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A comparison of estimates of mean annual precipitation from different proxies: a pilot study for the European Neogene

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ABSTRACT

Question: How well does the precipitation estimate method based on fossil mammal evidence correspond with results from the paleobotanical co-existence approach?

Data: Large herbivorous fossil mammals and plants for Western Eurasia. Data cover 23 to 2 million years ago. The data come from the NOW database and data compilation of the NECLIME Project.

Research method: We used standard statistical methods and GIS to compare plant and mammal proxies at different resolutions and through time.

Conclusions: The mammal and paleobotanical proxies give precipitation estimates that are very close to each other. On the regional scale, the integrated patterns are consistent. Overall, paleobotanical reconstruction gives higher precipitation estimates than those based on fossil mammals.

Keywords: Europe, fossil mammals, Neogene, paleobotany, paleoclimate.

INTRODUCTION

There is increasing interest in reconstructing the climate of the past. Various methods are available for climate reconstruction, including leaf margin analysis (Wolfe, 1979), the Climate Leaf Analysis Multivariate Program [CLAMP (Wolfe, 1993)], the co-existence approach (Mosbrugger and Utescher, 1997), and the climate amplitude method (Fauquette *et al.*, 1998). Reconstructions are used for various purposes, such as to derive quantitative climate estimates to validate climate models and to make comparisons between past, present, and future environmental conditions. Yet the applicability of, and differences between, methods in

different settings are not yet fully understood. This is especially true for older time periods, such as the Neogene (from 23 to 2 million years ago, Ma).

During the Cenozoic, the climate changed from the warm climate of the Paleogene into the Quaternary glacial phase (e.g. Zachos *et al.*, 2001). The Neogene is in the middle of this development, having large climatic oscillations. The Early Miocene was still warmer and more humid than today (e.g. Bruch *et al.*, 2004; Mosbrugger *et al.*, 2005), but towards the Late Miocene and Pliocene it changed towards cooler conditions (e.g. Fauquette *et al.*, 2007). The changes in the vegetation and mammalian faunas reflect this (e.g. Fortelius *et al.*, 2002; Utescher *et al.*, 2011). Major ecosystems changes include diminishing subtropical forests and the spread of grasslands during the Miocene (e.g. Jacobs *et al.*, 1999; Fortelius *et al.*, 2002, 2006; Willis and McElwain, 2002; Mosbrugger *et al.*, 2005).

The present pilot study aims to investigate differences in precipitation estimates in deep time, derived from two different fossil sources. We explicitly limit our investigation to just two methods, the co-existence approach and large mammal hypsodonty method (see below), and to the Neogene period, to allow us to compare these methods fully. In future studies, other proxy methods will also be taken into account, but that is beyond the scope of the present paper.

We are interested in whether different preservation potential causes discrepancies in the two proxy methods. We also investigate whether there might be other possible causes for discrepancies. For example, mammals can move – and track – their preferred habitat within their lifespan, while in plants migrations occur at the generation level. This raises the question of whether mammals react faster to changes in paleoprecipitation, i.e. their tolerance level is lower than that of plants. On the other hand, it has been suggested that plant proxy methods might have difficulties with precipitation reconstruction when water comes from sources other than rainfall (Utescher *et al.*, 2000).

Based on the above hypothesis, our focus is on whether paleobotany provides higher estimates of precipitation in drier climates, while in humid environments the two proxy methods are in better agreement. In other words, our aim is to investigate whether there are certain areas or situations where the methods do not perform well, and whether there are consistent differences between them. It is beyond the scope of this paper to investigate the causes of the differences in detail. Here we highlight possible areas or situations where there are differences in proxies for further studies and discuss their possible causes.

METHODS AND MATERIALS

Data

The plant data we use are from the NECLIME data set as published in the PANGAEA database (http://www.pangaea.de). The set comprises a total of 248 macro (fruits and seeds, leaves) and micro (pollen/spores) floras. For the mammal data set used in this study, we downloaded a dataset from the NOW database on 24 April 2009 (Fortelius, 2009: see http://www.helsinki.fi/science/now). We use all large mammal data between 23 and 2 Ma, encompassing the European Neogene mammal units MN1 to MN17. Only large herbivorous mammals are considered; all small mammals (orders Lagomorpha, Chiroptera, Rodentia, Insectivora) as well as carnivores (orders Carnivora and Creodonta) are deleted from the data set. We use only herbivorous large mammal localities that have at least

two tooth crown height data recorded. The data set comprises a total of 729 fossil mammal localities.

We limit our investigations to Europe for which there are enough reliable data for most of the Neogene and enough data to correlate plant and mammal localities. To average regional variation and substitute our lack of data from many areas, we re-plot them to a relatively coarse grid. For grouping the plant and mammal localities together, we use a Gaussian grid with a horizontal resolution of $3.75° \times 3.75°$ for longitudes and latitudes. Global climate model experiments for the Late Miocene use the same grid resolution (Micheels *et al.*, 2007, 2011). The use of a specific grid is arbitrary, but for this study it is sufficient to use a relatively coarse grid, because the sites are scattered. Our choice of $3.75° \times 3.75°$ represents a good compromise to overcome the representation of regional details of single localities and to avoid missing data of some regions either from the botanical or the mammal record. The use of a grid similar to the one used in climate models also allows our results to be readily compared with climate model data in future studies.

We divided our data into five time slices, using the MN-units from the NOW database as a base, according to Steininger (1999): Early Miocene (MN1–MN4, 23–17 Ma), Middle Miocene (MN5–MN7+8, 17–11 Ma), early Late Miocene (MN9–MN11, 11–8 Ma), late Late Miocene (MN12–MN13, 8–5 Ma), and Pliocene (MN14–MN17, 5–2 Ma). We also define three areas of interest (Central Europe, Northern Black Sea area, Eastern Mediterranean). The Northern Black Sea coast and the Eastern Mediterranean are areas where mammal fauna suggest open environments, or drier conditions, while plant fossils do not support the existence of these (for more details, see Bruch *et al.*, 2011). For control, we also include Central Europe, where conditions remained more stable throughout the Neogene.

Estimation of precipitation values

For the paleobotanical data, the quantitative data available for mean annual precipitation (MAP) originate from the application of the co-existence approach (for a detailed description, see Mosbrugger and Utescher, 1997). The basic idea of the co-existence approach is very simple and follows the nearest living relative philosophy, which assumes that the climatic requirements of a fossil taxon are similar to those of a taxonomically very close living relative. Based on the assumption that the climatic requirements of Cenozoic plant taxa are similar to those of their nearest living relatives, the aim of the co-existence approach is to find the climatic ranges in which a maximum number of nearest living relatives of a given fossil flora can co-exist. The co-existence approach provides the lower and upper limit of, for example, mean annual precipitation, the co-existence interval in which the fossil flora existed. These co-existence intervals are then considered the best description of the paleoclimatic situation under which the fossil flora lived.

The co-existence approach is based on only a few assumptions. These are:

1. For fossil taxa, systematically closely related nearest living relatives can be identified.
2. The climatic requirements of a fossil taxon are similar to those of its nearest living relative.
3. The climatic requirements or tolerances of a nearest living relative, and thus of the fossil taxon, can be derived from its area of distribution. Implicitly, it is also assumed

that the meteorological stations provide adequate and reliable data to describe the climatic tolerances of modern taxa.

4. The modern climatic data used are reliable and of good quality (for a detailed description, see Mosbrugger and Utescher, 1997).

The MAP data used here originate from the following sources: Bruch (1998), Utescher *et al.* (2000, 2007a), Bruch *et al.* (2002, 2004, 2006, 2007), Ivanov *et al.* (2002), Mosbrugger *et al.* (2005), Akgün *et al.* (2007), Erdei *et al.* (2007), and Syabryaj *et al.* (2007). For the present study, we use only sites that can be dated within the time slices described above. A direct correlation with the mammal zones is only possible for about 10% of cases. The major part is allocated to the five time slices using indirect correlations, as has been published for the sites. The paleobotanical data set is not only heterogeneous with respect to the quality of dating but also with regard to the climate resolution obtained. The resolution strongly depends on biodiversity and organ type of the fossil floras. This drawback is tolerated so as to have substantial data at our disposal when analysing consistency of precipitation data derived from paleobotanical and mammal proxies.

For the large mammal data set, we use a new method developed by Eronen *et al.* (2010). According to this method, we use large herbivorous mammal molar tooth crown height and its distribution and variation at the community level to derive estimates for mean annual precipitation. It is based on the calibration of the present-day herbivorous mammalian fauna to precipitation. This method works well for precipitation estimates up to 1500 mm per year. In excess of 1500 mm, the method saturates and the values should be understood as 'greater than 1500 mm'. Here we use the actual values, but note that the extremely high values are most likely overestimates (see discussion in Eronen *et al.*, 2010).

In this paper, we only use MAP values. The combined data set of mean annual precipitation estimates based on the co-existence approach and large mammal hypsodonty is available upon request from the authors.

Methods of comparison

To facilitate comparison, we calculate grid-specific values using both mammal and plant data. For the mammal data, we calculate the mean, the maximum, and the range of precipitation values for each grid cell using all localities within grid cells. For the plant data, we define the co-existence intervals for all plant localities, and then calculate the maximum range of the intervals, the intervals' average, and the average range within grid cells. This is necessary because the co-existence approach does not define any mean values within the co-existence interval (see Mosbrugger and Utescher, 1997). Finally, we calculate three different metrics for precipitation differences: (1) DIFF-1 compares the maximum ranges of both mammal and plant data; (2) DIFF-2 compares the averaged intervals; and (3) DIFF-3 is the difference between the mean of mammal data compared with the average range of plant data. It should be noted that a comparison of the averages of the mammal data with the averages of the botanical data is not meaningful. Plant proxy data are based on the co-existence approach providing a precipitation range but not an average value. Any value within the co-existence interval has the same likelihood. We calculate the metrics DIFF-1 to DIFF-3 for each time slice for the whole data set, for the selected regions, and for each grid cell. In the following analysis of results, we only consider those grid cells that have at least one plant and one mammal locality.

To estimate whether values between the two methods differ, we use the Gaussian error propagation equation:

$$\sigma_{\text{total}} = \sqrt{\sigma_{\text{LM}}^2 + \sigma_{\text{CA}}^2}$$
$$= \sqrt{(388 \text{ mm/a})^2 + (200 \text{ mm/a})^2} \qquad (1)$$
$$= 437 \text{ mm/a}$$

where σ_{LM} and σ_{CA} represent the standard deviations of the large mammal hypsodonty and the co-existence approach, respectively, and σ_{total} is the resulting total standard deviation. The large mammal data have an error of 388 mm per year (mm/a) (Eronen *et al.*, 2010). No data exist on statistical uncertainty for the co-existence approach. Based on possible uncertainties due to accuracy of extant climate data, nearest living relative interpretation, and evolutionary trait adaptations (see above discussion on co-existence approach methodology), we assume here an uncertainty of 200 mm/a for the co-existence approach. Equation (1) shows that precipitation differences between the two techniques >437 mm/a, rounded to 450 mm/a, can be considered as disagreement and those that are smaller than the threshold can be considered as agreement. Taking into account uncertainties, such as the assumed uncertainty of the co-existence approach, we prefer a more conservative assumption. In this study, we assume differences of ≤300 mm/a as agreement, whereas values ≥600 mm/a represent disagreement. In this study, values in between these two figures are regarded as potential disagreement:

≤300 mm/a	$< \sigma_{\text{total}} <$	≥600 mm/a
agreement	potential disagreement	disagreement

We apply the total standard deviation to the grid-specific values, to average over regional variation.

RESULTS

Overall trends

The comparison of mean precipitation estimates (Fig. 1a) at grid cell level shows that the values are quite similar. As a general observation, the plant data tend to have slightly higher precipitation estimates. The bias is not an effect of time, as all time periods we used seem to have similar differences. This tendency also holds for the regional mean precipitation values in the Eastern Mediterranean and the area north of the Black Sea. In Central Europe, the mean precipitation estimates match quite well (Fig. 1b, c, d).

The trends averaged over larger areas (Fig. 2) are similar in the two data sets. At continental level (Fig. 2a), both proxies depict a drying trend from the Early Miocene to late Late Miocene, and then more humid conditions for the Pliocene. For mammal data, this is more visible. The paleobotanical precipitation estimates show more stable conditions, with only slight drying towards the late Late Miocene. At regional level, Central Europe (Fig. 2b)

has very similar estimates from the two proxies, with very small differences of less than 100 mm on average. This is within the uncertainties of the methods. The estimated range of precipitation based on plant data is very narrow, and close to the estimated mean of mammal data. We lack data for the late Late Miocene from this area.

In the Eastern Mediterranean (Fig. 2c), the pattern is different. The diferences are larger, and during the late Late Miocene the estimated mean values are >100 mm. Still, they are within the uncertainties of the methods. During the Middle and early Late Miocene, the differences are smaller, but visible. The estimated range of precipitation based on plant data is very wide during the early Late and late Late Miocene. Also, the overall values are much low than in other areas, indicating generally drier conditions. In the area north of the Black Sea (Fig. 2d), the plant and mammal data show congruence, with mean estimates of mammal data within the estimated range of precipitation based on plant data for the Late Miocene (time slices 3 and 4). For the Middle Miocene, the differences are greater.

Spatial patterns

For the spatial patterns, we concentrate on DIFF-3 metrics (Figs. 3–6, the difference between the mean of mammal data compared with the average range of plant data). We provide figures for DIFF-1 (the maximum ranges of both mammal and plant data) and DIFF-2 (the comparison of the averaged intervals) in the supporting material online (supplementary figures available at: evolutionary-ecology.com/data/2659Appendix.pdf), but do not discuss them in detail.

For DIFF-1 (supplementary figures 1–4) there are no large differences. This is not surprising as the full ranges of both data sets are extremely large and cover most of the possible climatic space. DIFF-1 is the best metric to identify regions/sites where the different proxy data totally disagree. These are in Southern France and the Crimea during the Middle Miocene, and in Crete during the early Late Miocene.

There were also highly consistent patterns for DIFF-2 (supplementary figures 5–8), with few areas showing disagreement. In addition to the ones described above, there are two grid cells in the Early Miocene of Central Europe, as well as grid cells in the Eastern Mediterranean and north of the Black Sea in the Middle Miocene. During the early Late Miocene, there are some differences in Eastern Europe. The dry biases are in the eastern part, while the wet biases are in the Western part. Most of the differences are within 200 mm, so within the uncertainties of the comparison method. Note that DIFF-2 includes averaged intervals, so most local and sub-regional differences are smoothed.

DIFF-3 (the difference between the mean of mammal data compared with the average range of plant data) has the best potential to compare both approaches because it really shows areas where data are in agreement and where they are not. The values for different approaches used in DIFF-3 are also those that are usually quoted in publications (e.g. Eronen *et al.*, 2010).

For DIFF-3, the Early Miocene (Fig. 3) shows quite large discrepancies within Central Europe. There is one grid cell where there is a probable dry plant bias, and two grid cells where there is a large mammal dry bias. One of these is for certain (that of North Germany). In Spain, there is one grid cell with a slight mammal dry bias (180 mm), and one probable discrepancy of 317 mm for plant dry bias. In the Eastern Mediterranean, there is a small discrepancy of less than 100 mm.
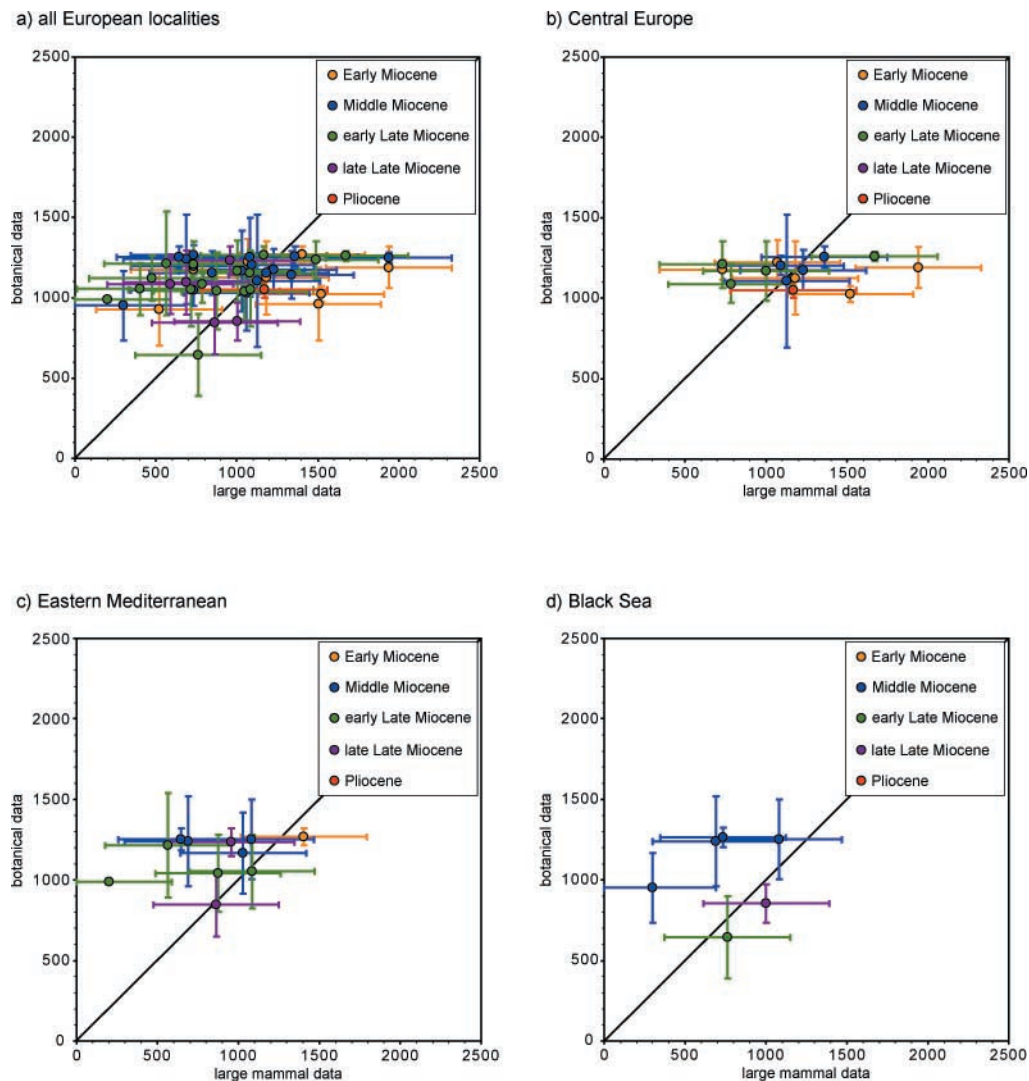
Fig. 1. The reconstructed mean annual precipitation (mm) based on botanical data (y-axis) plotted against estimates based on large mammal data (x-axis) for (a) all European localities, (b) Central Europe, (c) the Eastern Mediterranean, and (d) the Black Sea region. Early Miocene sites are shown in orange, Middle Miocene in blue, early Late Miocene in green, late Late Miocene in purple, and Pliocene in red. The dots refer to the means of the precipitation intervals and the bars represent the span width of the data. Data plotted above the diagonal line represent more humid conditions in the botanical data than in the mammal data; data plotted under the diagonal line represent more humid conditions in the mammal data than in the botanical data.

For the Middle Miocene (Fig. 4), there are disagreements in all parts of Europe. Most of the areas with differences have slight discrepancies (less than 300 mm), but many grid cells have larger discrepancies. Eastern Europe and the Eastern Mediterranean in particular have larger discrepancies where plants represent drier conditions, but none of these is for certain
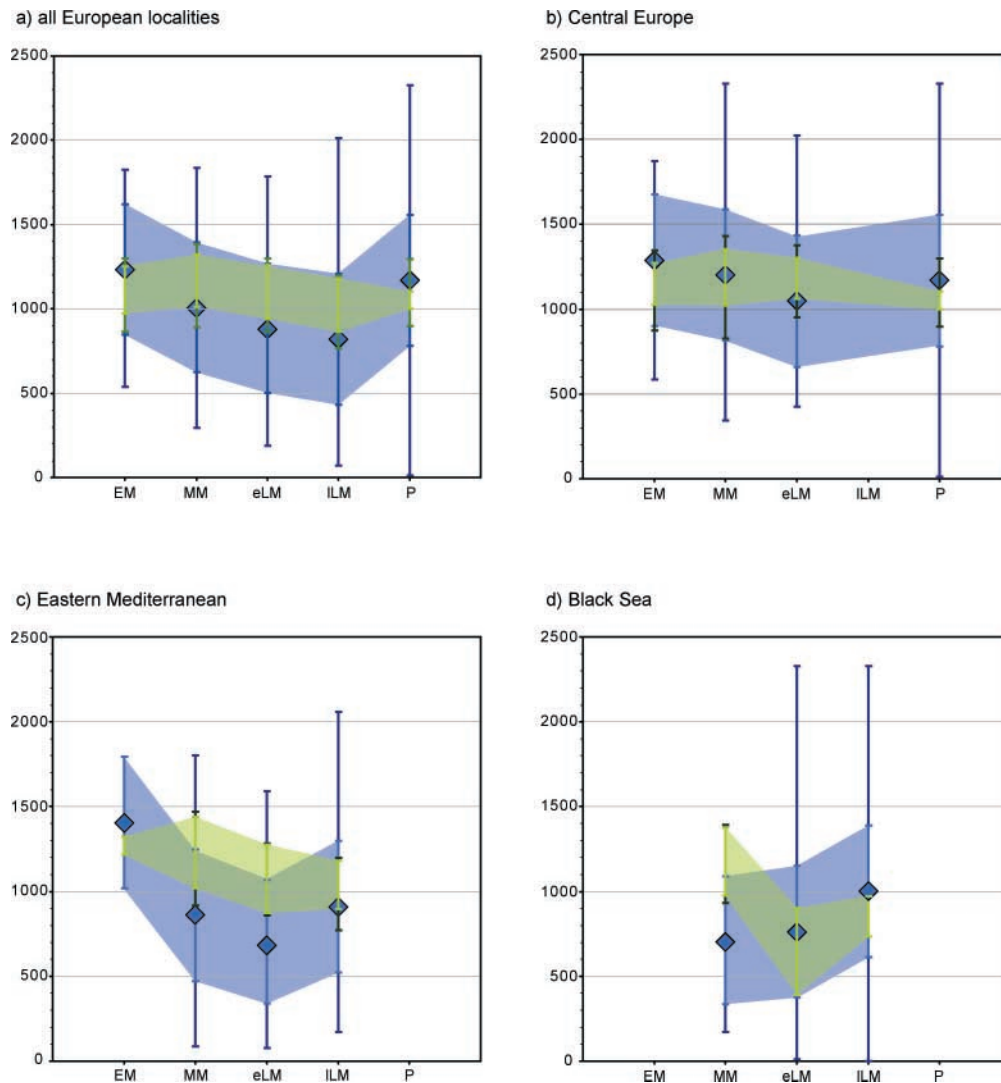
Fig. 2. The reconstructed mean annual precipitation (mm) based on botanical (green) and large mammal data (blue) for the five selected time intervals for (a) all European localities, (b) Central Europe, (c) the Eastern Mediterranean, and (d) the Black Sea region. Light green lines and shading illustrate the mean minimum–maximum ranges based on plants; light blue lines and shading illustrate the mean minimum–maximum ranges based on mammals; blue diamonds represent the centre of mean precipitation ranges based on mammals. EM = Early Miocene, MM = Middle Miocene, eLM = early Late Miocene, lLm = late Late Miocene, P = Pliocene.

beyond the uncertainties. In Southern France, there is one grid cell with a real discrepancy with mammal data indicating extremely wet conditions, while plants suggest more moderate humidity.

The same tendency is visible in the early Late Miocene (Fig. 5), with disagreement in particular in the eastern part of Central Europe and Eastern Europe. There are a number of

grid cells with some disagreement (over 300 mm), but an equal number of grid cells show agreement or minor differences. One grid cell in the Eastern Mediterranean represents a real difference (>600 mm) and grid cells in the Balkans (510 mm) and in Eastern Europe (493 mm) also show probable differences.

For the late Late Miocene (Fig. 6), we have few data that can be used for comparisons. In the late Late Miocene, there are grid cells that are in agreement, as well as a few where the differences are slight.

Grid-specific comparisons

To analyse cases where there are potential real discrepancies (>300 mm) between the mammal data and values calculated from paleobotany, we investigate the species lists of the localities. For paleobotanical data, we review primary floral lists as published by the authors and corresponding nearest living relatives. For fossil mammals, we mainly concentrate on those cases where mammals give higher mean estimates than paleobotany. To investigate this in more detail, we review the species list from the NOW database.

Early Miocene

For the Early Miocene (Fig. 3), the highest offset between the two data sets is observed for Central European grid cells. In the Early Miocene reconstruction (Fig. 3), there are two grid cells where fossil mammals give higher estimates than paleobotany.

For the northern grid cell, the most probable cause of differences is the geography. The paleobotanical sites are located in the northernmost part of the grid, whereas the mammal localities are in the southern part, and are just north of the wetland of the German Molasse Basin.

The grid cell further south is located in the southern part of the German Molasse Basin. There is large variation within the localities in this grid cell, from 700 to 1900 mm. Although values as high as 1900 mm are probably overestimates, there is much spatial variation, and this variation is reflected in the species lists of different localities. Eronen and Rössner (2007 and references therein) interpreted the German Molasse Basin as a highly mosaic wetland with large seasonal variation in precipitation. Although the paleobotanical localities have precipitation estimates that are within the large range of the mammal-based precipitation estimates, the average range falls outside the mean of mammal localities. Plant-based data for this grid cell refer to a single fruit and seed flora (Langenau). Shrubs and herbs confined to precipitation rates less than ~1100 mm (nearest living relatives are *Vitis vinifera* var. *sylvestris* and *Cleome lutea*) are responsible for the comparatively moderate MAP level of the reconstructed data. Apart from a local, aquatic component, vegetation can be interpreted as predominantly humid, mixed evergreen-deciduous forest. Monthly precipitation values calculated for the flora support the presence of a drier season. In addition, work by Kovar-Eder *et al*. (2008) using sclerophyllous and legume-type angiosperms as indicators for (seasonal) dryness point to the presence of sub-humid forests and seasonal rainfall for some late early to middle Miocene sites for the same grid cell.

A grid cell in north-west Germany (with a difference of 382 mm) has an unrealistically low estimate based on mammal data (733 mm), even though all species present were brachydont (low-crowned). This would indicate that it was humid. But because it has a short species list with only two species, the method produces lower estimates. The grid cell at
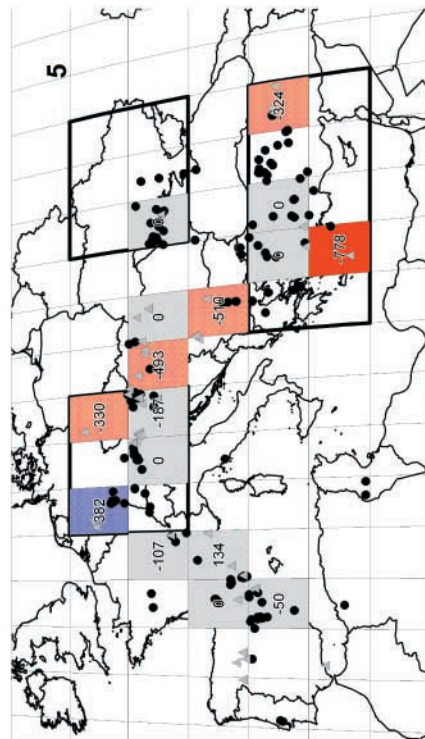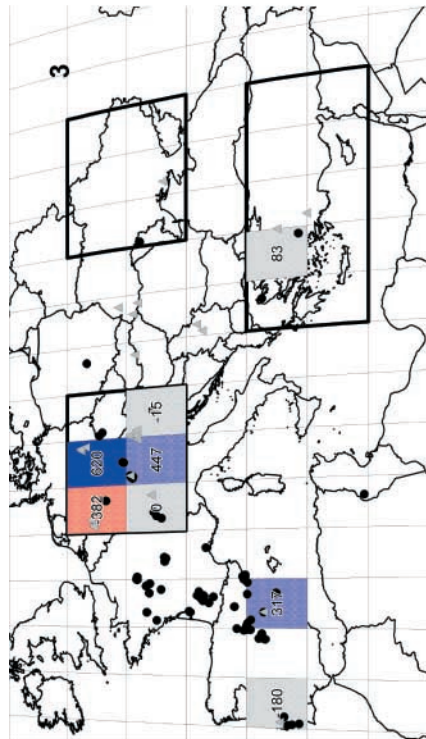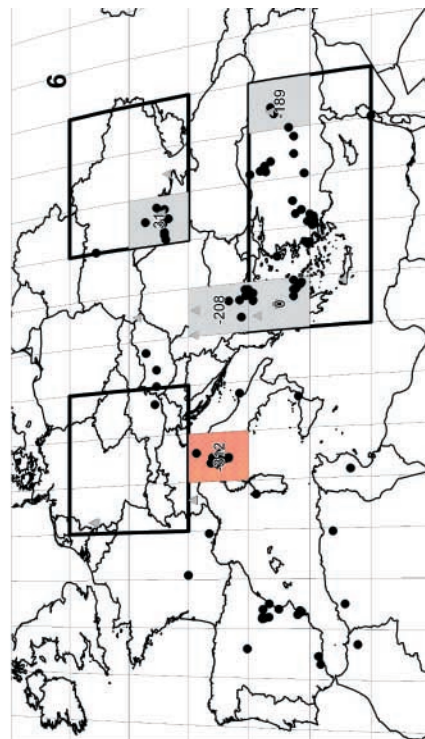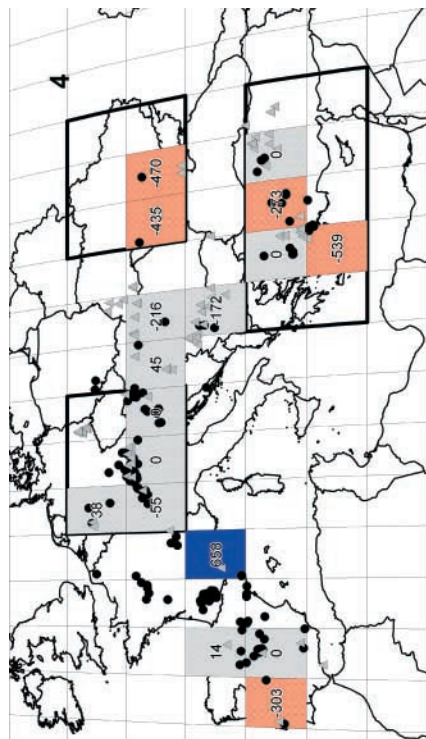
Figs. 3–6

the eastern coast of Spain has a number of species-rich mammal localities. All of these point towards very humid environments, so there the potential differences are not an artifact of the method.

Middle Miocene

For the Middle Miocene (Fig. 4), there are some discrepancies. The one grid cell where there is a large discrepancy is in Southern France/Northern Spain. The mammal estimates are more than 600 mm higher than those derived from paleobotany. Both mammal sites (Can Feliu and Castell de Barberà) have long species lists, with a large number of brachydont species, suggesting that the environments were humid. However, values as high as 1900 mm are probably overestimates. Plant-based data for this grid refer to a single flora (Baynna) with a precipitation estimate of 1280 mm. Although there is a real discrepancy, some of it is artificial, as it is based on an overly high estimate from one of the mammal localities. Both proxies nevertheless point towards humid conditions, with the plant data suggesting more moderate values than the mammal data.

The areas where there are potential discrepancies are the Northern Black Sea area, the eastern Central Paratethys (Serbian sites), and again Western Anatolia. For the Mid-Miocene sites of Ukraine, the two data sets hardly overlap. For the Korobki and Leninskoe sites located in the coastal areas of the Ukraine plain, there is some evidence for MAP well above 1000 mm from the microbotanical record (e.g. Cyatheaceae, *Cathaya*, *Trigonobalanus*). For the mammals, there is only one site with two brachydont taxa from the northern part of the grid cell. This suggests a similar underestimation of precipitation as in the Middle Miocene of north-western Germany (see above). At least for the early part of the time slice, diverse mesophytic forest cover with a subtropical character accounts for the southern part of Ukraine (Syabryaj *et al.*, 2007). However, herbaceous components became more important in the later part of the Middle Miocene. This increase of herbaceous components can in part be related to a drop in sea level and colonization of coastal mudflats (Syabryaj *et al.*, 2007). For the western grid cell (where the difference is 435 mm), there are two mammal sites, both with a short species list, suggesting bias in mammal estimates.

The grid cell 'Büyük Menderes region' (Western Anatolia) has also no overlap. High MAP rates around 1200 mm based on the paleobotanical data again refer to the presence of

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Fig. 3. The difference between the mean of mammal data compared with the average range of plant data for the Early Miocene for grid cells. For grid cells, grey denotes no difference, light blue denotes mammals giving slightly higher estimates than plants. Deep blue denotes disagreement between proxies, with the mammal estimate being more humid. Light red denotes plants giving slightly higher estimates than mammals. Bright red denotes disagreement between proxies, with the plant estimate being more humid.

Fig. 4. The difference between the mean of mammal data compared with the average range of plant data for the Middle Miocene for grid cells. For colour coding, see Fig. 3.

Fig. 5. The difference between the mean of mammal data compared with the average range of plant data for the early Late Miocene for grid cells. For colour coding, see Fig. 3.

Fig. 6. The difference between the mean of mammal data compared with the average range of plant data for the late Late Miocene for grid cells. For colour coding, see Fig. 3.

the genus *Trigonobalanus*. Regarding the floral record compiled for this region (Akgün *et al.*, 2007), precipitation below a threshold of about 800 mm is unlikely because in this case a closed forest cover would have existed at that time. On the other hand, relief and coastal exposition could have caused considerable local gradients in the considered region. The mammal sites are not rich and, therefore, they might slightly underestimate the precipitation. Probably the environment was not extremely dry (<400 mm precipitation), and the higher estimates from mammals suggest precipitation around 700 mm.

For Serbia, some diverse macrofloral records suggest MAP around 1200 mm (presence of the genera *Craigia* and *Persea*). Significant drying occurred in Serbia during the middle Miocene, with MAP falling well below 1000 mm (Utescher *et al.*, 2007a). Thus, paleobotany-derived data are within the range of mammal estimates. For some of the floras, for example Bozdarevac (Utescher *et al.*, 2007a), there is also evidence for a distinct dry season. Furthermore, the existence of a dry season in that area is supported by the analysis of diversity spectra of plant functional types for the floras Popovac, Melnica, and Misaca (Utescher *et al.*, 2007b). However, the minimum amount of annual rainfall as indicated by paleobotanical proxies stands against open landscapes in the Middle Miocene of Serbia. In addition, the northern grid cell of the two Serbian ones has only one mammal site, with a short species list (see discussion above about short lists). The southern Serbian cell has three mammal sites, with precipitation estimates ranging up to 1400 mm.

Early Late Miocene

In the early Late Miocene (Fig. 4), most of the disagreements between proxies are in the Eastern Mediterranean and in Serbia. In addition, there are two grid cells in Central Europe with a potential discrepancy (over 300 mm). The Northern German grid cell has multiple mammal localities. The estimates for mammal localities range from 1400 to 1900 mm. The variation is reflected also in the community structure. The most humid localities contain tapirs, chalicotheriums, cervids, and primates. These taxa are associated with humid and closed forest environments. Although the highest values (1900 mm) might be overestimates, the signal from these localities firmly points to very humid environments. Utescher *et al.* (2009) report values of 1300 mm that are close to the lower limit obtained from fossil mammals from the Lower Rhine Basin. That is about 500 mm higher than the present-day annual rainfall. Even with today's amount of rainfall, closed forest cover would be the natural vegetation. A Late Miocene climate model experiment also supports the wet conditions in Northern Central Europe due to increased moisture transport from the Atlantic Ocean into the European realm (Eronen *et al.*, 2009; Micheels *et al.*, 2011).

The northeastern Central European grid cell (with a difference of 330 mm) has many fossil mammal localities. The precipitation estimates have wide ranges, from as low as 300 mm up to 1900 mm. Most of the low values are caused by the underestimation of precipitation because of short species lists. Disregarding these, the mammal estimates are in a similar range as the paleobotanical evidence.

The grid cell with a potential difference of 493 mm has only one mammal locality, Csakvar. This is a species-rich locality, and while 500 mm might be underestimating the precipitation, the faunal composition suggests a mixed environment with quite low precipitation values. The paleobotanical data (Balatonszentgyörgi flora) located in the same grid cell might be slightly younger (base of MN12). The precipitation estimates are higher than those from mammals, based on the presence of *Rhus* sp., which indicates MAP rates over 730 mm (co-existence approach interval 735–1356 mm).

The grid cell in Serbia/Bulgaria (with a possible difference of 510 mm) has five mammal localities, all indicating dry conditions. The highest of these estimates is about 700 mm. The macrofloral record of Serbia clearly stands against dry conditions, with MAP above 1000 mm depending on the taxonomic interpretation of Lauraceae leaves as *Persea*. Being less specific, at least 800–900 mm result for this region, suggesting that estimates from mammals and botanicals are very close.

The southernmost paleobotanical site of the time slice is Makrilia on Crete. In Crete there is only one mammal locality during the early Late Miocene. This has only two species, and therefore the precipitation estimate is probably an underestimation. The diverse macroflora of Makrilia reflects mixed mesophytic vegetation with a clearly perhumid aspect. Consequently, the range cited in the paleobotanical data appears to be justified but might reflect local climate conditions (e.g. orographic precipitation). While for western Anatolia the two data sets are in good agreement, annual precipitation rates well above 800 mm [presence of Cycadaceae and *Engelhardia* in the microfloras (Akgün *et al.*, 2007)], as derived from East Anatolian botanical sites, stand against the dry end of the mammal data.

The grid cell in Eastern Turkey (with possible difference of 324 mm) has two mammal localities. Both of them have few species, with the majority brachydont species. This suggests that there might be a slight underestimation of precipitation. A Tortonian climate model run supports drier-than-present conditions in that area (Eronen *et al.*, 2009; Micheels *et al.*, 2011) and hence the presence of open landscapes. In the paleobotanical estimates, more than 10% of the taxa recorded indicate MAP > 800 mm, while the presence of *Lygodium* even points to rainfall rates > 1100 mm.

Late Late Miocene

In the late Late Miocene time slice, mammal and paleobotanical data are in quite good agreement. The Northern Italian grid cell shows some offset between the two data sets for part of the Velona microfloras. However, the high annual rainfall derived from the Velona palynofloras fits with the general model obtained when analysing Messinian vegetation of Northern Italy, i.e. the existence of hygrophilous, warmth-loving vegetation types, not only based on pollen but also on the macrofloral record using an integrative approach (e.g. Bertini and Martinetto, 2008). Most of the mammal localities are insular faunas with highly variable precipitation estimates. This suggests that there might be large local differences because of paleogeography during this time.

DISCUSSION

Based on our results, in some areas the differences in precipitation estimates are large, and cannot be easily accounted for. For the Middle Miocene these are the Eastern Mediterranean, especially Turkey, and one grid cell in Southern France. For the early Late Miocene, these include the Central European area where mammals suggest much more arid conditions, Makrilia, and Eastern Turkey. For the late Late Miocene, there is only one grid cell in Italy.

There are several reasons why differences are larger in these areas. First, most of them indicate arid conditions based on mammals, and humid or semi-humid conditions based on plants. In the dry parts of climate cycles, the preservation potential of plant remains and organic matter in general is low (for discussion, see Bruch *et al.*, 2011), and even palynomorphs consisting of comparatively chemically resistant sporopollenine may not outlast highly

oxidizing conditions. Hence, the fossil plant record in each case might represent the wetter part of a climate cycle.

Another important aspect that these places have in common is local geography, which affects facies development. The vast majority of sites are located in sedimentary basins where in general a high groundwater level can be assumed. Thus, water supply for the local vegetation did not necessarily depend on precipitation alone. This has to be considered when climatically interpreting taphocoenoses consisting of (par)autochthonous elements (mainly holds for leaf floras). Furthermore, sedimentary facies and the depositional environment at the plant sites are not arbitrary. In most cases, remnants are found in pelites and browncoal, deposits that often correspond to a higher level of the erosional base and thus to global warm and wet phases. On the other hand, precipitation reconstructions from microfloras of the Ukraine Plain show that the co-existence approach in general is well capable of resolving drying pulses (Syabryaj *et al.*, 2007).

Even when paleobotanical and fossil mammal localities are geographically proximal, one might be sampling different environments, especially since time-averaging the spatial scale the fossils represent is different between fossil palynological-, leaf-, and mammal-assemblages. Because of this, these different types of fossil may represent different ends of the local to regional environmental climatic spectrum. Under very dry climate conditions, preservation potential for plant remains in general is diminished (see above). For large mammal fossils, there is not so strong a bias, although deposits like coarser clastic successions favour preservation of fossil mammals in arid habitats over closed forest. For example, at the same time as there was close vegetation cover for the continental inland basins in Turkey, there might have existed open vegetation in the surrounding uplands, and because of preservation the different proxies reflect these differences. This results in a discrepancy where the paleobotanical data suggest the former, and the mammal data the latter kind of environment.

Another reason for discrepancies might be that the fossil mammal proxies seems to be more sensitive to changes. Our results also suggest that the within-grid variation in estimated precipitation is much higher between mammal fossil sites than in paleobotanical sites. This is surprising, as fossil mammals sites are thought to have plenty of temporal time-averaging (Jernvall and Fortelius, 2004), and therefore one would not expect so much variation. One possibility is that mammal evidence overestimates the precipitation gradients, because there are habitat-tracking (e.g. Eronen and Rook, 2004) and migration processes operating in addition to adaptation that decrease the response time of mammal assemblages to environmental changes. This discrepancy is especially visible in the Middle and early Late Miocene in our data. In addition to higher within-grid variation, at the European scale mammals reflect more humid conditions in the west, while in the east the mammal proxy estimates are much drier than those derived from paleobotanical sources. This difference is most prominent on a regional level. This is interesting, as one would expect that plants are more sensitive to precipitation changes, especially at the dry end of the climatic spectrum, because they are stationary and short-term drying pulses in the climate cycles lead to the disappearance of drought-intolerant components.

In addition to high spatial variation, also short-term temporal variation caused by, for example, orbital changes, in precipitation rates might cause discrepancies in the present data. For example, considerable changes up to 400 mm for MAP are recorded from a Pontian sequence of Northwestern Bulgaria (Utescher *et al.*, 2009). Also, significant differences are seen between the seasons. Unfortunately, such data are hard to infer

from the fossil record, and we rarely have the information about which season we are sampling.

Fortunately, in some cases, the reasons for proxy data discrepancies are fairly easy to decipher, as in the Northern German area during the Early Miocene, and the Crimean area during the Middle Miocene. In both areas, fossil mammal evidence clearly suggests more humid conditions than paleobotany, but the localities are situated in opposite corners of the grid cell. The long geographic distance between the mammal and botanical localities is the most probable cause for these differences.

Accounting for all the possible biases above, it is surprising that in most cases the differences between the two methods are less than the mean errors of the methods, and the trends in both methods are similar.

CONCLUSIONS

Overall, taking into account the extent and duration of the time slices, the paleobotanical and fossil mammal precipitation estimates are surprisingly similar. On a methodological level, our results suggest that much of the incongruence between our proxies is caused by short species lists in some of the fossil mammal localities that result in marked underestimation of precipitation. This effect is mainly seen in fossil mammal localities that have less than five species. In these cases even though all, or the large majority, of species are low-crowned (suggesting closed and humid environments), the precipitation estimates suggest too dry conditions compared with paleobotanical estimates. To confirm this, we need further studies focusing on sites where large mammals and plant remains originate from the same horizon.

On a more general level, our results highlight that there are more discrepancies between our proxies in the dry end of the spectrum, or when there are large-scale fluctuations in environmental conditions. In these conditions, the mammal proxy tends to result in slightly lower estimates of precipitation than the paleobotanical evidence, partly because the fossil record does not reflect the same part of the climate cycle. In stable conditions, the evidence from palaeobotany and fossil mammals is in good agreement, especially under humid conditions, like in the Neogene of Central Europe. Therefore, reconstructions from sites in potentially arid settings should rely on multiple proxies. Especially in paleobotany, both macro as well as micro remains should be investigated, to capture both local and regional conditions, respectively.

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REFERENCES

Akgün, F., Kayseri, M.S. and Akkiraz, M.S. 2007. Palaeoclimatic evolution and vegetational changes during the Late Oligocene–Miocene period in the Western and Central Anatolia (Turkey). *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **253**: 56–106.

Bertini, A. and Martinetto, E. 2008. Messinian to Zanclean vegetation and climate of Northern and Central Italy. *Bollettino Della Societa Paleontologica Italiana*, **47**: 105–121.

Bruch, A.A. 1998. Palynologische Untersuchungen im Oligozän Sloweniens – Paläo-Umwelt und Paläoklima im Ostalpenraum. *Tuebinger Mikropalaeontologische Mitteilungen*.

Bruch, A.A., Fauquette, S. and Bertini, A. 2002. Two quantitative approaches for climate reconstructions on Neogene palynofloras – an application on a late Miocene profile from the Velona Basin (Tuscany, Italy). *Acta Universitatis Carolinae – Geologica*, **46**: 27–37.

Bruch, A., Utescher, T., Alcalde Olivares, C., Dolakova, N., Ivanov, D. and Mosbrugger, V. 2004. Middle and Late Miocene spatial temperature patterns and gradients in Europe – preliminary results based on palaeobotanical climate reconstructions. *Courier Forschungsinstitut Senckenberg*, **249**: 15–27.

Bruch, A.A., Utescher, T., Mosbrugger, V., Gabrielyan, I. and Ivanov, D.A. 2006. Late Miocene climate in the circum-Alpine realm – a quantitative analysis of terrestrial palaeofloras. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **238**: 270–280.

Bruch, A.A., Uhl, D. and Mosbrugger, V., eds. 2007. Miocene climate in Europe – patterns and evolution. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **253**.

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

Erdei, B., Hably, L., Kazmer, M., Utescher, T. and Bruch, A.A. 2007. Neogene flora and vegetation development of the Pannonian domain in relation to palaeoclimate and palaeogeography. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **253**: 131–156.

Eronen, J.T. and Rook, L. 2004. The Mio-Pliocene European primate fossil record: dynamics and habitat tracking. *J. Human Evol.*, **47**: 323–341.

Eronen, J.T. and Rössner, G. 2007. Wetland paradise lost: Miocene community dynamics in large herbivore mammals from the German Molasse Basin. *Evol. Ecol. Res.*, **9**: 471–494.

Eronen, J.T., Mirzaie, M., Karme, A., Micheels, A., Bernor, R.L. and Fortelius, M. 2009. Distribution history and climatic controls of the Late Miocene Pikermian chronofauna. *Proc. Natl. Acad. Sci. USA*, **106**: 11867–11871.

Eronen, J.T., Puolamäki, K., Liu, L., Lintulaakso, K., Damuth, J., Janis, C. *et al.* 2010. Precipitation and large herbivorous mammals, Part I: Estimates from present-day communities. *Evol. Ecol. Res.*, **12**: 217–233.

Fauquette, S., Guiot, J. and Suc, J.-P. 1998. A method for climatic reconstruction of the Mediterranean Pliocene using pollen data. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **144**: 183–201.

Fauquette, S., Suc, J.-P., Jiminez-Moreno, G., Favre, E., Jost, A., Micheels, A. *et al.* 2007. Latitudinal climatic gradients in Western European and Mediterranean regions from the Mid-Miocene (≈15 Ma) to the Mid-Pliocene (≈3.6 Ma) as quantified from pollen data. In *Deep-Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies* (M. Williams, A.M. Haywood, F.J. Gregory and D.N. Schmidt, eds.), pp. 481–502, The Micropalaeontological Society, Special Publication. London: The Geological Society.

Fortelius, M., coordinator. 2009. *Neogene of the Old World Database of Fossil Mammals* (NOW), University of Helsinki. Available at: http://www.helsinki.fi/science/now/.

Fortelius, M., Eronen, J.T., Jernvall, J., Liu, L., Pushkina, D., Rinne, J. *et al.* 2002. Fossil mammals resolve regional patterns of Eurasian climate change during 20 million years. *Evol. Ecol. Res.*, **4**: 1005–1016.

Fortelius, M., Eronen, J.T., Liu, L., Pushkina, D., Tesakov, A., Vislobokova, I. *et al.* 2006. Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **238**: 219–227.

Ivanov, D.A., Ashraf, A.R., Mosbrugger, V. and Palamarev, E. 2002. Palynological evidence for Miocene climate change in the Forecarpathien Basin (Central Paratethys, NW Bulgaria). *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **178**: 19–37.

Jacobs, B.F., Kingston, J.D. and Jacobs, L.L. 1999. The origin of grass-dominated ecosystems. *Ann. Missouri Bot. Gard.*, **86**: 590–643.

Jernvall, J. and Fortelius, M. 2004. Maintenance of trophic structure in fossil mammal communities: site occupancy and taxon resilience. *Am. Nat.*, **164**: 614–624.

Kovar-Eder, J., Jechorek, H., Kvacek, Z. and Parashiv, V. 2008. The Integrated Plant Record: an essential tool for reconstructing Neogene zonal vegetation in Europe. *Palaios*, **23**: 97–111.

Micheels, A., Bruch, A.A., Uhl, D., Utescher, T. and Mosbrugger, V. 2007. A Late Miocene climate model simulation with ECHAM4/ML and its quantitative validation with terrestrial proxy data. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **253**: 267–286.

Micheels, A., Bruch, A.A., Eronen, J.T., Fortelius, M., Harzhauser, M., Utescher, T. *et al.* 2011. Analysis of heat transport mechanisms from a Late Miocene model experiment with a fully-coupled atmosphere–ocean general circulation model. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **304**: 337–350.

Mosbrugger, V. and Utescher, T. 1997. The coexistence approach – a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **134**: 61–86.

Mosbrugger, V., Utescher, T. and Dilcher, D. 2005. Cenozoic continental climatic evolution of Central Europe. *Proc. Natl. Acad. Sci. USA*, **102**: 14964–14969.

Steininger, F.F. 1999. Chronostratigraphy, geochronology and biochronology of the Miocene European Land Mammal Mega-Zones (ELMMZ) and the Miocene mammal-zones. In *The Miocene Land Mammals of Europe* (G.E. Rössner and K. Heissig, eds.). pp. 9–24. Munich: Verlag Dr. Friedrich Pfeil.

Syabryaj, S., Molchanoff, S., Utescher, T. and Bruch, A.A. 2007. Changes of climate and vegetation during the Miocene on the territory of Ukraine. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **253**: 153–168.

Utescher, T., Mosbrugger, V. and Ashraf, A.R. 2000. Terrestrial climate evolution in Northwest Germany over the last 25 million years. *Palaios*, **15**: 430–449.

Utescher, T., Mosbrugger, V., Bruch, A.A. and Milutinovic, D. 2007a. Climate and vegetation changes in Serbia during the last 30 Ma. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **253**: 141–152.

Utescher, T., Erdei, B., Francois, L. and Mosbrugger, V. 2007b. Tree diversity in the Miocene forests of Western Eurasia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **253**: 242–266.

Utescher, T., Ivanov, D., Harzhauser, M., Bozukov, V., Ashraf, A.R., Rolf, C. *et al.* 2009. Cyclic climate and vegetation change in the late Miocene of Western Bulgaria. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **272**: 99–114.

Utescher, T., Böhme, M. and Mosbrugger, V. 2011. The Neogene of Eurasia: spatial gradients and temporal trends – the second synthesis of NECLIME. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **304**: 196–201.

Willis, K.J. and McElwain, J.C. 2002. *The Evolution of Plants*. Oxford: Oxford University Press.

Wolfe, J.A. 1979. Temperature parameters of humid and mesic forests of Eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. *US Geol. Surv. Prof. Pap.*, **1106**: 1–37.

Wolfe, J.A. 1993. A method for obtaining climate parameters from leaf assemblages. *US Geol. Surv. Bull.*, **2040**: 1–71.

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