Precipitation and large herbivorous mammals II: application to fossil data

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ABSTRACT

Background: We developed a method to estimate precipitation using mammalian ecomorphology, specifically the relative height of the molars of herbivores (see companion paper, this issue).

Question: If we apply the new method to paleoenvironments, do the results agree with previous results from fossil mammals and paleobotanical proxies?

Data: Large herbivorous fossil mammals of Eurasia. Data from NOW database covers 23–22 Ma and is Eurasia-wide.

Method: We apply the new precipitation estimation method (based on present-day mammalian ecomorphology) to fossil assemblages from different localities.

Conclusions: The early Miocene retained the overall humid conditions of the late Paleogene. A shift to more arid conditions began during the middle Miocene. The late Miocene as a whole was a time of large changes, and there was continent-wide restructuring of the distribution of environments. Our new results agree with previous investigations and the mammal proxy data are in good agreement with palaeovegetation data. Mammals and vegetation produce similar precipitation values and large-scale patterns.

Keywords: climate, Eurasia, fossil mammals, hypsodonty, Neogene, precipitation.

INTRODUCTION

The structure of large mammal communities has been used to describe habitats and their environmental characteristics qualitatively. Mammals have been used to describe and reconstruct paleoenvironments for at least a century (e.g. Matthew, 1915). The first researchers to

use mammalian communities in a paleontological context to quantify aspects of past environments were Andrews *et al.* (1979), who collected an extensive data set of present-day habitats and the characteristics of their mammalian inhabitants. The analysis concentrated on tropical Africa, and used the features of taxonomic groupings, body size, locomotion, and diet to characterize the modern environments. They used the correlations obtained from these data to analyse the community structure of fossil localities, inferring differences in habitats based on differences in community structure. The method was not fully quantitative, but used ecological indexes in addition to visual interpretation in the form of histograms. Other methods for quantifying the environments based on mammalian community structure include the use of cenograms (Legendre, 1986; see next paragraph), small mammal communities (Legendre *et al.*, 2005; Van Dam, 2006), and large mammal community structure (Janis *et al.*, 2000; Fortelius *et al.*, 2002).

Legendre (1986) developed the methodology of cenogram analysis of mammalian community structure. Cenograms plot the distribution of the body sizes of mammals (on a logarithmic scale) in a particular community, and differences in these distributions for extant mammals characterize different types of modern environments. These correlations can then be used to examine paleocommunities and to draw inferences for paleo-environments. The body mass of a fossil mammal is estimated from the crown area of the first lower molar based on regression equations of extant mammals of known body mass. The interpretation of the type of paleoenvironment relies on visual inspection of the cenogram graph in comparison with those from extant communities. This method is controversial (Travouillon and Legendre, 2009). Its lack of statistical power has also drawn criticism (e.g. Rodriguez, 1999). Hernández-Fernández *et al.* (2006) argue that it can be used to infer the paleobiome type. Travouillon and Legendre (2009) note that the method cannot reliably infer habitat type from cenograms alone, but requires additional measurements.

Legendre *et al.* (2005) have also used small mammal communities to quantify environmental variables. Their method uses the number of species of sigmodontine rodents in North, Central, and South America to infer the mean annual temperature. However, sigmodontine rodent species diversity is related mainly to temperature; the correlation with rainfall is weak (Legendre *et al.*, 2005). Van Dam (2006) developed a method to calculate precipitation estimates based on the community structure of small mammal communities. The method uses regression of mean annual and minimum monthly precipitation on diet and locomotion and habitat information to calculate locality-specific precipitation estimates. The method has a reported mean error of 350–400 mm per year. But this approach requires a virtually complete faunal list, with ecomorphological characterization of all species, thus limiting its applicability at large scales. Also, arguably, small mammal fossil localities reflect the local microhabitat more than the regional mean values.

The link between mammals and environmental conditions that we use here is the relationship between food properties and dental wear observed in living mammals. Tooth crown height (specifically of the cheek teeth used for mastication) is a measure of dental durability. Brachydont – or low crowned – teeth are seen in herbivores that eat relatively non-abrasive food, such as soft browse (leaves of dicotyledonous plants) in a relatively grit-free environment. Higher crowned teeth indicate a diet that is more abrasive. This usually means a diet containing greater amounts of grass. But eating other plants in more arid areas may entail consuming a good deal of abrasive dust and grit (see Janis and Fortelius, 1988). Janis *et al.* (2002) presented data to show how the tooth crown height index (the hypsodonty index, HI) varies with both diet and habitat in 125 species of living ungulates of known

dietary preference. The average hypsodonty index for browsers (i.e. animals consuming < 10% grass) in woodland and forest habitats was around 1.5 (with a slightly greater upper range of variation in the more open woodland habitats). Savanna-dwelling browsers were more mesodont (average HI of 2.0, ranging as high as 3.5). Mixed feeders (i.e. animals eating > 10% but < 90% grass) were always at least mesodont (i.e. HI > 1.5) and ranged into the hypsodont values (HI > 3.0) for those species taking a greater percentage of grass in the diet and/or living in more open habitats such as grassland and prairie. All grazers (i.e. animals consuming > 90% grass) were hypsodont. Grazers in more open habitats tended to be more hypsodont (average HI of ~4.5 in savannas and ~6.2 in prairies).

These data show that ungulate hypsodonty values capture aspects of both diet and habitat, relating both to the abrasive nature of the food itself (i.e. browse vs. grass) and to environmental effects on this food (i.e. accumulation of dust and grit). The separation between animals predominantly browsing in closed habitats (forest and woodland) and those eating predominantly other types of diets in open habitats (savanna and prairie) is a hypsodonty index of around 2.5. Thus hypsodont animals reflect more arid habitats, whatever their actual diet. Damuth and Fortelius (2001) introduced and Fortelius *et al.* (2002) applied the use of mean hypsodonty to estimate past precipitation values from fossil molar teeth of large herbivorous mammals. This method was also applied by Fortelius *et al.* (2003, 2006), Eronen and Rook (2004), and Eronen (2006). Hypsodonty-based estimates have also been used, including by Jernvall and Fortelius (2004) and Eronen *et al.* (2009). Furthermore, Damuth *et al.* (2002) introduced and Janis *et al.* (2004) used a technique called 'per species mean hypsodonty' (PMH), where the predictor variable is an index incorporating both mean hypsodonty and number of large mammals species, closely akin to the key estimator variables that also emerge in the new method (Eronen *et al.*, 2010). A simple regression using PMH explains over 60% of the variance in mean annual precipitation for modern mammal communities (Damuth *et al.*, 2002), and in this regard is an extension of the method of Fortelius *et al.* (2002) when applied to well-sampled, individual fossil localities. The method used here, although similar in some ways, is based on a slightly different set of assumptions and a different statistical model. Significantly, for reference, the new method uses a data set of modern species occurrences on a geographical grid, rather than deriving them from point localities. Therefore, it applies at a somewhat different scale than the previous methods – a scale that, among other things, can be more directly interfaced with quantitative climate models.

In this paper, our objective is to compare the published results of the method of Fortelius *et al.* (2002) with those of this new method (Eronen *et al.*, 2010), both having been applied to a set of fossil localities covering the same time-span and geographical extent.

MATERIALS AND METHODS

We used the NOW database (Fortelius, 2009: http://www.helsinki.fi/science/now) to supply data on Miocene and Pliocene mammals. We downloaded the data on 24 April 2009. We used only the large herbivorous mammals (Orders Artiodactyla, Perissodactyla, Primates, and Proboscidea). We used only those localities that had at least two scorings for hypsodonty together with existing coordinate information. Three classes of molar tooth crown height are recorded in the NOW database: brachydont, mesodont, and hypsodont. The criteria for assigning species to these classes are ultimately up to the taxonomic coordinators of the NOW advisory board but the rule of thumb is based on the ratio of height to length of

Table 1. Miocene and Pliocene times used in the analysis

Time-slice	Age (Ma years)	MN time unit equivalents
Miocene		
Early	23–15	MN1–MN5
Middle	15–11	MN6–MN8
Early late	11–8	MN9–MN11
Late late	8–5	MN12–MN13
Pliocene		
Early	5–3.4	MN14–MN15
Late	3.4–2	MN16–MN17

Note: Ages are approximate. Based on Fortelius *et al.* (2002) and Eronen (2006) as well as some unpublished material.

the second molar (upper or lower). Brachydont teeth have a ratio of less than 0.8, mesodont teeth a ratio of 0.8–1.2, and hypsodont teeth a ratio of more than 1.2. For this study, the crown-height classes were assigned values of 1 (brachydont), 2 (mesodont), and 3 (hypsodont). We used similar criteria for the fossil data set as for the present-day data set (i.e. for the decision tree using hypsodonty, we used only those localities where there were at least two crown-height values recorded). Eronen *et al.* (2010) excluded the two extant species of elephants from their analysis but we include them here. Extant species have an exceptionally broad environmental range but extinct proboscideans are morphologically and ecologically diverse and there is good evidence that sympatric species had different dietary preferences (Calandra *et al.*, 2008). We used Fortelius *et al.* (2002) and Eronen (2006) as well as some unpublished material to define the time-slices of this study (Table 1).

Using the method of Fortelius *et al.* (2002), we calculated the mean crown height for each locality by averaging the assigned molar crown heights and plotting them on a map. Fortelius *et al.* (2002; and subsequent investigations, e.g. Fortelius *et al.*, 2003, 2006) used only relative interpretations within each time-slice. They inferred habitats and environments by comparing mean hypsodonty values with the present-day patterns and present-day habitats. In contrast, the new method for estimating precipitation that we also use here was developed with data from present-day large herbivorous mammal communities and present-day mean annual precipitation values (Eronen *et al.*, 2010). The method estimates precipitation using regression tree analysis on large herbivorous-mammal molar crown height, its distribution, and its variation at the community level. This method describes today's precipitation patterns fairly well ($R^2 = 0.665$; s.e. = 388 mm).

In this work, we apply the new method to fossil assemblages to test its use in a paleontological context. We use the regression tree in which the only variable is the molar crown height of species (see Eronen *et al.*, 2010). The regression tree uses the following input variables: NHYP (number of species with crown height data); NHYP1 (number of low crowned species); NHYP2 (number of medium crowned species); NHYP3 (number of high crowned species); pHYP1 (proportion of low crowned species); pHYP2 (proportion of medium high crowned species); and pHYP3 (proportion of high crowned species).

Eronen *et al.* (2010) developed their estimates with a data set that had 53,054 grid cells and 584,341 taxon occurrences (i.e. 11.014 species per locality). To use the method on the fossil

data set, its numbers of species must be adjusted. (The numbers include only those grid cells/localities where at least two hypsodonty values are recorded.) The fossil data set has 1266 localities and 7594 species occurrences. That amounts to 5.998 species per locality. So the ratio between present-day and fossil localities is 1.836 (11.014/5.998). Because present-day localities have on average 1.84 times more species than fossil localities, we multiplied all fossil diversity input variables (see above) for fossil localities by 1.84. For example, if a fossil locality has three species of mammals with a high molar tooth crown (NHYP3 = 3) and one species with a low molar tooth crown (NHYP1 = 1), we would count these as NHYP3 = 5.5 (i.e. 3×1.84) and NHYP1 = 1.8 for our regression tree analysis.

We applied the adjustments to the data and then used the method of Eronen *et al.* (2010) to estimate mean annual precipitation for each locality. To investigate the spatial patterns, we plotted these precipitation estimates onto present-day maps. Then we interpolated between the localities using MapInfo 8.5. For the interpolations, we used the thematic mapping and grid interpolation, with the following settings: 30 km grid size; 600 km search radius; 600 grid border. For the interpolation method, we used an inverse distance weighted algorithm (IDW). Then, we imported the interpolated maps as grids into Vertical Mapper, where they were assigned to classes and contoured to connect areas with similar values. We used five inflections for the mean hypsodonty map, and seven for the predicted precipitation based on the hypsodonty regression. We show results for both mean hypsodonty (method of Fortelius *et al.*, 2002) and estimated precipitation (method of Eronen *et al.*, 2010) to facilitate comparison with previous results (e.g. Fortelius *et al.*, 2002, 2003, 2006; Eronen and Rook 2004; Eronen, 2006).

Our method assumes that all localities are similarly preserved and studied, and that their faunal list is representative of the fossil fauna. Previous studies (Damuth, 1982; Jernvall and Fortelius, 2004) have shown that the community structure and group proportions are indeed preserved in the fossil assemblages. Recently, Western and Behrensmeyer (2009) showed that there is high fidelity between bone assemblages and the living, large mammal communities of East Africa. Their results show that the bone assemblages track the changes in the living mammal community over intervals as short as 5 years, as well as on longer time-scales.

RESULTS

The early Miocene (Fig. 1A,B) had overall humid conditions. The mean hypsodonty values [Fig. 1A, based on the method of Fortelius *et al.* (2002)] and our new precipitation estimates [Fig. 1B, based on the method of Eronen *et al.* (2010)] show similar patterns. There were drier areas in the Iberian Peninsula and in eastern Europe/eastern Mediterranean area, as well as in central western China. The mean hypsodonty values are between 1.4 and 2.2 for most of these drier areas. The highest values within the time-slice were around 1.8–2.2 in central western China (Fig. 1A). The precipitation estimates for these areas range from around 300 to 700 mm per year (Fig. 1B).

We estimate that the middle Miocene (Fig. 1C,D) was quite a humid interval. Mean hypsodonty values indicate humid conditions for all of central Europe, and the only less humid areas were parts of China and the eastern Mediterranean (Fig. 1C). Central China and eastern Europe (including the eastern Mediterranean) had more arid conditions than before. Precipitation estimates (Fig. 1D) indicate a slightly drier pattern compared with estimates from the mean hypsodonty values. According to our new precipitation estimates, central China in the middle Miocene had similar precipitation to that in the early Miocene, but the more northern part of China became more humid (700–1200 mm per year). In

western Eurasia, the less humid environments spread from the east towards the eastern parts of central Europe. However, eastern European precipitation estimates fall into about the same range as the humid parts of northern China (over 800 mm per year). Western Europe retained its very humid environments.

During the early late Miocene (Fig. 1E,F), the spread of arid conditions is visible on a continental scale. Both the mean hypsodonty values and the precipitation estimates suggest a similar increase in aridity (Fig. 1E,F). The mean hypsodonty values show drying in China and central Asia. In addition, the mean hypsodonty values for the eastern Mediterranean are quite high (Fig. 1E). The central European region had low mean hypsodonty values, indicating persisting humid conditions. Northeastern Spain had very humid conditions, and westernmost localities in Portugal show extremely humid environments (Fig. 1E). Our new precipitation estimates show a similar pattern. The precipitation estimates indicate less than 700 mm rainfall for most parts of China, and even as little as 300 mm per year for some areas (Fig. 1F). The Mongolian localities were very dry, as were areas of eastern Kazakhstan and Pakistan/Afghanistan. The Mongolian localities had precipitation estimates of only about 200–500 mm per year. Eastern Kazakhstan and the Pakistan/Afghanistan areas had precipitation estimates of less than 500 mm per year (Fig. 1F). Similar conditions also prevailed in the Caucasus area, while northern Iran and the eastern Mediterranean had precipitation estimates of around 700–800 mm per year, with some areas being drier and others more humid. Central Europe also had precipitation estimates of about 800–1200 mm per year. The very humid areas in western central Europe diminished, persisting only in northern Germany and northeastern Spain (Fig. 1F).

The patterns for the late late Miocene (Fig. 2A,B) are quite different from the previous time-slice. The mean hypsodonty values show an increase in humidity in northern China (Fig. 2A). The eastern Mediterranean became a little drier while the western Mediterranean became much drier (Fig. 2A). The estimated precipitation values (Fig. 2B) show that the humidity in northern China increased considerably to around 800–1200 mm per year for many localities. Some localities in central northern China retained more arid conditions with estimated precipitation of around 500–700 mm per year, whereas more western parts of northern China were humid. The Uzbekistan/Afghanistan/northern India area also showed increased humidity with precipitation estimates of around 700–1200 mm per year. Central Asia as a whole was very heterogeneous, with scattered arid and humid localities (Fig. 2B). In western Eurasia, the eastern Mediterranean area (south of the Black Sea) experienced 500–800 mm per year, with Greek localities being more humid, around 800–1200 mm per year. The Caucasus area was dry. The area north of the Black Sea, as well as central Europe, was more humid than before, although not to a great extent, with precipitation estimates of around 700–1200 mm per year. The western Mediterranean became very dry, with precipitation estimates ranging from 200 to 700 mm per year (Fig. 2B), a marked change from the previous time-slice. The mean hypsodonty values and the precipitation estimates show a very similar picture overall. The main differences between them are that central northern China was not so dry, and the western and eastern Mediterranean had more comparable conditions.

During the early Pliocene (Fig. 2C,D), reorganization of the continental scale pattern is visible. The mean hypsodonty values illustrate uniform humidity in central Europe, and also humid conditions in Ukraine (Fig. 2C). In addition, hypsodonty values indicate that the western Mediterranean was more humid than the eastern Mediterranean. In China, conditions were drier than previously (Fig. 2C). The estimated precipitation (Fig. 2D)
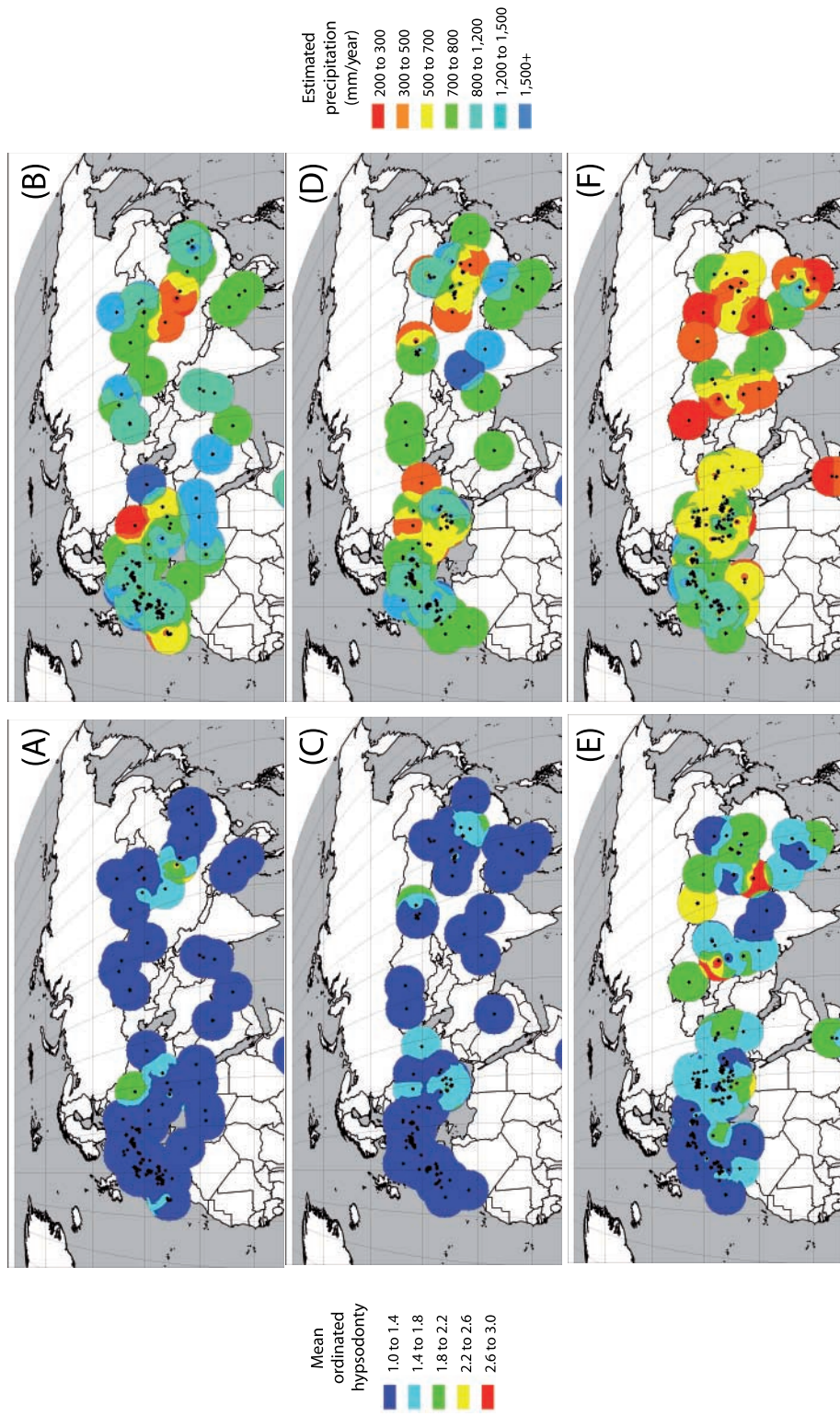
Fig. 1. (A) Mean hypsodonty values for the early Miocene (MN1–MN5, 23–15 Ma). (B) Estimated precipitation for the early Miocene. (C) Mean hypsodonty values for the middle Miocene (MN6–MN7 + 8, 15–11 Ma). (D) Estimated precipitation for the middle Miocene. (E) Mean hypsodonty values for the early late Miocene (MN9–MN11, 11–8 Ma). (F) Estimated precipitation for the early late Miocene.
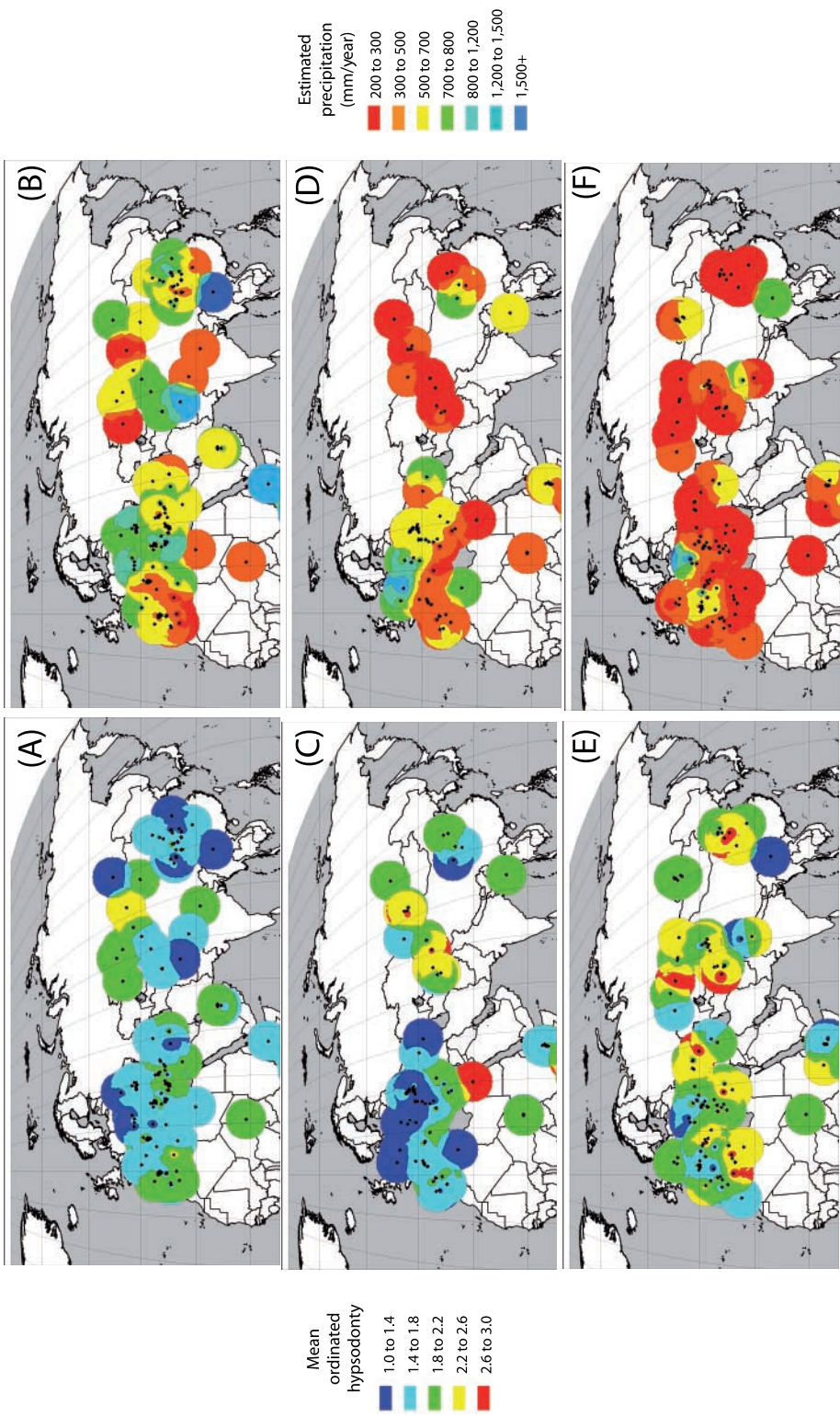
Fig. 2. (A) Mean hypsodonty values for the late late Miocene (MN12–MN13, 8–5 Ma). (B) Estimated precipitation for the late late Miocene. (C) Mean hypsodonty values for the early Pliocene (MN14–MN15, 5–3.4 Ma). (D) Estimated precipitation for the early Pliocene. (E) Mean hypsodonty values for the late Pliocene (MN16–MN17, 3.4–2 Ma). (F) Estimated precipitation for the late Pliocene.

Estimated
precipitation
(mm/year)

200 to 300
300 to 500
500 to 700
700 to 800
800 to 1,200
1,200 to 1,500
1,500+

Mean
ordinated
hypsodonty

1.0 to 1.4
1.4 to 1.8
1.8 to 2.2
2.2 to 2.6
2.6 to 3.0

shows a very similar pattern to the mean hypsodonty values. According to the estimated precipitation, the conditions in China changed dramatically towards drier environments, with rainfall of only 200–500 mm per year (Fig. 2D). Similar conditions were prevalent across central Asia. The Caucasus area was now more humid, with precipitation estimates for some localities as much as 800 mm per year. The eastern Mediterranean area was completely different from the previous time-slice: southwestern Turkey and Greece were very dry, with precipitation estimates of less 500 mm per year. The Balkans were more humid, with precipitation estimates of 500–700 mm per year, with some localities having up to 800 mm per year. The Ukranian area was drier, having precipitation patterns estimates of only about 800 mm per year. Central Europe was still humid. The central and western Mediterranean was very dry, with precipitation estimates of only 300–500 mm per year. There were some localities with more humid conditions (Fig. 2D).

The late Pliocene (Fig. 2E,F) shows similar patterns from the mean hypsodonty values and the precipitation estimates. Both methodologies indicate very dry environments throughout Eurasia, with only a few humid regions. Most of Eurasia had estimated precipitation between 200 and 500 mm per year (Fig. 2F). Southeastern France and northwestern Italy had more humid environments, with 500–700 mm per year. In addition, the Hungarian/Slovakian area was more humid, with about 1200–1500 mm per year (Fig. 2F). Other areas that had more humid conditions were the Caucasus and localities around the Mongolian/Russian border. The mean hypsodonty pattern (Fig. 2E) was very similar to that obtained from the precipitation estimates.

DISCUSSION

At the continental level, the precipitation estimates obtained from our new precipitation method are very similar to those obtained from the mean hypsodonty patterns. The new precipitation estimation method confirms the results of previous investigations (e.g. Fortelius *et al.*, 2002, 2003, 2006). The results obtained here are also comparable to those obtained in other studies, including vegetation-based reconstructions of paleoenvironmental conditions (Utescher *et al.*, 2000; Ivanov *et al.*, 2002; Bruch *et al.*, 2004, 2007; Mosbrugger *et al.*, 2005). Our results can be used to test computational climate model results (e.g. Steppuhn *et al.*, 2006). The precipitation estimates can also be used as an input to paleoclimate model boundary conditions. Let us now concentrate on understanding the environmental patterns and relating them to vegetation and climate model studies.

According to Fortelius *et al.* (2002), the early Miocene was a relatively uniform and humid time interval. But the precipitation estimates presented here indicate a drier climate. Our new method uses more a diverse set of variables than does the mean hypsodonty method (see Eronen *et al.*, 2010), but the main patterns obtained by the two methods are similar. Bruch *et al.* (2007) present a detailed climatic reconstruction based on the paleobotanical record of the Neogene of Europe. According to them, the early to middle Miocene of Europe was characterized by precipitation of between 800 and 1500 mm per year. According to paleobotanical proxies, the early Miocene was a time of weak seasonality and shallow temperature gradients (Utescher *et al.*, 2000; Mosbrugger *et al.*, 2005; Bruch *et al.*, 2007), which is in line with our estimates presented here. When comparing the pattern for the Langhian interval in Figure 1 of Bruch *et al.* (2007) to our Fig. 1A, we see that both patterns show that the Iberian Peninsula and eastern Mediterranean area were slightly drier than the rest of Europe.

Our new middle Miocene precipitation estimates show distinct east–west differences in Europe, with the eastern part being drier. Paleovegetation studies show that in the late early Miocene there were more broad-leaved evergreen taxa from Austria westwards (Jechorek and Kovar-Eder, 2004), with more broad-leaved deciduous taxa in the east, showing cooler conditions there. At the same time, central Europe had a high percentage of sclerophyllous taxa, probably because of low precipitation or pronounced seasonality of rainfall (Jechorek and Kovar-Eder, 2004). There was no clear latitudinal differentiation of the vegetation during the late early to middle Miocene, but a clear east–west differentiation (Jechorek and Kovar-Eder, 2004). This agrees with our precipitation estimates. In addition, our precipitation estimates show that the Iberian region remained drier than central Europe.

Late Miocene environments differed from those of the previous time-slices. During the early late Miocene, arid conditions spread at a continental scale. In western Eurasia, we see the emergence of the Pikermian paleobiome (Eronen *et al.*, 2009). The Pikermian paleobiome had a vast geographic range: its core area was the sub-Paratethyan region that extended from the Balkans in the west to the Caspian Sea and beyond in the east. Our precipitation estimates for the early late Miocene reflect this pattern to a great extent. But note that our division of time-slices differs slightly from that of Eronen *et al.* (2009). To enable more precise comparison, we plotted the corresponding time-slice as supporting information (evolutionary-ecology.com/data/2539.pdf). According to our estimates, northern Iran and the eastern Mediterranean had precipitation of around 700–800 mm per year, except for Greek localities, which were more humid (800–1200 mm per year; see Figs. 1A and 1B in evolutionary-ecology.com/data/2539.pdf). This is extremely close to the 1000 mm mean annual precipitation that Quade *et al.* (1994) and Solounias *et al.* (1999) suggested for the Pikermian paleobiome based on stable isotopes and paleosol profiles. In addition, our precipitation estimations suggest that precipitation was greater in the area north of the Black Sea (Fig. 1B), and especially in central Europe. This confirms the results of Eronen *et al.* (2009), which show patterns similar to the results presented here for the late late Miocene. The driving factors for this pattern are the hypsodonty values of the MN12 time-equivalent faunas, which, in our present division of time-slices, extend into the late late Miocene (Fig. 2A,B). According to Eronen *et al.* (2009), the Pikermian chronofauna had its climax 8 Ma ago, after which it started to diminish. This is reflected in our precipitation estimates, which suggest more variable conditions for the eastern Mediterranean area during the early Pliocene (Fig. 2B).

During the early late Miocene, the most humid places in western Eurasia, according to our precipitation estimates, were northeastern Spain and northern Germany. According to Utescher *et al.* (2000) and Mosbrugger *et al.* (2005), based on paleobotanical evidence, the mean annual precipitation in central Europe was at a constant level of 1250 mm until the late Pliocene (Zanclean). This accords with our results, although we lack localities and faunal data for north central Europe during the late late Miocene. The case for northeastern Spain is interesting. This is the region where the faunal Vallesian crisis at 9.7 Ma is best documented (Agusti and Moya-Sola, 1990; Agusti *et al.*, 2003). During this crisis, several faunal elements that were adapted to wet-subtropical conditions declined abruptly in western Europe: primates disappeared completely, and the smaller large mammals (those less than 30 kg) in general and carnivores in particular were strongly reduced in diversity (Fortelius *et al.*, 1996). Among ungulates, the rhinoceros *Lartetotherium sansaniense*, tapirs, the suids *Listriodon* and *Schizochoerus*, and forest-adapted cervids and moschids declined considerably (see Agusti and Moya-Sola, 1990; Agusti *et al.*, 2003). The Vallesian crisis corresponds to a reduction of the

sub-tropical evergreen forests and their replacement by more deciduous forests (Agusti *et al.*, 2003). The pre-crisis localities have a very diverse fauna with species representing both the autochthonous forest community and more open-adapted immigrants from the evolving Pikermian communities of western Asia and eastern Europe (Agusti *et al.*, 2003; Eronen *et al.*, 2009). This diversity led Fortelius *et al.* (1996) to suggest that these communities were ecologically supersaturated. A dramatic example is the sympatric occurrence there of two species of sabertooth hypercarnivores, *Sansanosmilus jourdani* and *Machairodus aphanistus*, at multiple localities (Fortelius, 2009: NOW). Nevertheless, the high number of species in these communities might simply reflect high productivity. The abrupt decline in diversity at the Vallesian crisis, when arid conditions spread to the westernmost parts of Europe 10–9 Ma ago (Agusti *et al.*, 2003), might favour the latter interpretation.

Eastern Eurasia became more arid from the middle Miocene to early late Miocene, as did the western part of the continent. The precipitation pattern seems to be reversed during the late late Miocene when precipitation increased in northern China. Fortelius *et al.* (2002) interpreted this increase as the start of strong summer monsoon precipitation. Passey *et al.* (2009) further demonstrate that the likely mechanism of environmental change in China at this time was a response to increased summer monsoon precipitation. During the same time-slice, the western Mediterranean experienced very arid conditions. From the early late Miocene to the late late Miocene, the wetter parts of the continent became drier and the dry parts got wetter. During times of humid conditions in the western Mediterranean, eastern Asia was arid, and during humid conditions in eastern Asia, the western Mediterranean was more arid. This is an interesting reciprocal pattern that we do not yet understand.

In western Eurasia, the precipitation gradient between a wetter west and a drier east started to change during the late Miocene. During the early late Miocene, there was only a slight gradient, and during the late late Miocene the gradient reversed, then going from an arid west to a less arid east. During the early Pliocene, this gradient changed to reflect a more north–south gradient. Fortelius and Hokkanen (2001) suggest that this reflects the emerging temperature difference between a colder northern and a warmer southern Europe. Kovar-Eder and Kvacek (2003) show a reconstructed vegetation pattern for the late Miocene: the macrofloral assemblages show north–south trends of evergreen versus deciduous broad-leaved taxa in central Europe and higher percentages of sclerophyllous taxa in southern Europe and the Balkans, implying cooler temperatures in the north. During the latest Miocene/earliest Pliocene, the Black Sea coast and the Pannonian Basin had few sclerophyllous taxa and many humid subtropical evergreen taxa, implying relatively humid conditions (Kovar-Eder and Kvacek, 2003). This agrees with our estimated precipitation patterns. Mosbrugger *et al.* (2005) conclude that the increase of seasonality in Europe during the late Miocene was due mostly to lower winter temperatures. Although we do not have temperature estimates for our localities, the change in pattern from the late late Miocene to early Pliocene does not contradict their conclusions.

The estimated precipitation patterns and mean hypsodonty values seem to diverge more from other proxy results during the Pliocene. Our proxies do not capture well the apparent increase of humidity during the earliest Pliocene in the Mediterranean area, nor do they capture the continued humid conditions in the earliest Pliocene in China. Our methods seem to represent middle Pliocene conditions better, although we do not see the warm and humid conditions as clearly as the literature suggests we should (Salzmann *et al.*, 2008).

CONCLUSIONS

The new method introduced by Eronen *et al.* (2010) for estimating the precipitation based on large herbivorous fossil mammal communities can reproduce the humidity–aridity patterns that have been published previously (e.g. Fortelius *et al.*, 2002, 2003, 2006; Eronen and Rook, 2004; Eronen, 2006; Eronen *et al.*, 2009). The method confirms earlier studies on the environmental changes during the Neogene of Eurasia, and allows us to quantify the patterns. This opens up the possibility to analyse paleoenvironmental changes in more detail and readily compare them to other quantitative proxies, such as climate estimates from paleovegetation data.

Our results show that during the Neogene, a drying trend started in Eurasia around middle Miocene times (c. 15–11 Ma). The late Miocene (c. 11–5 Ma) as a whole was a time of large changes, a continent-wide restructuring of the distribution of environments. The most important physical drivers were the rise of the Tibetan Plateau, changes in the ocean currents, and continentalization of the Eurasian inland sea, the Paratethys. These events resulted in the redistribution of precipitation on a continental scale, with some areas drying and others becoming more humid. The mammal proxy data agree well with paleovegetation data, showing similar large-scale patterns and estimated precipitation values. However, there are small-scale differences that should be studied further.

This study concentrated on the Eurasian continent in order to test how well the method works in a setting with well-known and well-studied fossil mammal data. We have shown that the estimations of paleoprecipitation obtained for Eurasia from the hypsodonty values of fossil mammals agree well with other proxies, such as climatic modelling and paleovegetation data. This gives us confidence that these methods could be applied to other areas.

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