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Wetland paradise lost: Miocene community dynamics in large herbivorous mammals from the German Molasse Basin

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ABSTRACT

Questions: What was the distribution of fossil mammal taxa in the Miocene German Molasse Basin? Were there changes in community structure during the terrestrial development of the Molasse Basin? Were community dynamics similar in the Molasse Basin to those in the rest of Europe?

Data: We gathered the available Miocene large mammal herbivore occurrences from the southern German Molasse Basin [museum data mainly from Munich (Germany), with additional data from museums in Stuttgart (Germany) and Vienna (Austria)]. We used public data from NOW (Neogene of the Old World database, <http://www.helsinki.fi/science/now>) for comparison and as the source of ecological data for the species.

Methods: We combined ecological data from the NOW database with distributions of herbivorous mammals within the Molasse Basin. We plotted the occurrences of taxa on a base map, and used the associated body size and dietary categories to plot these data on the map. We investigated the differences in the structure of communities in different time periods. We compared different time periods and differences among areas. We also compared the Molasse Basin and NOW data.

Conclusions: The evolution of large-mammal communities in the Molasse Basin occurred in two phases: build up and decline. The build-up phase was characterized especially by a high abundance of small-sized browsers and mixed feeders. The diversity was especially high during the built-up phase, indicating a highly differentiated wetland habitat. The decline phase saw a very different community structure with fewer mixed feeders and with larger sized mammals dominating. The difference between these phases was largely the consequence of regional extinctions of species and genera. The Molasse Basin community dynamics also differ from those of the rest of Europe (NOW data).

Keywords: body size, community structure, diet, large mammals, Miocene, paleoecology, southern Germany.

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INTRODUCTION

From the late Early to the Late Miocene, the Molasse Basin, a northern foreland basin of the Alps, was a wetland area in southern Germany. Today, widely distributed limno-fluvial sediments with a rich fossil record of plants, invertebrates, and vertebrates (e.g. Fahlbusch *et al.*, 1972; Jung and Mayr, 1980; Gregor, 1982; Gregor *et al.*, 1989; Reichenbacher, 1989; Schwarz and Reichenbacher, 1989; Göhlich, 1998, 2002; Sach, 1999; Böhme 2003; Böhme and Reichenbacher, 2003; Sach *et al.*, 2003; Reichenbacher *et al.*, 2004; Rössner, 2004, 2006; Heissig, 2006; Reichenbacher and Prieto, 2006) document this ancient biome. Its community structure dynamics and seeming stability might be explained by an extremely diversified spatio-temporal habitat structure, controlled by external factors (e.g. climate and tectonics) (Heissig, 1989; Böhme, 2003), but this has never been substantiated.

Here, we use the herbivores of the large mammal record from the southern German Molasse Basin to reconstruct distribution patterns in space and time. We assume that community dynamics reflect changes in ecological conditions based on the relationship of primary producer and primary consumer.

Analysing such a large amount of data requires methods other than the ones conventionally applied in paleoecological research. Recently, there has been a growth in the number of investigations focusing on community dynamics of fossil mammals (Fortelius *et al.*, 1996, 2002, 2003; Alroy, 2000; Fortelius and Hokkanen, 2001; Barnosky and Carrasco, 2002; Jernvall and Fortelius, 2002; Barnosky *et al.*, 2004; McGill *et al.*, 2005; van der Meulen *et al.*, 2005; Eronen, 2006). This has been made possible by advances in the handling of great quantities of data and the introduction of effective computer-based modelling techniques. Fortelius *et al.* (2002, 2003) and Eronen and Rook (2004) recently developed techniques to analyse the patterns of faunal changes in large herbivore mammal communities during the Miocene on Eurasian (Fortelius *et al.*, 2002, 2003; Eronen, 2006) and European (Eronen and Rook, 2004) scales. These authors examined general faunal changes in order to reconstruct the response of mammal communities to climate change. In contrast, the aim of the present paper is to use these techniques for a geographically much more restricted area (the southern German Molasse Basin) and to trace changes in community structure of a certain paleohabitat in detail. As in the cited papers, we used GIS mapping to visualize spatio-temporal patterns of ecological adaptations.

We differentiated between five time intervals: European Land Mammal Zones MN4 (early Karpatian), MN5 (Karpatian and early Badenian), MN6 (late Badenian), MN7+8 (Sarmatian and early Pannonian), and MN9 (early Pannonian). They are correlated with the European Land Mammal Mega Zones from the late Orleanian to early Vallesian and the Central Paratethys Ages from the Karpatian to early Pannonian (Steininger, 1999).

Subsequently, we analysed the community structure of the faunas to determine the general patterns. We discuss community dynamics and their relation to the studied wetland environment. We are interested in whether diversification of community structure in this paleo-wetland could be comparable to diverse environments in present-day wetlands. Comparisons with the rest of Europe should elaborate the possible differences and similarities of the Molasse Basin to other regions in the Middle Miocene of Europe.

We use the word 'community' as a term for all fossil mammal species found at a certain locality (or the vicinity of it) even if there are only one or two species. Thus, 'community dynamics', as we use it here, describes the interactions of these local communities and changes that are seen in the temporal record.

GEOLOGICAL SETTING AND PALEOHABITAT

The Molasse Basin developed from the Eocene onwards as a result of subduction of the Eurasian plate under the Adriatic Plate. It has been filled with clastic erosion products under contemporary subsidence (Lemcke, 1988). Today the Molasse Basin extends from Genf in Switzerland to northwest of Vienna in Austria, with a length of 800 km. In Germany, the Molasse Basin comprises an area of 250 km in length and 100 km in mean width (Fig. 1). The northern border is formed by the underlying Jurassic limestone plateau. The widely distributed terrestrial deposits of the Miocene belong mainly to the so-called 'Upper

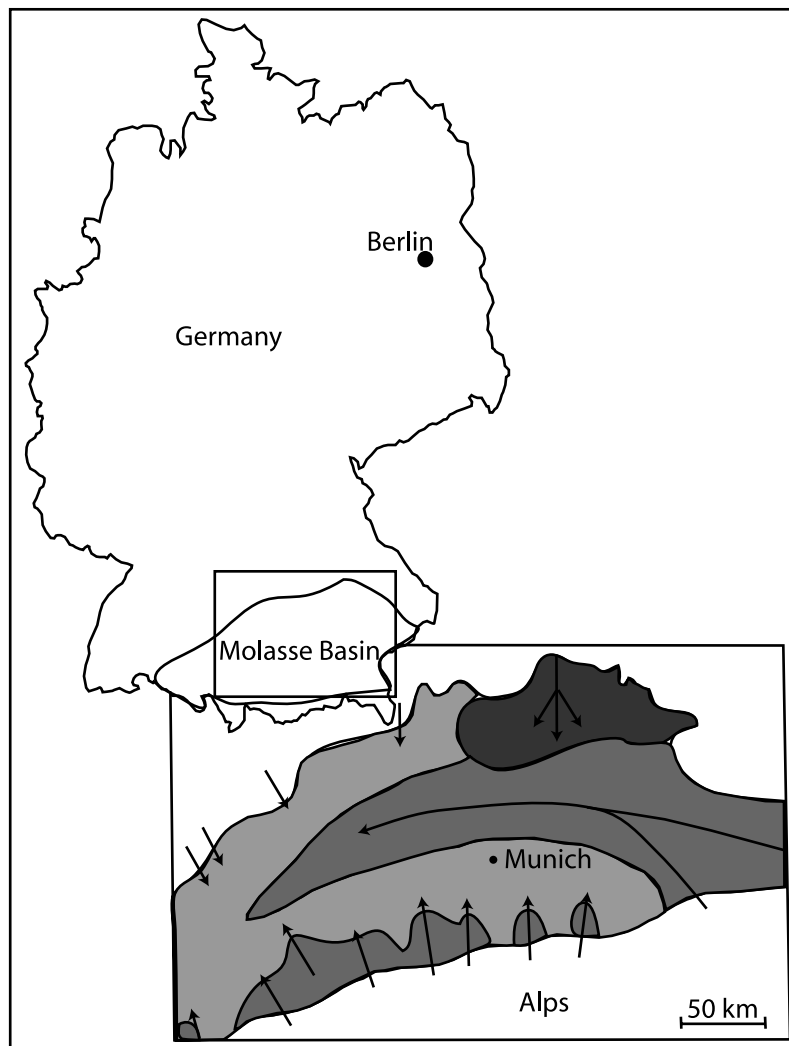


Fig. 1. Geographic location of the Molasse Basin in Germany and distribution of the terrestrial deposits of the Upper Freshwater Molasse (UFM) (adapted from Doppler and Schwerd, 1996). Light grey: UFM without pebbles. Medium grey: UFM with pebbles. Dark grey: UFM without pebbles and with coal and humic components. Arrows: Main drainage and side tributaries.

Freshwater Molasse' (UFM) and represent the youngest lithostratigraphic formation of the Molasse Basin. Directly underlying this is the ultimate, limnic member of the 'Brackwater Molasse', which also yields some large fossil mammal faunas. This lithological succession documents the final silting up of the continuously drying western Paratethys, a Cenozoic side arm of the Tethys, from the late Early Miocene (early Karpatian) to the early Late Miocene (early Pannonian) (Lemcke, 1988). This corresponds to the interval from approximately 17.25 to 10.0 Ma (MN4 to MN9) (Steininger, 1999). Low sea level allowed the development of a wetland with areas of marsh, fen, peatland, and forests. Fresh water was present in ponds and lakes or flowing in rivers or streams. This is documented by a variety of limno-fluviatile sediments composed of gravels, sands, marls, dark strata containing a highly concentrated humic substance, and freshwater limestones (e.g. Fahlbusch *et al.*, 1972; Fiest, 1989; Schmid, 2002; Seehuber, 2002; Heissig, 2006; Reichenbacher and Prieto, 2006; Abdul Aziz *et al.*, 2007). Primary draining to the west (Lemcke *et al.*, 1953; Blissenbach, 1957) and radial tributaries from the south caused accumulation of gravels in the east, in the central part, and in southern marginal areas (Sach, 1999) (Fig. 1). Sedimentation was cyclic, not continuous (Lemcke *et al.*, 1953; Heissig, 1989), and linked with alpine tectonic events. There was a phase of predominant erosion and relief development (early MN5 to early MN6) (Heissig, 1989; Reichenbacher and Prieto, 2006), resulting in several hiatuses (late MN5, early MN6 directly before the meteorite impact of the Ries event, late MN6 to late MN7+8) (Heissig, 1997; Reichenbacher *et al.*, 1998; Böhme *et al.*, 2001; Abdul Aziz *et al.*, 2007). Layers with allochthonous malm limestone boulders (e.g. Heissig, 1989; Reichenbacher *et al.*, 1998) are correlated with the meteorite impact of the Ries event at approximately 14.9 Ma (Reichenbacher *et al.*, 1998). Several key horizons of bentonite (Heissig, 1997; Schmid, 2002) and volcanic ash layers are present (e.g. Unger *et al.*, 1990; Ulbig, 1999). It is assumed that they are of Carpathian origin. In the late Pannonian, the last major orogenic event lifted the Molasse Basin and made it a denudation area. Approximately 100 to 200 m of sediments have been eroded (Lemcke, 1974), including the total removal of the most northern margin overlying directly the Jurassic Limestone Plateau (Swabian and Franconian Alb). The southern wing of the basin was folded and several kilometres pushed above its unfolded northern part. Thus, today the Molasse Basin area is much smaller than in the studied time interval and the central axis lies directly adjacent to the foot of the Alps. Due to the asymmetric U-shaped diameter of the basin, the outcrops of the older sediments [MN4, MN5, MN6; 'Ältere' and 'Mittlere Serie' according to Dehm (1955)] are found in the northern half and the outcrops of the younger sediments [MN7+8 and MN9; Jüngere Serie according to Dehm (1955)] in the southern half of the basin.

MATERIAL AND DATA

The dataset used includes 700 large mammal species occurrences, of which 559 are identified at least to genus level and have an age estimation. The number of studied localities is 293. The data were compiled mainly from specimens of the Bayerische Staatssammlung für Paläontologie und Geologie in München (BSPG) and completed by additional specimens from the Staatliches Museum für Naturkunde Stuttgart (SMNS) and the Naturhistorisches Museum Wien (NHW). We also compiled a list of the number of individual specimens (NISP) from the fossils that are housed in the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in München (BSPG). This subset comprises 128 localities with 400 occurrences and 5497 individual specimen. Most of the data are unpublished. The dating of localities is based on the local biostratigraphy of the Upper Freshwater Molasse in

Bavaria according to Heissig (1997; personal communication, October 2004) and in Baden-Württemberg according to Sach and Heizmann (2001), and the correlation with the Neogene European Land Mammal Units (Mein, 1975, 1989). The latter are recommended to be redefined as Neogene European Land Mammal Zones in Steininger (1999).

A list of the localities and taxa is given in the online appendix (<http://evolutionary-ecology.com/data/1941App.pdf>). We only consider large mammals; small mammals (orders Chiroptera, Lagomorpha, Rodentia, Insectivora) are not included. In addition, we have excluded carnivores and carnivory-dominated omnivores because of the unclear relationship between ecomorphology and vegetation. We have included the Suoidea as herbivory-dominated omnivores. We assigned ecomorphological characters to all taxa used in this study using the NOW database (<http://www.helsinki.fi/science/now>). [For further details on the structure and organization of the database and for downloading the latest public version, please visit the NOW homepage.] The dataset used for the present study is available upon request from the authors.

For a comparison of the Molasse Basin with the rest of Europe (including Turkey), we used the public NOW datafile (released 17 July 2003).

METHODS

In our analysis we used the ecomorphological categories 'Diet_3' and 'Svlength' from NOW. We do not consider the ecomorphological parameter hypsodonty, which is usually used to display habitat types with respect to climate (e.g. Janis *et al.*, 2000, 2002, 2004; Fortelius *et al.*, 2002, 2003; Eronen and Rook 2004; Eronen, 2006), because in the studied spatio-temporal unit the herbivorous mammals were exclusively brachyodont with only some mesodont exceptions.

The 'Diet_3' category is the most precise of three diet categories, separating different dietary adaptations within larger categories (herbivores in this case). We used the variables browser, br/gr (mixed feeder), grazer, and plant_dom (plant-dominated omnivores) for our analysis. For mapping we used only the variables browser, br/gr, and grazer. The results of Kaiser and Rössner (submitted) are incorporated.

The 'Svlength' category defines the approximate snout-to-anus length of the species. The variable spectrum is coarse, but can be used as a guideline to show at least regional size differences in communities. We used the four classes from the NOW database: 0.1–1 m, 1–2 m, 2–5 m, and 5 m+.

The faunal maps were produced using an IDW (inverse distance weighted) algorithm-interpolation, using MapInfo 8.0 GIS with Vertical Mapper, and the following criteria: cell size 10 km, search radius 50 km, grid border 50 km, number of classes 4, values rounded to 1 decimal place. For diet we plotted the percentage of browsers in the communities, separated into four classes: 0–25%, 25–50%, 50–75%, and 75–100%. For size we plotted the percentage of small and medium-sized (classes 0.1–1 m and 1–2 m) mammals, separated into four classes as for the diet maps. Only localities with known coordinates could be plotted. All singletons (only one species occurrence per locality) were deleted before calculations. Percentage values were calculated for each locality (community) and were plotted on the maps. The areas were defined by using contour interpolation.

We were only able to obtain the NISP values for a subset of localities in this dataset. The subset is representative of the whole dataset in terms of spatial and temporal coverage (G.E. Rössner and J.T. Eronen, unpublished data). We used this subset to investigate species diversity in the Molasse Basin, since we had very uneven sample sizes (number of localities) for different

time intervals in our basic dataset (see online appendix at <http://evolutionary-ecology.com/data/1941App.pdf>). We calculated the NISP for each locality in the subset and plotted this against the number of species. For the NISP calculation we omitted the excessively rich locality of Sandelzhausen, because of its different sampling history (G.E. Rössner, unpublished). We also divided the total number of species in each time interval by the duration of the time interval, and the total number of species by the total number of localities in each time interval, using the complete dataset.

We compared the Molasse dataset with the NOW data using differences in dietary adaptations, size classification, and taxonomical composition as an indicator of similarity. For this purpose, we calculated the percentage values of different dietary and size categories, and of taxonomical groups, for both the NOW data and Molasse Basin dataset. We then deducted the values of the NOW data from the requisite group of the Molasse Basin data. This results in a relative measure of similarity.

From the basic dataset we calculated the number of genera for the single time intervals, to show community dynamics at the taxonomic level and reconstruct relationships between ecological constraints and adaptative reactions. We included only the taxa that can be identified to genus level or below. For comparisons based on species numbers, we considered as species all taxa that could be identified to species level, or genus level if that was the only recorded occurrence during that time interval (e.g. there is only one Chalicotheridae in MN9, *Chalicotherium* sp., and this we count as one species; in MN6 there are five Chalicotheridae, *Metaschizotherium* sp., *C. grande*, *C. grande* sp., *C. sp.*, *C. goldfussi*, and these we count as three species). This is a conservative procedure, following Alroy (1996) and many others.

To reveal the rate of faunal change, we calculated relative turnover rates. We recorded the First Occurrence Datum (FOD) and Last Occurrence Datum (LOD) for each genus. The FODs were counted as happening at the beginning of the time interval of the first recorded occurrence. For the Molasse Basin record, we calculated all taxa as appearing for the first time in MN4. The LODs were counted as happening at the beginning of the next time interval after the last recorded occurrence. These were summed for each time interval to represent the turnover rate. This results in 16 genera that 'survived' to MN10, although the last records are from MN9. This is not true for the calculations using the NOW data, as they cover a much larger time span than the Molasse Basin record. We then calculated the relative turnover by counting the total number of genera present in each time interval and dividing the turnover rate by the number of genera.

Taphonomic and sampling bias affected our data sets, as this is the normal condition for the fossil record. Moreover, per taxon rates in combination with biochronological boundaries have to be used with caution, since they have been shown to be problematic in the interpretation of faunal dynamics (see, for example, Alroy, 1996).

RESULTS

Species richness

The variety in community composition and the relative overall representation of species in the communities change from interval to interval. In MN4 there are only a few species occurrences from a small number of communities. In contrast, the maps show high

community numbers in MN5 ($n = 87$) and MN6 ($n = 67$). MN7+8 ($n = 21$) and MN9 ($n = 33$) clearly differ from MN5 and MN6 in their community numbers.

With this record, the question arises of whether there are differences in species richness in different time intervals [for a review of problems with estimating species richness from fossil assemblages, see Barnosky and Carrasco (2002)]. We used a subset of our dataset to estimate the possible differences in species richness. The results (Fig. 2) show that MN6 and MN7+8 have significantly more species for certain NISP values than MN5 and MN9 (i.e. MN6 and MN7+8 have a steeper slope). Here, 'significant' means that the slopes of MN6 and MN7+8 are outside the 95% confidence interval of the slopes of MN5 or MN9. The high species/NISP ratio of MN7+8 is driven mainly by two rich localities: Massenhausen and Wartenberg bei Erding. If these localities are omitted, the slope is within the confidence intervals of MN5 and MN9 and outside the confidence interval of the MN6 slope. In comparison, MN6 has many localities with high species/NISP ratios. Furthermore, the number of species per million years (Fig. 3) shows that MN6 has the highest ratio, and the second highest ratio for number of species per locality (MN7+8 has the highest ratio, if Massenhausen is taken into account) (Fig. 3). We conclude from these results that species richness was highest during MN6, and might have been comparable in MN7+8. MN5 and MN9 had lower species richness. Thus, we believe that our results showing differences from MN5–MN6 to MN7+8–MN9 are real.

Throughout the time interval studied, the number of browsers is high, exceeding five in many localities and even nine in some, which is the maximum number of browsing ungulate species in modern habitats (Owen-Smith, 1982). For MN5, there are two localities with at least seven browsers (Walda 2, Gisseltshausen 1a). For MN6, at least ten browsing species are recorded for three localities (Griesbeckerzell 1a, Thannhausen, Stätzing) and for MN7+8

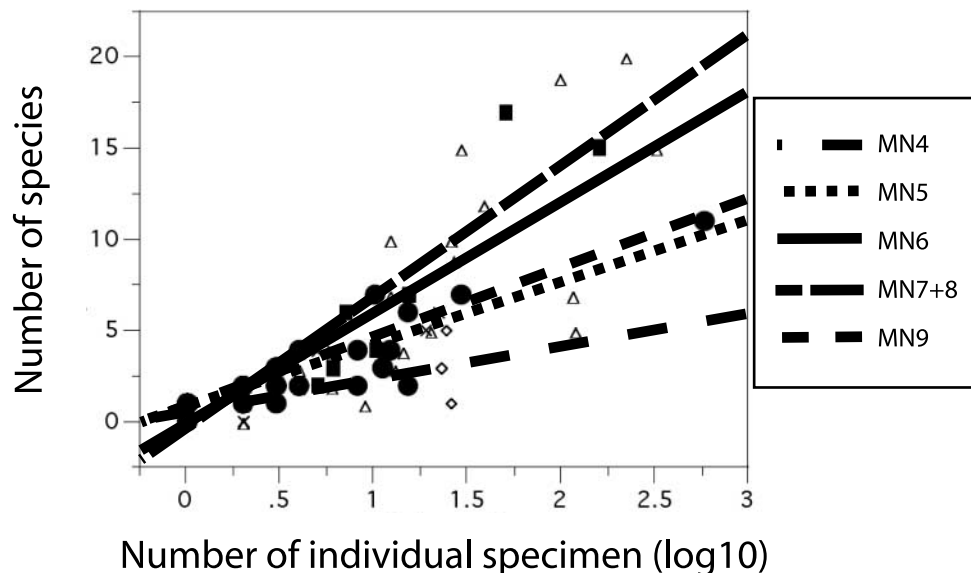


Fig. 2. The species richness estimates. Number of individual specimen counts (on logarithmic scale) are plotted against number of identified species for each locality. \diamond , MN4; \bullet , MN5; \triangle , MN6; \blacksquare , MN7+8; \times , MN9.

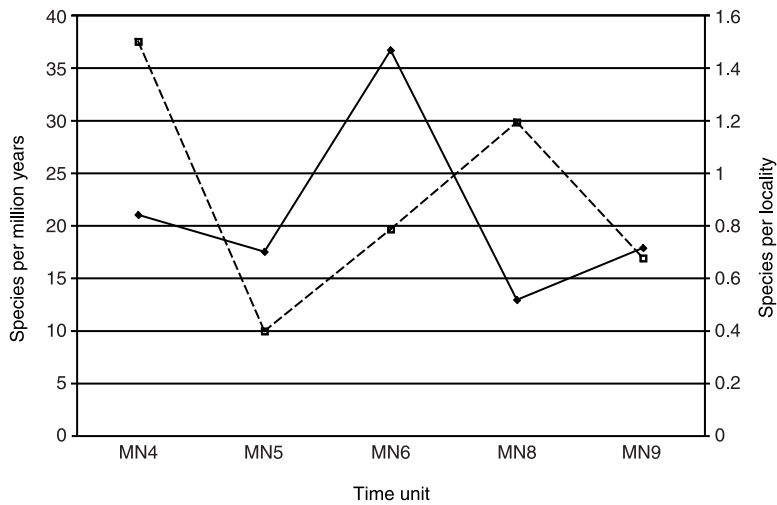


Fig. 3. Number of identified species per million years for each time interval (solid line) and number of identified species per locality for each time interval (dashed line).

one locality with ten browsers is recorded (Wartenberg bei Erding) in the Molasse Basin. This reflects extraordinary conditions compared with the modern world and is in congruence with developments in North-American Middle Miocene ungulate faunas (Janis *et al.*, 2000, 2002, 2004). Since this peak is in parallel with the highest species richness observed for the investigated time span, the probability is high that it was a real event.

Spatial dynamics

Figures 4 and 5 show a chronological series of maps for diet and body size distribution in the Molasse Basin from MN4 to MN9, and form the background for the following reconstructions and interpretations. MN4 is represented by only a few communities and a low species occurrence value (see online appendix at <http://evolutionary-ecology.com/data/1941App.pdf>). Despite an incomplete geographic coverage, we decided to include these data in our analysis as part of the initial evolutionary stage of the Miocene large mammal communities in the Molasse Basin. Data for MN7 are missing, because deposits from that interval are lacking in the Molasse Basin (see above). We therefore treat the time intervals MN7 and MN8 as one time interval (MN7+8), as this is the usual procedure among specialists nowadays (see de Bruijn *et al.*, 1992). Generally, the map sequence from MN4 to MN7+8 shows a change from communities dominated by small-sized browsers to communities dominated by larger-sized mixed feeders. If we exclude MN4, the maps reflect differences in western and eastern communities for those time intervals. In MN9, the dominance of browsers reappeared but mean body sizes remain large.

MN4 is characterized by browser-dominated communities with only some elements that fed on a small proportion of abrasive food (Fig. 4). The size map (Fig. 5) reflects a similar uniform picture of mainly small (up to 1 m) species. The MN5 diet map differs from the MN4 diet map, with an overall browser-dominated fauna with mixed feeder-dominated spots (Fig. 4). This is caused by a much higher community number than in MN4. The MN5

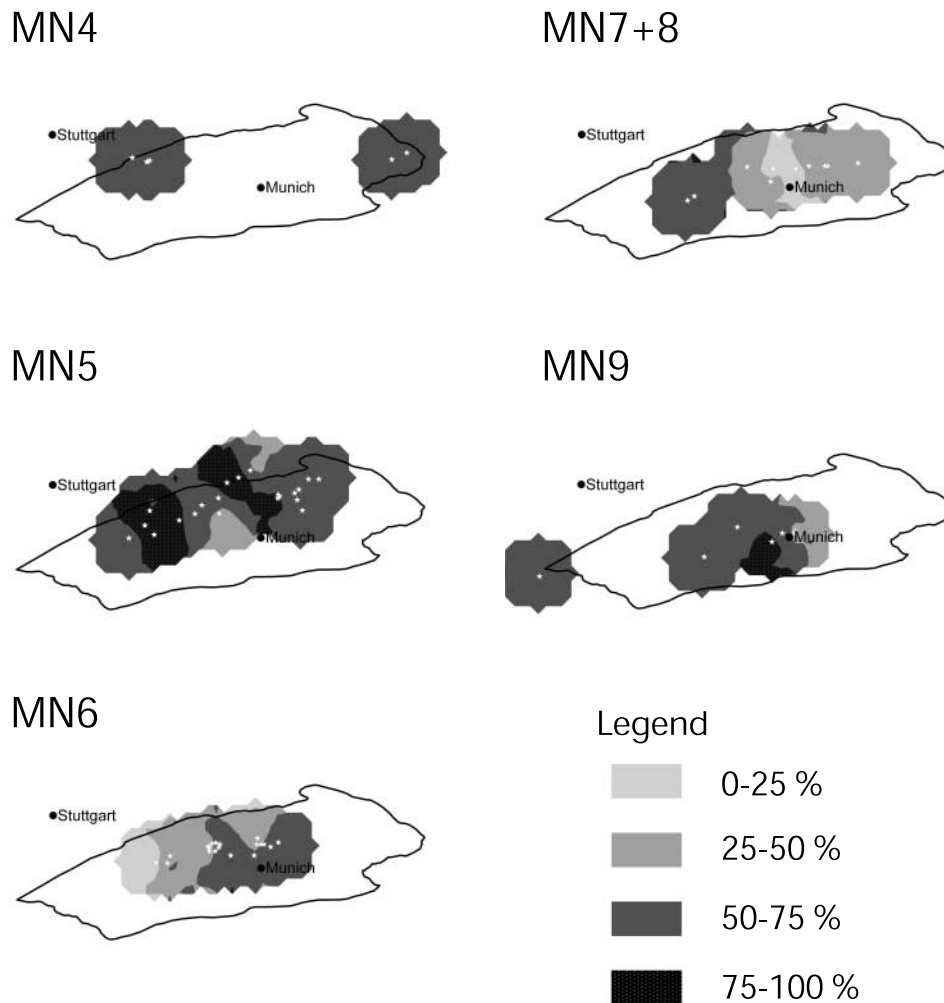


Fig. 4. IDW-interpolated diet maps for the Miocene German Molasse Basin area. Asterisks mark the geographic position of the localities. The percentages represent the amount of browsers in the faunas.

size map (Fig. 5) shows that in the east the communities comprise larger forms. Overall, the diet and size maps of MN5 reflect a mosaic pattern that cannot be interpreted in great detail. The MN6 diet map (Fig. 4) shows an increasing proportion of mixed feeders. The MN6 size map reflects the ‘spreading’ of more large-form dominated communities in the east, while in the west small forms remained dominant. It is interesting that the mixed feeders were largely of small size, while browsers were larger.

In MN7+8, diets return to browser dominated in the west and remain mixed-feeder dominated in the east (Fig. 4). During MN9, most of the Molasse Basin communities changed to browser dominated. Mean body sizes of the communities are dominated much more by larger forms than before (Fig. 5).

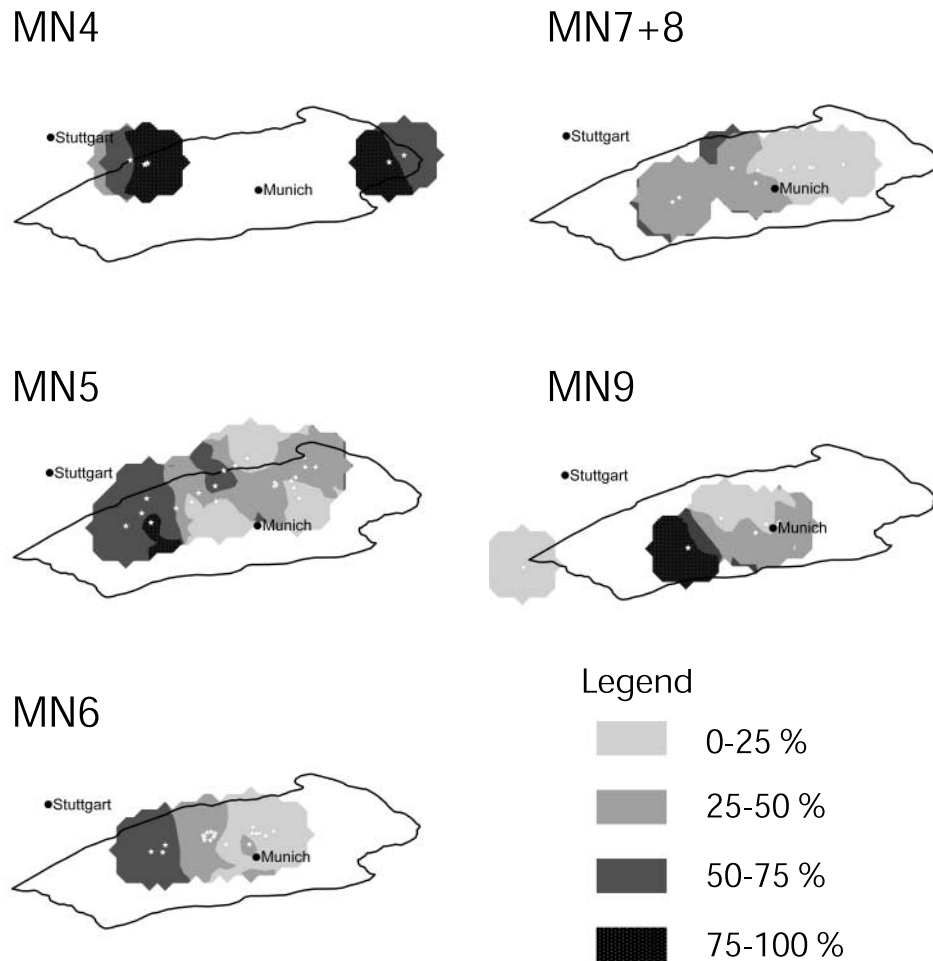


Fig. 5. IDW-interpolated body size maps for the Miocene German Molasse Basin area. Asterisks mark the geographic position of the localities. The percentages represent the amounts of small and medium-sized mammals (0.1–2 m body length) in the faunas.

General community dynamics

In Fig. 6b, the dietary characterizations of all occurrences are lumped together. This shows that in the Molasse Basin, the most numerous large mammals are the browsers. It is noteworthy that mixed feeders show a unimodal curve, with a peak in MN6 and diminishing afterwards. The plant-dominated omnivores (suoids) are a small but stable part of the communities. In Fig. 6a, all size data reflect an increase of large-sized species in relative abundance in the Molasse Basin. The small forms are diminishing from MN4 onwards in relative abundance, with a slight increase in MN6.

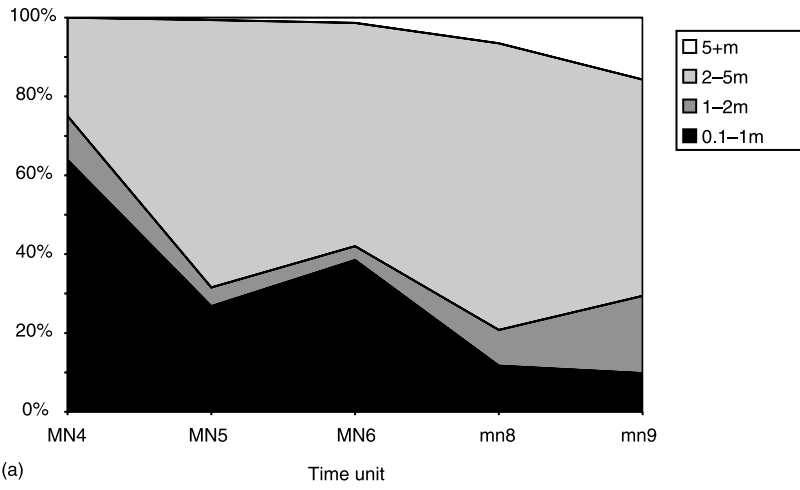
Over the studied time interval, the taxonomic composition changed in the Molasse Basin, especially in Ruminantia. In MN4, MN5, and especially in MN6, the ruminants show high

species numbers, caused by the species diversity of the Cervidae (see online appendix at <http://evolutionary-ecology.com/data/1941App.pdf>). Correspondingly, they formed one-fifth of the total occurrences and show high abundance (Fig. 6c). Remembering that the species richness estimates show that MN6 (and probably MN7+8) has higher species richness than MN5 and MN9, changes in the taxonomic composition seem to reflect this. Within small-sized browsers, cervids and the tragulid *Dorcatherium* are the most abundant taxa. Interestingly, contemporaneously with the decrease in the number of cervid species, *Dorcatherium* was reduced to one species and clearly had fewer species occurrences (see online appendix at <http://evolutionary-ecology.com/data/1941App.pdf>). Moreover, from MN5 to MN6 the ratio of browsers to mixed feeders changes drastically in the cervid population. In MN5, most of the cervids are browsers, and the only mixed feeder occurrences are a few *Stehlinoceros elegantulus*. In MN6, there are two mixed-feeding cervid species, *Stehlinoceros elegantulus* and *Dicrocerus elegans*, with many more occurrences. After MN6, the number of cervids diminishes drastically, and there are no more mixed-feeding cervids. *Dorcatherium* populations do not show a change between MN5 and MN6. In MN6, there are still more browsers than mixed feeders. After MN6 there is the same kind of drop in the number of occurrences of *Dorcatherium* as in the cervids.

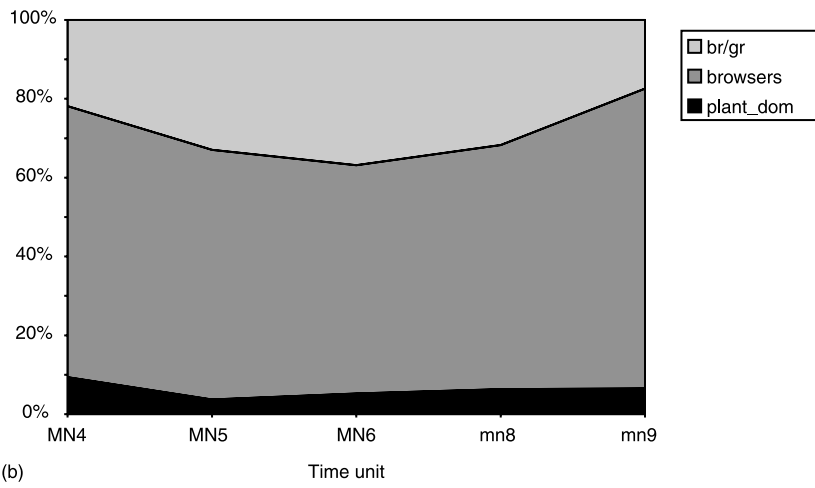
The most abundant large-sized community elements are the rhino *Brachypotherium* and the proboscidean *Gomphotherium* (Fig. 6c; see also online appendix at <http://evolutionary-ecology.com/data/1941App.pdf>). Both genera are represented over the whole study interval. Chalicotheres are missing in MN4, appear in MN5, are best represented in MN6 (widely outnumbering equids), decrease until MN7+8, and are again missing in MN9. The equid *Anchitherium* was a rare but consistent element over the study interval. The hominoid *Pliopithecus* was only represented during MN5 and MN6 (see online appendix at <http://evolutionary-ecology.com/data/1941App.pdf>). Finally, the Bovidae have a very different occurrence pattern from all the other large herbivores (see online appendix at <http://evolutionary-ecology.com/data/1941App.pdf>). Generally, they are rare elements of the Molasse Basin communities. Nevertheless, there are communities with *Eotragus* in the oldest time interval (MN4), demonstrating that bovids had already appeared in the Molasse Basin with all the other characteristic large mammals. However, in all the MN5 communities (the highest number in our analysis), there is not a single bovid specimen. In MN6, *Eotragus* reappeared and disappeared again before MN7+8. This second gap in bovid representation in the Molasse Basin is followed by a comparatively bovid-rich phase in MN9 (*Miotragocerus*).

Comparison with the rest of Europe

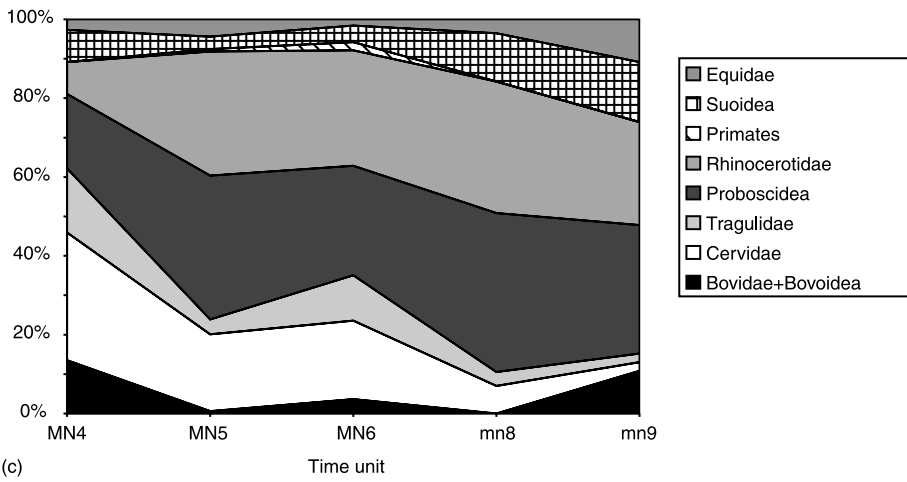
The taxonomic composition of the Molasse Basin at the family level does not show any important changes through time except for the drastic decrease of ruminants from MN6 onwards. The NOW data contain about the same proportion of cervids in the faunas during MN5 as in the Molasse Basin, and a higher number of tragulids (Fig. 7c). The NOW data had also a higher proportion of bovids, which are absent from the Molasse Basin record. During MN6, the proportion of cervids and tragulids rose in the Molasse Basin and decreased in other regions of Europe. In contrast, the proportion of bovids in Europe is on the rise throughout, from MN4 to MN9, and in MN9 there are more bovids than cervids. Although giraffids are a common faunal component in Europe from MN7+8 onwards, they are totally missing from northwest Europe (Austria, Czech Republic, Germany,



(a)



(b)



(c)

France, Switzerland) with one newly described exception from the western edge in Austria (Vislobokova, 2005).

The relative composition of diet categories in Europe reflects a gradual increase of browsers (Fig. 7b), which differs from the Molasse Basin, whose record documents a decrease in MN5 and MN6 as well as an increase in MN7+8 and MN9 (Fig. 6b). The size categories (Fig. 7c) show differences from the Molasse Basin. The Molasse Basin had relatively more large-sized mammals than the rest of Europe throughout the interval studied. In MN6, there were relatively fewer large-sized mammals. However, there were more large-sized mammals than in general in Europe.

Compared with the Molasse Basin, the relative turnover rates differ in the rest of Europe (NOW data) (Fig. 8). While turnover rate is lowest in the Molasse Basin in MN6 and highest in MN5 and MN7+8, the principal trend in Europe is the lowest relative turnover rate in MN7+8 and high relative turnover rates in MN5 and MN9.

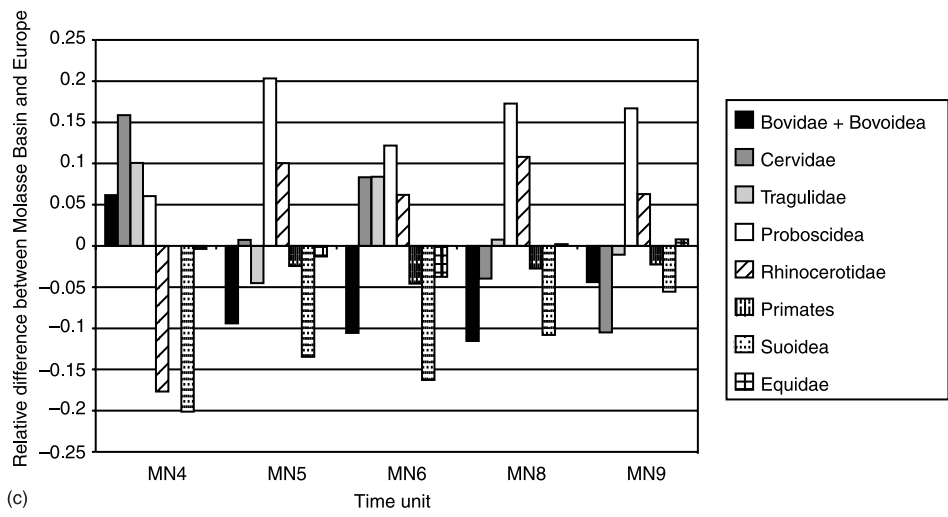
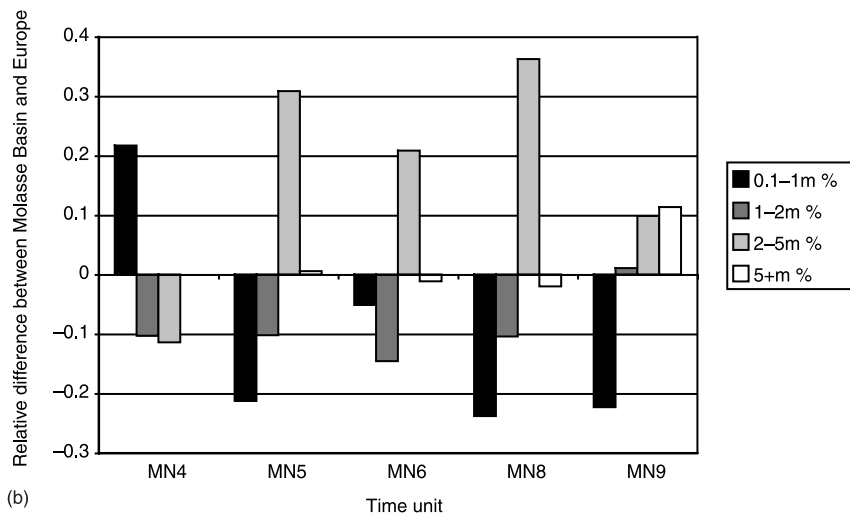
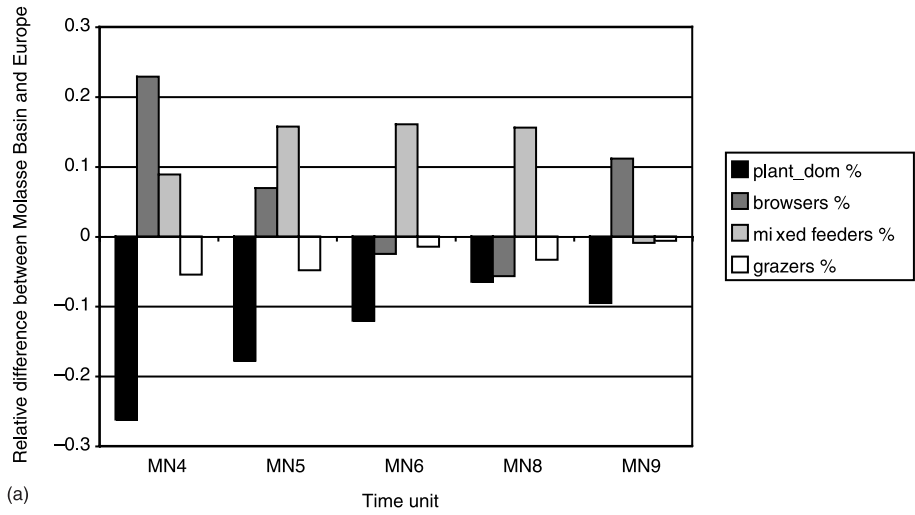
The NOW data imply that Europe generally experienced an immigration and radiation boom in large mammals in the Middle Miocene with accompanying extinction events (e.g. Bernor *et al.*, 1996; Rössner and Heissig, 1999). Interestingly, in the Molasse Basin only a few extinctions occurred at that time of immigration/radiation, but there was a high diversification of feeding strategies in MN6, reflected by a large number of mixed feeders (see also Kaiser and Rössner, submitted).

DISCUSSION

Taxonomic composition and faunal turnover

The herbivore large mammal record of the Molasse Basin displays changes in diversity and community composition. Our results clearly differ from the hypothesized MN5–MN6 species impoverishment of Jung and Mayr (1980). Our results are in line with the especially high numbers of species in the large herbivore mammal faunas of North America and Africa from the late Early and Middle Miocene (Janis *et al.*, 2000, 2002, 2004), which are not comparable to any modern habitat and reflect optimal conditions for large terrestrial mammals. The Ruminantia have extremely high species numbers per locality (up to 10), mainly cervids and to a lesser extent tragulids, as already shown by Rössner (2004). This picture takes a striking turn from MN6 to MN7+8, where the ruminants, in particular the cervids and tragulids, diminished drastically in terms of species (one-third) and occurrences (less than one-tenth). Pliopithecids disappear and chalicotheres remain reduced to a minimum. Suoids, rhinos, and proboscideans retained their previous species numbers. The pattern described above is supported by relative turnover rates, which show the lowest value in MN6 and the highest value in MN7+8.

Fig. 6. (a) Distribution of body size categories of large herbivore mammals from the Miocene German Molasse Basin. (b) Distribution of diet categories of large herbivore mammals from the Miocene German Molasse Basin. (c) Relative taxonomic composition at the family level of large herbivore mammals from the Miocene German Molasse Basin.



Changes and relationships in diet adaptations and body size

Changes in dietary adaptations of the communities in the Molasse Basin from exclusively, or nearly exclusively, browsing to a higher proportion of abrasive food from MN4 to MN6 (Fig. 6b) provides evidence of increasing diversification in community structure. In MN4 and MN5, mixed feeders formed only one-third of the genera and occurrences. In MN6, the number of mixed feeders increased to two-thirds. In contrast, from MN6 to MN9 the community structure returns to browser dominated.

The species turnover from MN6 to MN7+8 only partially changed the mixed-feeder guild. Most of the mixed-feeding ruminants went extinct. The mixed-feeding proboscideans (*Gomphotherium*, *Tetralophodon*) and rhino *Brachypotherium* remained a major part of the communities. From MN7+8 to MN9, the occurrences of these large-sized mixed feeders decreased significantly and they formed only a small part of the browser-dominated communities.

The change in the body size distribution from MN4 to MN9 is notable (Fig. 6a). In MN4, more than half of the occurrences in the communities were small (0.1–1 m). During MN5, the number decreased to the still considerable proportion of about 40% and remained the same for MN6. Between MN6 and MN7+8, the number of larger animals increased markedly (more than 70% were > 2 m).

The described changes coincide with the fall in the number of cervids and tragulids from MN6 to MN7+8. Most of the cervids were small- or medium-sized, and all the tragulids were small. This resulted in a higher proportion of large-sized taxa in the fauna formed by proboscideans and rhinocerotids. Within the small to medium ruminants, all mixed feeders and most of the browsers disappeared. But the proportion of mixed feeders in the large body size group remained quite stable and was even increasing after the loss of the small ones, which retained an abundance of mixed feeders in the communities. During MN9, the situation changed to large-sized browser-dominated communities, formed by deinotheriids and rhinocerotids.

This diversity in feeding strategies requires a concomitant diversification in the habitat/vegetation structure, which did not generally take place in Europe at this time, and most probably offered more niches. In MN7+8, the situation was changed by an especially high extinction rate accompanied by a small number of invaders, at a time when the rest of Europe experienced a comparably low relative turnover rate (see Fig. 8). The increasing similarity of the Molasse Basin fauna with the general European browser-dominated feeding assemblage is suggested by the taxonomic composition: the relative numbers of suids and equids (*Anchitherium*) increased from MN6 onwards, while those of cervids and tragulids decreased (Fig. 6c). Also, the differences between the Molasse Basin and Europe lessen from MN6 onwards. This suggests a successive homogenization of the habitat/vegetation structure, followed by the extinction of narrowly adapted species and the

Fig. 7. Differences in community structure and taxonomic composition of Miocene large herbivorous mammals between the Molasse Basin and the rest of Europe (NOW data) during the studied time interval. The histograms show the relative difference of Molasse faunas to Europe. Negative values denote that Molasse faunas had less described elements; positive values denote that Molasse faunas had more described elements. (a) Differences in the diet categories. (b) Differences in body size categories. (c) Differences in taxonomic composition.

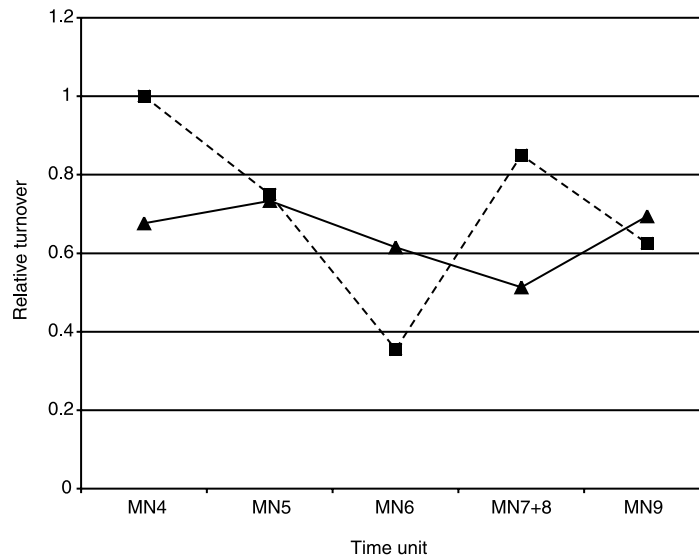


Fig. 8. Relative turnover rates of large herbivore mammals from the German Molasse Basin (dashed line) and from Europe (NOW data, solid line) in the late Early to early Late Miocene European Land Mammal Zones. Relative turnover is calculated as: $FOD + LOD / \text{number of taxa}$.

invasion of new species to a changing ecosystem. Before MN7+8 in the Molasse Basin and Europe (without the Molasse Basin), ruminants form one of the most numerically important components, besides rhinocerotids and proboscideans, within communities. They mainly contributed to the small- and medium-sized group. But the changing environmental conditions in the Molasse Basin caused the loss of nearly all of them, thus reflecting their inability to adapt to the new ecological circumstances.

General community structure

Within the context outlined above, the most outstanding change in community structure in the Molasse Basin appears to be the disappearance of small forms, which begs the question of taphonomic bias. Indeed, the Molasse Basin sediments deposited by the main drainage from the east (see Fig. 1) are much coarser in the east than in the west. Since the sediments of many of the MN8 and MN9 communities belong to the coarser section east of Munich, they might reflect a general bias by size-sorting. However, it is likely that we are observing a real phenomenon in community structure from the late Middle Miocene record onwards, because not all of those communities come from coarse-grained sediments. There are also several communities from the fine-grained sections to the west of Munich (e.g. Hammerschmiede), and richer communities from the coarser-grained sections to the east of Munich with small- and medium-sized forms (e.g. Massenhausen). We also excluded the one-specimen-communities (singletons, see above), typically comprising a proboscidean tooth, from the analysis.

The changes in the Molasse Basin might be connected to the global phenomenon of over-rich brachyodont communities and their subsequent disappearance in the Middle Miocene (described in Janis *et al.*, 2004). Almost all of the previously widespread cervids

disappeared in the Molasse Basin together with most of the other small browsers and mixed feeders. The large browser *Metaschizotherium* disappeared at the same time. Compared with Europe, the numbers of cervids and tragulids diminished, but not to the same extent as the changes in the Molasse Basin between MN6 and MN7+8 (Fig. 7c). Between MN6 and MN7+8, Europe is characterized by the lowest relative faunal turnover rate within the time span studied (Fig. 8) and does not show much change in the number of cervids and tragulids. There are still communities present during the Late Miocene that retain the same kind of community structure as in the Molasse Basin during the Middle Miocene (e.g. Can Llobateres in Spain, Rudabanya in Hungary). All these show a similar pattern of community structure to the Molasse Basin area, with primates, chalicotheres, tragulids, and cervids (Rudabanya is 9.9–10.3 Ma and Can Llobateres is 9.4–9.6 Ma).

Climatic interpretations, vegetation record, and ecological implications

When we look for reasons for the almost total disappearance of small browsers in the Miocene Molasse Basin ecosystem, the two most obvious are changes in habitat or vegetation structure and climate change.

The climatic conditions of the late Early and Middle Miocene of Europe are well documented as warm and humid (Kovar-Eder *et al.*, 1996; Esu, 1999; Utescher *et al.*, 2000; Ivanov *et al.*, 2002; Böhme, 2003; Jechorek and Kovar-Eder, 2004; Reichenbacher *et al.*, 2004; Jiménez-Moreno *et al.*, 2005). During the late Middle Miocene and early Late Miocene, a change towards stronger seasonality is suggested (e.g. Utescher *et al.*, 2000; Fortelius *et al.*, 2002, 2003; Böhme, 2004; Bruch *et al.*, 2004; Eronen and Rook, 2004; Mosbrugger *et al.*, 2005; Böhme *et al.*, 2006). This is most likely connected to decreasing mean annual precipitation to the west of the Tibetan Plateau (Kutzbach *et al.*, 1993). As a consequence, the environments became dryer at the beginning of the Late Miocene (10–11 Ma) (van der Burgh *et al.*, 1993; Ivanov *et al.*, 2002), causing a vegetational change from warm temperate deciduous forests to warm temperate deciduous woodlands in Europe (van der Burgh *et al.*, 1993; Agustí *et al.*, 2003). Therefore, the observed change in community structure from MN6 to MN7+8 (middle Middle to late Middle Miocene) in the Molasse Basin appeared contemporaneously with a general climatic change with increasing seasonality in Europe.

These events are probably connected to the global change towards cooler temperatures [Mid-Miocene cooling (e.g. Miller *et al.*, 1991; Flower and Kennett, 1994)] during the Middle Miocene. It has been dated in the marine record at 14.1 Ma. Although in the continental MN-chronologies, obtained from central Europe and from Spain, there is currently disagreement on the timing of this cooling [according to the correlation scheme of Steininger (1999), 14.1 Ma ago is the latest MN6; according to the correlation scheme of Agustí *et al.* (2001), 14.1 Ma ago is during MN5], a general cooling beginning in the Middle Miocene can be observed in the paleontological record. The Molasse Basin paleoenvironment must have been affected by a strong increase in seasonal distribution of precipitation and a subsequent decrease in temperature in the Middle to Late Miocene. This change in climatic conditions does not support a principal change in vegetation and habitat structure. As the sedimentary conditions (wetland) seem to have remained stable, the woody plant composition of the hinterland flora comprised an increasingly greater number of deciduous trees. Those trees produced leaves and fruit in rhythm with the seasons and caused reduced food availability for herbivores for some times during the year. This change in food availability must have been significant for browsers feeding mainly on leaves and buds, but not to mixed feeders, which fed also on grass and fallen leaf material. So the decreasing abundance of several

browsing large mammal species in the Sarmatian/Pannonian (MN7+8 and MN9) – for example, *Pliopithecus*, *Metaschizotherium*, *Taucanamo*, *Bunolistriodon*, *Archaeobelodon*, *Plesiaceratherium*, and *Prosantorhinus* – as well as nearly all Badenian (MN5 to MN6) Ruminantia, might have been connected to the inability of those species to subsist exclusively on plant material that was hard to digest.

The change in food availability outlined above conflicts with the resurgent dominance of browsers in MN9 (Figs. 5 and 6b). Those browser guilds were mainly composed of large-sized proboscideans and rhinocerotids (see online appendix at <http://evolutionary-ecology.com/data/1941App.pdf>). Since documentation of vegetation and climate changes is supported by several parameters, the interpretation of specifically preferred diets may be wrong or insufficient, especially in the case of large-sized mammals, which would have fed on large amounts of browsing material. Based on these data, the interpretation of the paleodiet of the Pannonian proboscideans and rhinocerotids from the German Molasse Basin needs to be re-evaluated.

CONCLUSIONS

We hypothesize the evolution of the Miocene Molasse Basin mammal faunas as a two-phase model: paradise time and loss.

Paradise time – build-up and ‘paradise’ phase

In MN5, a wetland ‘paradise’ was built up. The size distribution was mosaic (Fig. 5) and the diet distribution was still browser dominated, but with spots of an increasing number of mixed feeders (Fig. 4). Although there were already all the elements that suggest a wetland environment (e.g. tragulids, different dietary categories well represented), it appears that this was not the structure of the ‘paradise time’. When we compare the large mammal record of this time interval to the previous and the subsequent intervals, it reflects a ‘successional stage’ towards the composition of communities in MN6.

In MN6, the wetland ‘paradise’ environment was completely established. The diet distribution shows an increased proportion of mixed feeders in the Molasse Basin area. The mixed feeders were largely small in size, while browsers were larger (Fig. 4). The size distribution shows small-form dominated communities in the west and large-form dominated communities in the east, and an overlap in the central area (Fig. 5). Cervids, tragulids, and rhinocerotids (see online appendix at <http://evolutionary-ecology.com/data/1941App.pdf>) were widespread components of the communities. The relative proportion of mixed feeders (Fig. 6b) was high, with most of these individuals being cervids and tragulids. There were relatively more small (0.1–1 m) mammals than before (Fig. 6a). Chalicotheriidae and Pliopithecidae, already present in MN5, were rare but a constant part of the communities.

In relation to the studied environment – a wetland with forest and woodland hinterland, abundant water bodies surrounded by riparian vegetation, and floodplains with seasonal grass cover – hard-to-digest fibrous plants were probably widely distributed. This kind of environment surely supported a broad array of dietary adaptations and niche occupation in a highly diversified habitat structure.

Paradise loss – consequent phase

In the late Middle to Late Miocene, the transition from marine to continental conditions (continentalization) of Western Europe increased with the rising Alps. The resulting shift towards exclusively limno-fluvial environments in residual basins (Meulenkamp and Sissingh, 2003) must have provided further opportunity for mammals to invade the Molasse Basin. From MN7+8 to MN9, the fossil record reflects restructuring of the communities. Cervids and tragulids almost disappeared, and the relative number of mixed feeders diminished (Fig. 6b). The geographic distribution of body size (Fig. 5) implies a higher abundance of larger forms in the eastern part of the basin with a probable immigration from the east into the drying basin.

We hypothesize that this loss of ‘paradise’ conditions was triggered by two interacting processes: (1) the increase in seasonality and (2) the general drying of the basin area. This environmental change was forced by another major uplift event within the early Late Miocene (MN9, 11 Ma) (Meulenkamp and Sissingh, 2003) and progressed from east to west following the main draining direction. Both caused a much stronger fluctuating water content in the Molasse Basin. The consequence was an increase in the duration of the dry phase and spatial spread of dryness. This affected the degree of mosaic habitat differentiation by drying small rivers, marshes, and tree stands. Land was drier longer during the year and the availability of associated plants diminished. The need to exploit more mixed dietary resources forced the extinction of species, especially ruminants (see online appendix at <http://evolutionary-ecology.com/data/1941App.pdf>), with poorly adapted digestive organ anatomy and physiology (see Hofmann, 1973; van Soest, 1994). Although faced with changing dietary resources, proboscideans and rhinos adapted as reflected in their increasing body size (Clausen *et al.*, 2003). *Hippotherium*, a herald of upcoming open environments, is not recorded in the Molasse Basin; it is known only from neighbouring biomes in the south (Höwenegg, MN9, Germany) and east (Wolfsegg, MN9, Austria).

We hypothesize that during MN6 the Molasse Basin wetland offered an extremely diverse spatio-temporal habitat structure with a large variety of niches with browsing and mixed feeding. The mosaic landscape was formed by the alternation of seasonal flooding and dry seasons. When seasonality started to increase in Europe, the sensitive seasonal cycle was altered, causing the break up of the mosaic wetland environment. Also, because of the rising land masses and the retreating Paratethys, more areas became dry land. It is common knowledge that wetlands are one of the most fragile parts of global biomes, and there is no reason to believe that this was different 10 million years ago.

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