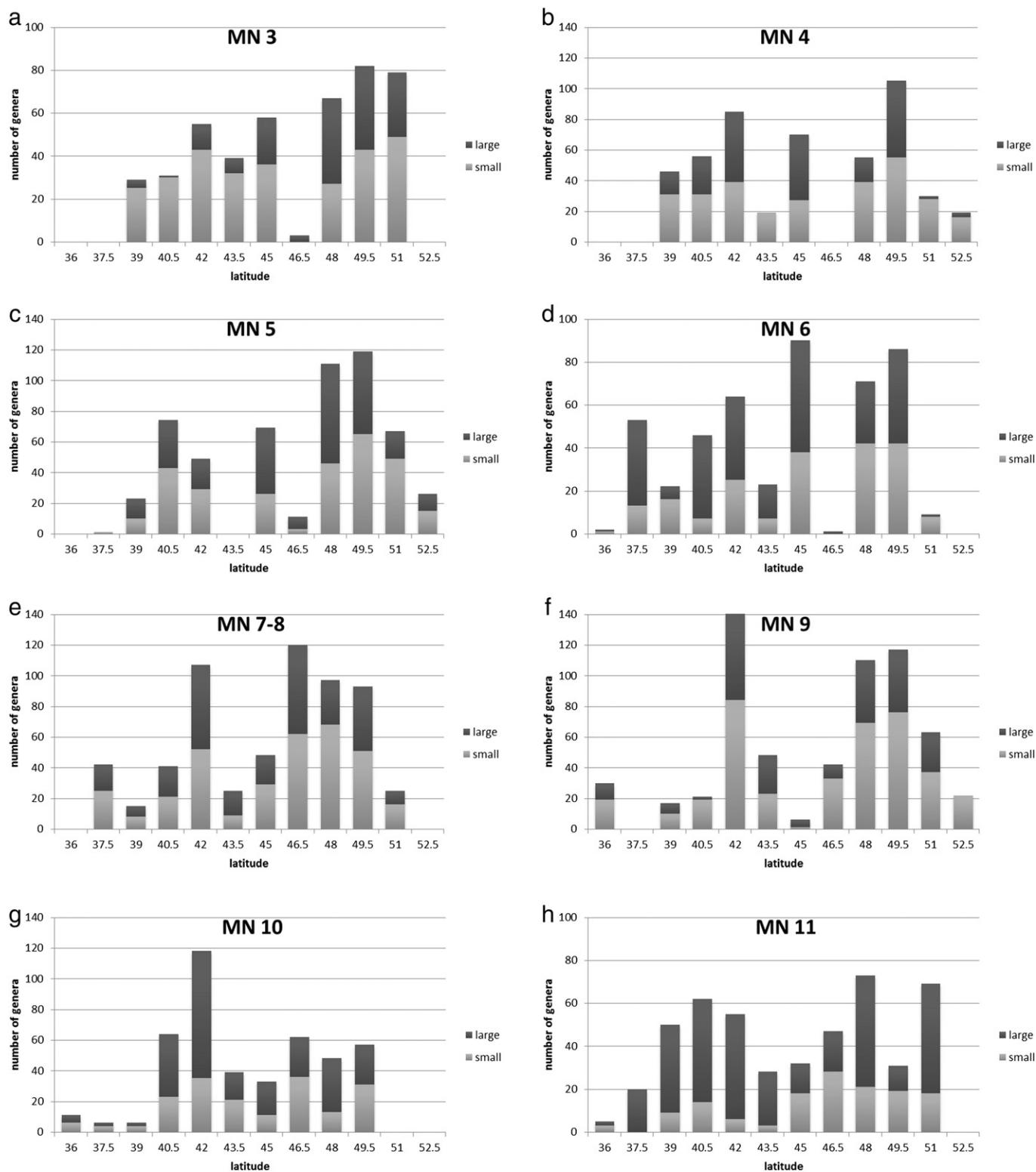


Fig. 2. a-h. Bar graphs showing the number of genera for the hotspots per latitude per MNEQ for large and small mammals (resp. dark and light colors in the bar graphs). The location of the richest latitude changes through time, going from rich higher latitudes in MNEQ 3 to MNEQ 7 + 8 to a more southern hotspot in MNEQ 9.

While the sampling bias is considered negligible, there is still some geographic bias present in the data. During the late Miocene, for instance, localities in the higher latitudes are lacking. This northern hiatus appears to be a conservation bias. Likewise, the patchiness

is emphasized by empty spaces on the map (e.g., France, Croatia), as data from the various countries have not been entered equally into the NOW. Together, these amount to reservations to be kept in mind and not reasons to dismiss this type of comprehensive data.

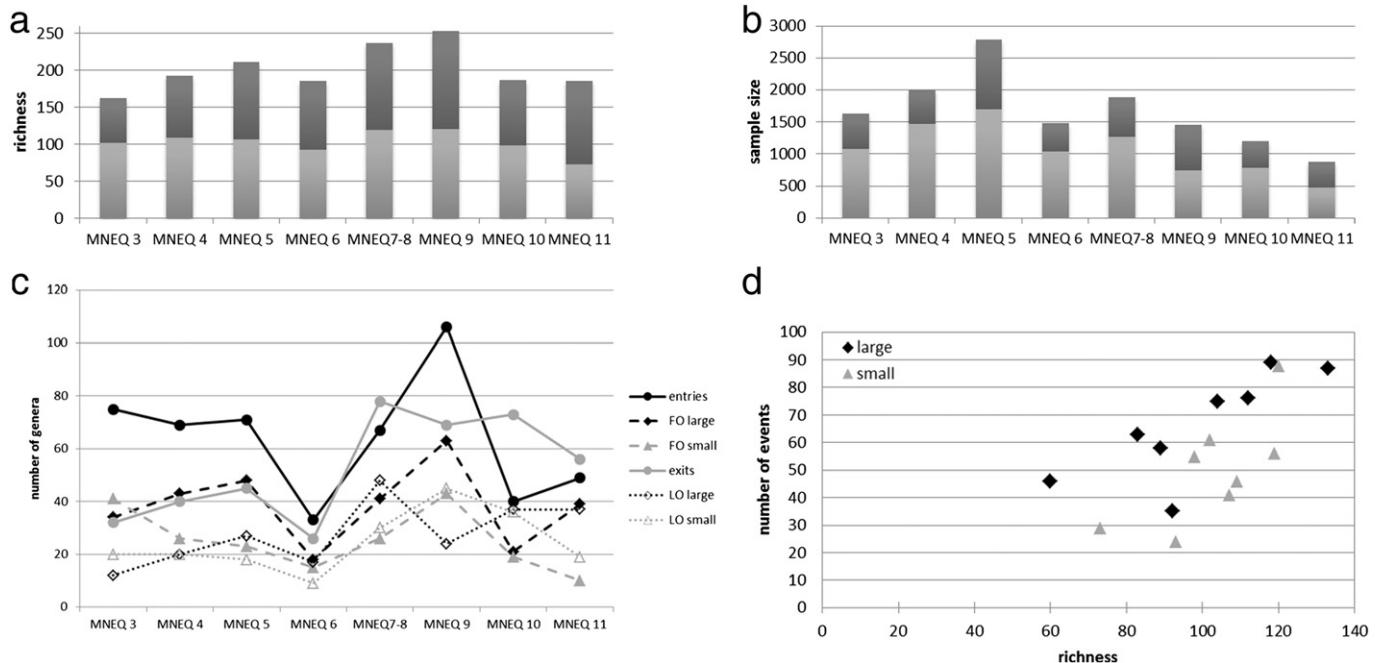


Fig. 3. Genus biodiversity explored through time (per MNEQ) for large and small mammals (resp. dark and light colors in the bar graphs), both separately and combined. (a) Richness in number of genera. (b) Sample size in number of data points. (c) Number of first (FO) and last (LO) occurrences. (d) Relationship between number of events (FO + LO) and richness per time interval.

4. Discussion

4.1. Data accuracy

Consistency of the data is a major difficulty of constructing a complete overview of all Eurasian Miocene mammals. Reconstructing ancient communities based on fossil assemblages depends on accurate and consistent identifications and the level of completeness as defined by Foote and Raup (1996).

The fossil record holds a great amount of information about the original living fauna (Alba et al., 2001). There is a high level of fidelity between modern bone assemblages and living populations, likewise changes in community structure can be accurately tracked in fossil assemblages (Western and Behrensmeyer, 2009). Furthermore, by comparing data from the NOW database with information about fossil communities with those from a database about recent populations, Saarinen et al. (2010) found that grid cell data from fossil localities give a good estimate of the total fauna and show ca. 60% of the total species diversity, implying that this percentage will be even higher for genus level biodiversity.

The differences within and between small and large mammal communities could be a problem, as they can vary greatly in completeness and dispersal ability. Previous studies of the NOW showed that the set of localities included in the database does not represent homogeneous sampling for the large mammals (Peláez-Campomanes and Van der Meulen, 2009). However, the NOW database is continuously being updated, and with numerous additions in the last few years (such as Casanovas-Vilar et al., 2010), the evolving dataset becomes more complete and accurate for new compilations (Fortelius, 2013).

4.2. Spatial diachrony

The long-distance correlations commonly utilize Mammal Neogene (MN) biochronology (Mein, 1999; Agustí et al., 2001), which is widely used in European mammal palaeontology. However, Van der Meulen et al. (2011, 2012) recently demonstrated the asynchrony of parts of

this zonation by comparing long-term Miocene mammal sections from Spain and the North Alpine Foreland Basin of Germany and Switzerland that were correlated with the palaeomagnetical time-scale (Van der Meulen et al., 2011). The observed diachrony by taxa entering the various areas at different times has strong biogeographical implications, as it shows the expansions and retractions of species distribution zones, and ultimately of ecosystems.

4.3. Pattern related to climate

In the early to late Miocene diversity hotspots drifted to lower latitudes, followed by a shift in diversity patterns from MNEQ 10 on. The changes in the Vallesian were characterized by the disappearance of certain mammal groups, in particular those adapted to stable humid or closed environments and specialized herbivores, that is, frugivores (fruit eaters) or folivores (leaf eaters) (Van der Made et al., 2003). New immigrants may have been more adapted to dry or open landscapes or less predictable environments. Numerous studies suggest the late Miocene (after MNEQ 11) was becoming more dry, cold and seasonal (Agustí et al., 2003; Van der Made et al., 2003; Mosbrugger et al., 2005; Eronen et al., 2009, 2010, 2012). Vegetation patterns showed the development of continentality, where both temperature and precipitation seasonality increased (Bruch et al., 2011) together with the appearance of extensive grasslands (Stromberg et al., 2007).

Besides several groups declining and ultimately disappearing, the late Miocene Vallesian Crisis also involved a change towards communities with a lower species richness (Casanovas-Vilar and Agustí, 2007). Even though a small number of studies based on pollen records and stable isotopes do not show drastic changes in regional vegetation or climatic conditions on the Iberian Peninsula during the Vallesian (Jiménez-Moreno et al., 2010), several others similarly link the Vallesian Crisis to changing climate. Maps based on mean hypsodonty (i.e., increased tooth height, used as a proxy of mean annual palaeoprecipitation) show increased aridification in south-west Europe (Fortelius et al., 2002). In addition, the transition from a hot and wet 'washhouse' climate sensu Böhme et al. (2008), with temperatures and precipitation higher than

present to drier conditions timed between 9.7 and 9.5 Ma, and the associated cooling episode, seemed to have triggered faunal turnover (Böhme et al., 2008, 2011).

However, the inland areas also experienced faunal transitions right at the beginning of the Vallesian and during the Vallesian Crisis (Van Dam et al., 2006). Astronomical forcing influenced the Earth's climate and in that way triggered faunal events. The Milankovic theory describes the cumulative effects of changes in the Earth's cyclic movements (orbital shape/eccentricity, axial tilt/obliquity and precession of the Earth's axis) on climate (Hays et al., 1976). Van Dam et al. (2006) argued that astronomical cycles could trigger analogous faunal events. At times when these different Milankovic cycles strengthen each other, they can change the climate to such a degree that the stability of ecosystems is affected. This, in its turn, may precipitate faunal events like migrations and extinctions.

Finding a pattern of southward movement of a diversity hotspot is one thing, recognizing the causes behind it quite another. In order to do so, the genera present in each diversity peak need to be evaluated, which is outside the scope of the present paper. It is possible, however, to speculate and attempt to draw up a working hypothesis for further research.

Insectivores are starting to become more widely recognized as good humidity indicators. Furió et al. (2011) showed that insectivore diversity is continuously higher in the north than in the south, and postulated a latitudinal humidity gradient across Europe throughout the late early to early late Miocene (ca. MN 2 to MN 10). As they analysed the data from the various MN units separately, they did not look at the development of this gradient through time. It is clear, that the south of Europe was drier than the central parts. Van Dam noted this for the late Neogene, but showed (van Dam, 2006 fig. 9a) it also held true for the late middle Miocene. According to Böhme et al. (2006), precipitation rates in the early middle Miocene in Central Europe were about three times higher than those in the Iberian Peninsula. A southward movement of the more humid ecosystems in itself is not enough to explain the decreasing latitudes of the maximum diversity. Given a humidity gradient, one might expect the hotspot to remain in the most forested environments in the north. The pattern indicates a shift, particularly in MNEQ units 5 to 9, i.e., the middle and early late Miocene.

Similar to this study, the work of Furió et al. (2011) was based on data ordered in MN units. Van der Meulen et al. (2011, 2012) noted that the system shows a certain amount of diachronicity, particularly in MN units 5, 6 and 7 + 8, the very period in which the area of high richness was moving in a southern direction. This implies that the correlation methods used would have impeded the recognition of the relation between the dry south and humid north, as MN units would in part have followed the ecosystem expansion, making them less suitable as a time frame (which may account also for the diachronicity found). The southward expansion culminated in the most southern hotspot in the Vallès-Penedès (MNEQ 9), when moist loving Eulipotyphla as heterosoricids and dimylids thrived in the area (Furió et al., 2011, 2015), and the basin became one of the most important spots for hominoid diversity (Agustí et al., 2003; Casanovas-Vilar et al., 2011; DeMiguel et al., 2014).

The observed hotspots seem to have represented the fringes of a southward expanding humid ecosystem. Diversity was higher in the periphery, because of a spatial fragmentation of the environment, resulting in a mosaic where both southern and northern faunal elements lived in close proximity. In addition, this paper's methodology combines data from an area over an extended period of time. Minor oscillations in the position of the ecosystem boundaries would therefore lead to time averaging, leading to an even higher observed diversity.

Although diversity reached its acme in MNEQ 7 + 8, the most remarkable hotspot was arguably the one found in MNEQ 9. It represents the most southern r, and, moreover, it is somewhat paradoxical to have the highest diversity in Europe on a peninsula. Most important, however, is that here the southward movement ended. During MNEQ 10

diversity is far more equitable, which seems to indicate that ecosystems throughout Europe were more uniform.

5. Conclusions

These data reveal a trend of a southward moving area with the highest richness from the early to middle Miocene. This trend can be explained by an expansion of a humid ecosystem and subsequently closed environments from higher into lower latitudes, where high richness results from temporal and spatial mixing at the boundary of ecosystems. This trend culminated in the early Vallesian Iberian Peninsula. Notably, areas surrounding this most southern hotspot did not show the same richness.

During the late Vallesian and the Vallesian Crisis (at 9.7 Ma), the distribution of mammals in Europe became more even and areas of high richness not as sharply defined as before. This was the time of the disappearance of most humid-adapted and forest dwelling groups, meaning the end of the hominoids in Europe as well. The number of exits in MNEQ 10 is barely higher than in MNEQ 9 (Fig. 3c), which would be predicted if the Vallesian Crisis were more than a local event. Notably, the number of genera did not change in Eastern Europe. This is in line with the notion that the Vallesian Crisis was indeed local, not continent wide.

Acknowledgments

We would like to express gratitude to the team of the NOW database, especially Mikael Fortelius, Jussi Eronen and Emilia Oikarinen. For the help with GIS and R, we wish to thank Willem Snitger, Niels Raes, Peter van Welzen and Thomas Olszewski. We are also grateful for the funding by the Alida M. Buitendijk Fund and Leiden University Fund International Study Fund (LISF). Furthermore, we want to thank the editor and anonymous reviewers for their suggestions. And last, a special thank you to Steve Donovan for being the 'editor from hell', much appreciated.

References

- Agustí, J., 1981. *Roedores Miomorfos del Neógeno de Cataluña*. Universitat de Barcelona, Barcelona, p. 288.
- Agustí, J., Cabrera, L., Garces, M., Pares, J.M., 1997. The Vallesian mammal succession in the Valles-Penedès basin (northeast Spain): paleomagnetic calibration and correlation with global events. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 133, 149–180.
- Agustí, J., Cabrera, L., Garces, M., Krijgsman, W., Oms, O., Pares, J.M., 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. *Earth-Sci. Rev.* 52, 247–260.
- Agustí, J., de Siria, A.S., Garces, M., 2003. Explaining the end of the hominoid experiment in Europe. *J. Hum. Evol.* 45, 145–153.
- Agustí, J., Garces, M., Krijgsman, W., 2006. Evidence for African–Iberian exchanges during the Messinian in the Spanish mammalian record. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 238, 5–14.
- Agustí, J., Cabrera, L., Garces, M., 2013. The Vallesian Mammal Turnover: a Late Miocene record of decoupled land–ocean evolution. *Geobios* 46, 151–157.
- Alba, D.M., Agustí, J., Moyà-Solà, S., 2001. Completeness of the mammalian fossil record in the Iberian Neogene. *Paleobiology* 27, 79–83.
- Alroy, J., 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127, 285–311.
- Alroy, J., 2002. How many named species are valid? *Proc. Natl. Acad. Sci. U. S. A.* 99, 3706–3711.
- Alroy, J., 2003. Taxonomic inflation and body mass distributions in North American fossil mammals. *J. Mammal.* 84, 431–443.
- Alroy, J., 2010. Fair sampling of taxonomic richness and unbiased estimation of origination and extinction. *Quant. Methods Paleobiol.* 16, 55–81.
- Ataabadi, M.M., Liu, L.P., Eronen, J.T., Bernor, R.L., Fortelius, M., 2013. Continental scale patterns in Neogene mammal community evolution and biogeography: a Europe–Asia perspective. In: Xiaoming, W., Flynn, Lawrence J., Fortelius, Mikael (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York.
- Badgley, C., Gingerich, P.D., 1988. Sampling and Faunal Turnover in Early Eocene mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 63, 141–157.
- Barry, J.C., Morgan, M.L.E., Flynn, L.J., Pilbeam, D., Behrensmeyer, A.K., Raza, S.M., Khan, I.A., Badgley, C., Hicks, J., Kelley, J., 2002. Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. *Paleobiology* 28, 1–71.
- Barry, J.C., Behrensmeyer, A.K., Badgley, C., Flynn, L., Pelttonen, H., Cheema, I.U., Pilbeam, D., Lindsay, E.H., Raza, S.M., Rajpar, A.R., Morgan, M.E., 2013. *The Neogene Siwaliks*

of the Potwar Plateau, Pakistan. In: Xiaoming, W., Flynn, Lawrence J., Fortelius, Mikael (Eds.), *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York.

Behrnsmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.D., Wing, S.L., 1992. *Terrestrial Ecosystems Through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals*. The University of Chicago Press, Chicago.

Bernor, R.L., 1984. A zoogeographic theater and a biochronologic play: the time/biofacies phenomena of Eurasian and African Miocene mammal provinces. *Paléobiol. Cont.* 14, 121–142.

Bernor, R.L., Fahlbusch, V., Andrews, P., De Bruijn, H., Fortelius, M., Rögl, F., Steininger, F.F., Werdelin, L., 1996. The evolution of Western Eurasian mammal faunas: a chronologic, systematic, biogeographic and paleoenvironmental synthesis. In: Bernor, R.L., Fahlbusch, V., Mittmann, H.W. (Eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York, pp. 449–469.

Böhme, M., 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 195, 389–401.

Böhme, M., Ilg, A., Ossig, A., Kuchenhoff, H., 2006. New method to estimate paleoprecipitation using fossil amphibians and reptiles and the middle and late Miocene precipitation gradients in Europe. *Geology* 34, 425–428.

Böhme, M., Ilg, A., Winklhofer, M., 2008. Late Miocene "washhouse" climate in Europe. *Earth Planet. Sci. Lett.* 275, 393–401.

Böhme, M., Winklhofer, M., Ilg, A., 2011. Miocene precipitation in Europe: temporal trends and spatial gradients. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 304, 212–218.

Broccoli, A.J., Manabe, S., 1997. Mountains and midlatitude aridity. In: Ruddiman, W.F. (Ed.), *Tectonic Uplift and Climate Change*. Plenum, New York, pp. 89–121.

Bruch, A.A., Utescher, T., Mosbrugger, V., Members, N., 2011. Precipitation patterns in the Miocene of Central Europe and the development of continentality. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 304, 202–211.

Casanovas-Vilar, I., Agustí, J., 2007. Ecogeographical stability and climate forcing in the Late Miocene (Vallesian) rodent record of Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 248, 169–189.

Casanovas-Vilar, I., García-Paredes, I., Alba, D.M., Van den Hoek Ostende, L.W., Moyà-Solà, S., 2010. The European far west: Miocene mammal isolation, diversity and turnover in the Iberian peninsula. *J. Biogeogr.* 37, 1079–1093.

Casanovas-Vilar, I., Alba, D.M., Garces, M., Robles, J.M., Moyà-Solà, S., 2011. Updated chronology for the Miocene hominoid radiation in Western Eurasia. *Proc. Natl. Acad. Sci. U. S. A.* 108, 5554–5559.

Casanovas-Vilar, I., Van den Hoek Ostende, L.W., Furió, M., Madern, P.A., 2014. Patterns as pretty as can be: the range and extent of the Vallesian Crisis in its type area. *J. Iber. Geol.* 40, 29–48.

Costeur, L., Legendre, S., 2008. Mammalian communities document a latitudinal environmental gradient during the Miocene climatic optimum in western Europe. *Palaios* 23, 280–288.

Costeur, L., Legendre, S., Aguilar, J.P., Lecuyer, C., 2007. Marine and continental synchronous climatic records: towards a revision of the European Mid-Miocene mammalian biochronological framework. *Geobios* 40, 775–784.

De Bruijn, H., Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P., Morales, J., Heinemann, E., Mayhew, D.F., Van der Meulen, A.J., Schmidt-Kittler, N., Telles Antunes, M., 1992. Report of the RCMNS working group on fossil mammals, Reisensburg 1990. *Newsl. Stratigr.* 26, 65–118.

DeMiguel, D., Alba, D.M., Moyà-Solà, S., 2014. Dietary specialization during the evolution of western Eurasian hominoids and the extinction of European great apes. *PLoS ONE* 9, 1–13.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. *Science* 345, 401–406.

Domingo, M.S., Alberdi, M.T., Azanza, B., 2007. A new quantitative biochronological ordination for the Upper Neogene mammalian localities of Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 255, 361–376.

Domingo, M.S., Badgley, C., Azanza, B., deMiguel, D., Teresa Alberdi, M., 2014. Diversification of mammals from the Miocene of Spain. *Paleobiology* 40, 196–229.

Erónen, J.T., Ataabadi, M.M., Micheels, A., Karme, A., Bernor, R.L., Fortelius, M., 2009. Distribution history and climatic controls of the Late Miocene Pikermian chronoфаuna. *Proc. Natl. Acad. Sci. U. S. A.* 106, 11867–11871.

Erónen, J.T., Puolamäki, K., Liu, L.P., Lintulaakso, K., Damuth, J., Janis, C., Fortelius, M., 2010. Precipitation and large herbivorous mammals II: application to fossil data. *Evol. Ecol. Res.* 12, 1–14.

Erónen, J.T., Fortelius, M., Micheels, A., Portmann, F.T., Puolamaki, K., Janis, C.M., 2012. Neogene aridification of the Northern Hemisphere. *Geology* 40, 823–826.

Foote, M., Raup, D.M., 1996. Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology* 22, 121–140.

Forcino, F.L., Stafford, E.S., Leighton, L.R., 2012. Perception of paleocommunities at different taxonomic levels: how low must you go? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 365, 48–56.

Fortelius, M., 2013. Neogene of the Old World Database of Fossil Mammals (NOW). University of Helsinki (<http://www.helsinki.fi/science/now/> - downloaded November 2013).

Fortelius, M., Werdelin, L., Andrews, P., Bernor, R.L., Gentry, A., Humphrey, L., Mittmann, W., Viranta, S., 1996. Provinciality, diversity, turnover and paleoecology in land mammal faunas of the later Miocene of western Eurasia. In: Bernor, R.L., Fahlbusch, V., Mittmann, W. (Eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, pp. 414–448.

Fortelius, M., Erónen, J., Jernvall, J., Liu, L.P., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I., Zhang, Z.Q., Zhou, L.P., 2002. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evol. Ecol. Res.* 4, 1005–1016.

Fortelius, M., Erónen, J., Liu, L.P., Pushkina, D., Tesakov, A., Vislobokova, I., Zhang, Z.Q., 2006. Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 238, 219–227.

Furió, M., Casanovas-Vilar, I., Van den Hoek Ostende, L.W., 2011. Predictable structure of Miocene insectivore (Lipotyphla) faunas in Western Europe along a latitudinal gradient. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 304, 219–229.

Furió, M., Prieto, J., Van den Hoek Ostende, L.W., 2015. Three million years of "Terror-Shrew" (Dinosorex, Eulipotyphla, Mammalia) in the Miocene of the Vallès-Penedès Basin (Barcelona, Spain). *C.R. Palevol* <http://dx.doi.org/10.1016/j.crpv.2014.12.001>.

Gómez Cano, A.R., Hernandez Fernandez, M., Álvarez-Sierra, M.A., 2011. Biogeographic provincialism in rodent faunas from the Iberocitlan Region (southwestern Europe) generates severe diachrony within the Mammalian Neogene (MN) biochronologic scale during the Late Miocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 307, 193–204.

Harzhauser, M., Piller, W.E., 2007. Benchmark data of a changing sea–palaeogeography, palaeobiogeography and events in the Central Paratethys during the Miocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 253, 8–31.

Harzhauser, M., Kroh, A., Mandic, O., Piller, W.E., Goehlich, U., Reuter, M., Berning, B., 2007a. Biogeographic responses to geodynamics: a key study all around the Oligo-Miocene Tethyan Seaway. *Zool. Anz.* 246, 241–256.

Harzhauser, M., Latal, C., Piller, W.E., 2007b. The stable isotope archive of Lake Pannon as a mirror of Late Miocene climate change. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 249, 335–350.

Hays, J.D., Imbrie, J., Shackleton, N.J., 1976. Variations in Earth's orbit–pacemaker of ice ages. *Science* 194, 1121–1132.

Heikinheimo, H., Fortelius, M., Erónen, J., Mannila, H., 2007. Biogeography of European land mammals shows environmentally distinct and spatially coherent clusters. *J. Biogeogr.* 34, 1053–1064.

Hijmans, R.J., van Etten, J., 2012. Raster: geographic analysis and modeling with raster data. R Package Version 2.0-8 (<http://CRAN.R-project.org/package=raster>).

IPCC, 2007. *Climate Change 2007: The Physical Science Basis*. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (996 pp.).

Jernvall, J., Fortelius, M., 2002. Common mammals drive the evolutionary increase of hypodonty in the Neogene. *Nature* 417, 538–540.

Jiménez-Moreno, G., Suc, J.P., 2007. Middle Miocene latitudinal climatic gradient in Western Europe: evidence from pollen records. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 253, 208–225.

Jiménez-Moreno, G., Fauquette, S., Suc, J.P., 2010. Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. *Rev. Palaeobot. Palynol.* 162, 403–415.

Krijgsman, W., Stoica, M., Vasiliiev, I., Popov, V.V., 2010. Rise and fall of the Paratethys Sea during the Messinian Salinity Crisis. *Earth Planet. Sci. Lett.* 290, 183–191.

Lewin-Koh, N.J., Bivand, R., 2012. maptools: tools for reading and handling spatial objects. R Package Version 0.8-16 (<http://CRAN.R-project.org/package=maptools>).

Lewis, A.R., Marchant, D.R., Ashworth, A.C., Hedenas, L., Hemming, S.R., Johnson, J.V., Leng, M.J., Machlus, M.L., Newton, A.E., Raine, J.L., Willenbring, J.K., Williams, M., Wolfe, A.P., 2008. Mid-Miocene cooling and the extinction of tundra in continental Antarctica. *Proc. Natl. Acad. Sci. U. S. A.* 105, 10676–10680.

Maridet, O., Costeur, L., 2010. Diversity trends in Neogene European ungulates and rodents: large-scale comparisons and perspectives. *Naturwissenschaften* 97, 161–172.

Maridet, O., Escarguel, G., Costeur, L., Mein, P., Hugueney, M., Legendre, S., 2007. Small mammal (rodents and lagomorphs) European biogeography from the Late Oligocene to the mid Pliocene. *Glob. Ecol. Biogeogr.* 16, 529–544.

Martín-Suárez, E., Freudenthal, M., Civís, J., 2001. Rodent palaeoecology of the continental Upper Miocene of Crevillente (Alicante, SE Spain). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 165, 349–356.

Mein, P., 1975. Biozonation du Néogène Méditerranéen à partir des Mammifères. In: Senes, L. (Ed.), *Report on Activity of RCMNS Working Groups (1971–1975)*. Vth Congress of the Regional Committee of Mediterranean Neogene Stratigraphy, Bratislava, pp. 78–81.

Mein, P., 1999. Biochronology and dispersal events among Cenozoic vertebrates. *Bull. Soc. Geol. Fr.* 170, 195–204.

Merceron, G., Costeur, L., Maridet, O., Ramdarshan, A., Gohlich, U.B., 2012. Multi-proxy approach detects heterogeneous habitats for primates during the Miocene climatic optimum in Central Europe. *J. Hum. Evol.* 63, 150–161.

Mosbrugger, V., Utescher, T., Dilcher, D.L., 2005. Cenozoic continental climatic evolution of Central Europe. *Proc. Natl. Acad. Sci. U. S. A.* 102, 14964–14969.

Peláez-Campomanes, P., Van der Meulen, A.J., 2009. Diversity of mammals in the Neogene of Europe: comparing data quality of large and small mammals in the NOW database. *Hell. J. Geosci.* 44, 105–115.

Popov, S.V., Shcherba, I.G., Ilyina, L.B., Nevesskaya, L.A., Paramonova, N.P., Khondkarian, S.O., Magyar, I., 2006. Late Miocene to Pliocene palaeogeography of the Paratethys and its relation to the Mediterranean. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 238, 91–106.

R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Renema, W., Bellwood, D.R., Braga, J.C., Bromfield, K., Hall, R., Johnson, K.G., Lunt, P., Meyer, C.P., McMonagle, L.B., Morley, R.J., O'Dea, A., Todd, J.A., Wesselingh, F.P., Wilson, M.E.J., Pandolfi, J.M., 2008. Hopping hotspots: global shifts in marine Biodiversity. *Science* 321, 654–657.

Rögl, F., 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). *Geol. Carpath.* 50, 339–349.

Saarinen, J., Oikarinen, E., Fortelius, M., Mannila, H., 2010. The living and the fossilized: how well do unevenly distributed points capture the faunal information in a grid? *Evol. Ecol. Res.* 12, 363–376.

Shevenell, A.E., Kennett, J.P., Lea, D.W., 2004. Middle Miocene Southern Ocean cooling and Antarctic cryosphere expansion. *Science* 305, 1766–1770.

Steininger, F.F., 1999. Chronostratigraphy, Geochronology and Biochronology of the Miocene “European Land Mammals Mega-Zones” (ELMMZ) and the Miocene “Mammal-Zones (MNzones)”. In: Rössner, G.E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr Friedrich Pfeil, pp. 9–24.

Steininger, F.F., Berggren, W.A., Kent, D.V., Bernor, R.L., Sen, S., Agustí, J., 1996. Circum-Mediterranean Neogene (Miocene–Pliocene) marine continental chronologic correlations of European mammal units. In: Bernor, R.L., Fahlbusch, V., Mittmann, H.W. (Eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, pp. 7–46.

Stromberg, C.A.E., Werdelin, L., Friis, E.M., Sarac, G., 2007. The spread of grass-dominated habitats in Turkey and surrounding areas during the Cenozoic: Phytolith evidence. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 250, 18–49.

Sun, J., Zhang, Z., 2008. Palynological evidence for the Mid-Miocene Climatic Optimum recorded in Cenozoic sediments of the Tian Shan Range, northwestern China. *Glob. Planet. Chang.* 64, 53–68.

Van Dam, J.A., 2006. Geographic and temporal patterns in the late Neogene (12–3 Ma) aridification of Europe: The use of small mammals paleoprecipitation proxies. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 238, 190–218.

Van Dam, J.A., Alcalá, L., Alonso-Zarza, A.M., Calvo, J.P., Garces, M., Krijgsman, W., 2001. The upper Miocene mammal record from the Teruel–Alfambra region (Spain). The MN system and continental stage/age concepts discussed. *J. Vertebr. Paleontol.* 21, 367–385.

Van Dam, J.A., Aziz, H.A., Álvarez-Sierra, M.A., Hilgen, F.J., Van den Hoek Ostende, L.W., Lourens, L.J., Mein, P., Van der Meulen, A.J., Peláez-Campomanes, P., 2006. Long-period astronomical forcing of mammal turnover. *Nature* 443, 687–691.

Van der Made, J., Agustí, J., Morales, J., 2003. The Vallesian Crisis in the Iberian and European mammal records. EEDEN—Environments and Ecosystem Dynamics of the Eurasian Neogene, Birth of the New World. Stará Lesná, Slovakia, November, 12–16th 2003.

Van der Made, J., Morales, J., Montoya, P., 2006. Late Miocene turnover in the Spanish mammal record in relation to palaeoclimate and the Messinian Salinity Crisis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 238, 228–246.

Van der Meulen, A.J., Daams, R., 1992. Evolution of Early–Middle Miocene rodent faunas in relation to long-term paleoenvironmental changes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 93, 227–253.

Van der Meulen, A.J., García-Paredes, I., Álvarez-Sierra, M.A., Van den Hoek Ostende, L.W., Hordijk, K., Oliver, A., Lopez-Guerrero, P., Hernandez-Ballarin, V., Peláez-Campomanes, P., 2011. Biostratigraphy or biochronology? Lessons from the Early and Middle Miocene small Mammal Events in Europe. *Geobios* 44, 309–321.

Van der Meulen, A.J., García-Paredes, I., Álvarez-Sierra, M.A., Van den Hoek Ostende, L.W., Hordijk, K., Oliver, A., Peláez-Campomanes, P., 2012. Updated Aragonian biostratigraphy: small mammal distribution and its implications for the Miocene European Chronology. *Geol. Acta* 10, 159–179.

Western, D., Behrensmeyer, A.K., 2009. Bone assemblages track animal community structure over 40 years in an African savanna ecosystem. *Science* 324, 1061–1064.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292, 686–693.