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Dental functional traits of mammals resolve productivity in terrestrial ecosystems past and present

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We have recently shown that rainfall, one of the main climatic determinants of terrestrial net primary productivity (NPP), can be robustly estimated from mean molar tooth crown height (hypsodonty) of mammalian herbivores. Here, we show that another functional trait of herbivore molar surfaces, longitudinal loph count, can be similarly used to extract reasonable estimates of rainfall but also of temperature, the other main climatic determinant of terrestrial NPP. Together, molar height and the number of longitudinal lophs explain 73 per cent of the global variation in terrestrial NPP today and resolve the main terrestrial biomes in bivariate space. We explain the functional interpretation of the relationships between dental function and climate variables in terms of long- and short-term demands. We also show how the spatially and temporally dense fossil record of terrestrial mammals can be used to investigate the relationship between biodiversity and productivity under changing climates in geological time. The placement of the fossil chronofaunas in biome space suggests that they most probably represent multiple palaeobiomes, at least some of which do not correspond directly to any biomes of today's world.

Keywords: herbivorous mammals; dental traits; net primary production; fossil mammals; neogene; palaeoclimate

1. INTRODUCTION

It is well established that molar tooth crown height (hypsodonty, HYP) in herbivorous mammals is related to both habitat and diet [1]. Specifically, it has been shown that the HYP of 'large' (i.e. non-rodent) herbivores that coexist in a community is a robust proxy for humidity, including mean annual rainfall [2,3]. How this relationship comes about is not known in detail, but the general principles are clear enough. Dental durability [4] and capability [5] increase when the availability of easily edible plant parts is limited. Typically, these conditions occur where net primary productivity (NPP) is low, in climates that are arid, cold or both, seasonally or permanently [6]. From the point of view of tooth function, food properties also include a habitat effect through extrinsic mineral matter adhering to the vegetation [1,4,7,8]. The distribution of dental functional traits in the community of coexisting herbivores in any one location reflects the distribution of variously demanding plant foods, and ultimately the climatic conditions that in turn control the vegetation. In addition to HYP, ecometric traits [9] such as loph count [10] and molar crown complexity [11] have been used to quantify the relationships between food properties and dental function.

NPP is limited in the terrestrial realm mainly by three interactive components: temperature, radiation and water availability [6,12]. Apart from the tropical area, where neither water nor temperature limits the productivity, NPP is limited by radiation only in the extreme polar regions. Outside these extremes, NPP is mainly limited by interactions of temperature and availability of water (mainly precipitation) [6,12–14]. In principle, it should, therefore, be possible to estimate terrestrial NPP from adequate proxies of temperature and precipitation. Here, we show that dental ecometrics do reveal precipitation and temperature, the two main determinants of NPP, and that robust estimates of NPP can indeed be derived from mammal teeth. Using the rich fossil record of mammalian teeth, we show two examples of how these estimates can be used to map past ecosystems alongside present-day biomes in humidity-temperature space.

2. MATERIAL AND METHODS

(a) *Dental variables longitudinal lophs count and hypsodonty*

We follow Fortelius [5] in using a crown-type scheme developed by Jernvall *et al.* [10] to describe the functional topography of the tooth surface. Instead of combining lophedness and HYP as a measure of 'functional capability' [5], we here contrast the two traits in order to separate their effects. By counting only longitudinal lophs count (LOP)

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as our measure of cutting capacity, we also emphasize the largest and most abundant clades of large mammals herbivores, across diets and habitats. For the criteria of cusp number and the cut-off point of cusp shape and loph, we followed Jernvall *et al.* [15]. We also include HYP as a dental variable by using the same definition and data as in previous studies [3,16,17]. The LOP and HYP data of large herbivores can be found in the electronic supplementary material, dataset S1.

(b) *Climate and net primary productivity variables*

To relate the occurrence of these dental traits to observed spatial patterns in climate and vegetation, we use a global dataset which includes climate variables, biome type and distribution of herbivorous large mammal species. Data sources of climate variables are from <http://www.worldclim.org> [18]. Biome type and distribution of herbivorous large mammal species (Orders: Perissodactyla, Artiodactyla, Primates, Proboscidea) are from WWF WildFinder. For mammal data, see 'data and tools' under <http://www.worldwildlife.org/science/>. For delineation of WWF biomes, see Olson *et al.* [19] and Home >> Our Earth >> Places >> About Global Ecoregions >> Major habitat types >> Terrestrial ecoregions, under <http://wwf.panda.org/>. For more details, see previous work [3].

NPP is calculated using the classic formula from Lieth [20]. The formula are: (i) $NPP_t = 3000 / (1 + \exp(1.315 - 0.119 \times MAT))$, where mean annual temperature (MAT) is the annual mean temperature in Celsius; (ii) $NPP_p = 3000 \times (1 - \exp(-0.000664 \times MAP))$, where mean annual precipitation (MAP) is annual precipitation in millimetres; and finally (iii) $NPP = \min(NPP_t, NPP_p)$, where NPP is grams carbon in $m^{-2} year^{-1}$ dry matter. Because of its empirical basis and its ability to generate reasonable global patterns of NPP, the model of Lieth [20] is still used as a baseline for NPP evaluation, even while more sophisticated models have been developed [21].

(c) *Regression models for estimating mean annual temperature, mean annual precipitation and net primary productivity from longitudinal loph count and hypsodonty*

All climate, NPP, biome and species data have been converted to a gridded format with a resolution $0.5^\circ \times 0.5^\circ$ (ca 55 km at the equator). In each gridded map cell, dental variables LOP and HYP are calculated for all large herbivorous species in this cell, and the mean values are used in our analysis. Based on previous results [3,16], we only included grid cells with at least three species in the analysis. For recent mammal data, the restriction to grid cells with at least three species excluded large parts of the high latitudes and North America (electronic supplementary material, figure S1), but had no significant effect on the correlation pattern nor the performance of the regression models (electronic supplementary material, table S1 and figures S2–S3). Each map cell thus has values for LOP and HYP as well as for the respective climate and NPP variables.

We use an ordinary least-squares (OLS) linear regression model to estimate the MAT, MAP and NPP, using LOP and HYP as covariates. We experimented with several statistics to summarize the distribution of dental variables in a map cell and choose the mean because of its simplicity, and because using more complex statistics did not substantially improve the estimation accuracy. Notice that random resampling of species in a map cell adds variance to the fit but it will not create bias to the means of dental

variables nor to the estimates given by the OLS regression models; hence, the mean can be used even if only a random subset of species in a grid cell is observed. We report Pearson correlation coefficients among variables across the map cells.

In order to verify that our results are not only owing to the spatial autocorrelation, we first found the range of the positive short-range spatial residual autocorrelation (SSRA) for the three OLS regression models [22]. The ranges turned out to be 6000, 3500, and 4000 km for the models for MAT, MAP and NPP, respectively. As in Hawkins *et al.* [22], we resampled sets of map cells in which the distance between the cells is at least the range of the SSRA. We then fitted the OLS models on the resampled dataset to obtain empirical *p*-values for the null hypothesis that the regression coefficients of both HYP and LOP are zero. We were able to reject the null hypothesis for all three models ($p \leq 0.01$).

(d) *Fossil data*

We use presence–absence data from the NOW database [23] to estimate past NPP for the Pikermian and Sansan fossil chronofaunas. As in previous work [16,17], we include in a chronofauna that all localities with a Dice faunal resemblance index to a chosen 'standard locality' higher than 0.2. The localities and fossil occurrence data were derived from our previous work [16,17].

3. RESULTS AND DISCUSSION

The correlation pattern among the climate and dental variables are shown in table 1 and in the electronic supplementary material, table S1 for a full set of climate variables in the Worldclim dataset, denoted by bio1, bio2 etc.

(a) *Temperature*

LOP shows a good correlation to temperature, while the temperature correlation of HYP is lower. Estimating MAT with both HYP and LOP as covariates gives substantially better accuracy ($r^2 = 0.69$) than by using either HYP ($r^2 = 0.01$) or LOP ($r^2 = 0.47$) alone. Among the 11 temperature variables in the Worldclim dataset (electronic supplementary material, table S1), LOP has a more significant correlation with cold, e.g. minimum temperature of coldest month (bio6) and mean temperature of coldest quarter (bio11), than to warm conditions (bio5 and bio10).

(b) *Precipitation*

Previous research [3] shows a strong correlation among HYP and precipitation. This is supported here (electronic supplementary material, table S1) by the highest correlation of HYP to precipitation of the driest month (bio14) and precipitation of the driest quarter (bio17). Both variables express seasonal aridity and high values of HYP seem to be specifically related to the presence of a dry season. LOP has a strong correlation with precipitation of wettest month (bio13) and precipitation of wettest quarter (bio16), but does not resolve the dry end well. Again, using both HYP and LOP to estimate MAP gives a better accuracy ($r^2 = 0.63$) than by using either of them alone ($r^2 = 0.33$ and $r^2 = 0.56$, respectively).

Table 1. The Pearson correlation coefficients among MAT, MAP, NPP and the dental variables HYP and LOP. (We also show the r^2 values of the OLS linear regression which estimates MAT, MAP and NPP using HYP and LOP (rightmost column). r^2 is conventionally defined as $r^2 = 1 - \text{VAR}_{\text{RES}}/\text{VAR}_{\text{DEP}}$ where VAR_{RES} is the variance of the residual and VAR_{DEP} is the variance of the dependent variable. High r^2 is better.)

	HYP	LOP	r^2 for OLS linear regression using LOP and HYP as covariates
MAT	0.12	-0.69	0.67
MAP	-0.57	-0.75	0.63
NPP	-0.54	-0.83	0.73

(c) Net primary productivity

Both LOP and HYP have a strong correlation to NPP. Using LOP and HYP together to estimate NPP gives a better accuracy ($r^2 = 0.73$) than using either LOP ($r^2 = 0.69$) or HYP ($r^2 = 0.29$) alone. LOP and HYP together also estimate MAT and MAP better than either of them does on its own. To estimate NPP, MAT and MAP more accurately, and to be able to separate biomes in a bivariate space spanned by LOP and HYP, we therefore use both LOP and HYP as covariates.

(d) Regression models for estimating mean annual temperature, mean annual precipitation and net primary productivity by longitudinal lophs count and hypsodonty

The respective OLS regression models to estimate MAT, MAP and NPP from LOP and HYP are given as $\text{MAT} = 24.7 + 13.8 \times \text{HYP} - 25.1 \times \text{LOP}$, $\text{MAP} = 2727.7 - 411.9 \times \text{HYP} - 859.7 \times \text{LOP}$ and $\text{NPP} = 2957.8 - 304.3 \times \text{HYP} - 1043.7 \times \text{LOP}$ (figure 1).

(e) Biomes

The computed estimates of NPP by LOP and HYP for individual biomes (electronic supplementary material, table S2) are concordant with those computed using Lieth's model [20] and field observation [24]. Tundra has the lowest productivity ($406 \text{ g C m}^{-2} \text{ year}^{-1}$ dry matter), followed closely by desert ($475 \text{ g C m}^{-2} \text{ year}^{-1}$ dry matter) while tropical and subtropical moist broadleaf forests have the highest productivity ($1885 \text{ g C m}^{-2} \text{ year}^{-1}$ dry matter). Our estimates of NPP are generally consistent with those from compilations of NPP measurements and estimates [25–27], with the estimates for forest biomes being particularly similar. Our computed estimates for tundra and desert are high, which is expected from the fact that mammals in these biomes survive by concentrating the available growth over wide areas; however, the estimates for these biomes are still the lowest obtained from dental traits. NPP values previously reported for grasslands, savannahs and shrublands are highly variable between studies and our estimates for these biomes are within reported extremes (electronic supplementary material, table S2). Underestimate of NPP for various types of 'grasslands' is a known issue [28]. Moreover, the WWF ecoregions classification used here splits the widely used savannah biome into subtypes of grassland, shrubland and woodland biomes, making direct comparisons with studies using different classifications problematic.

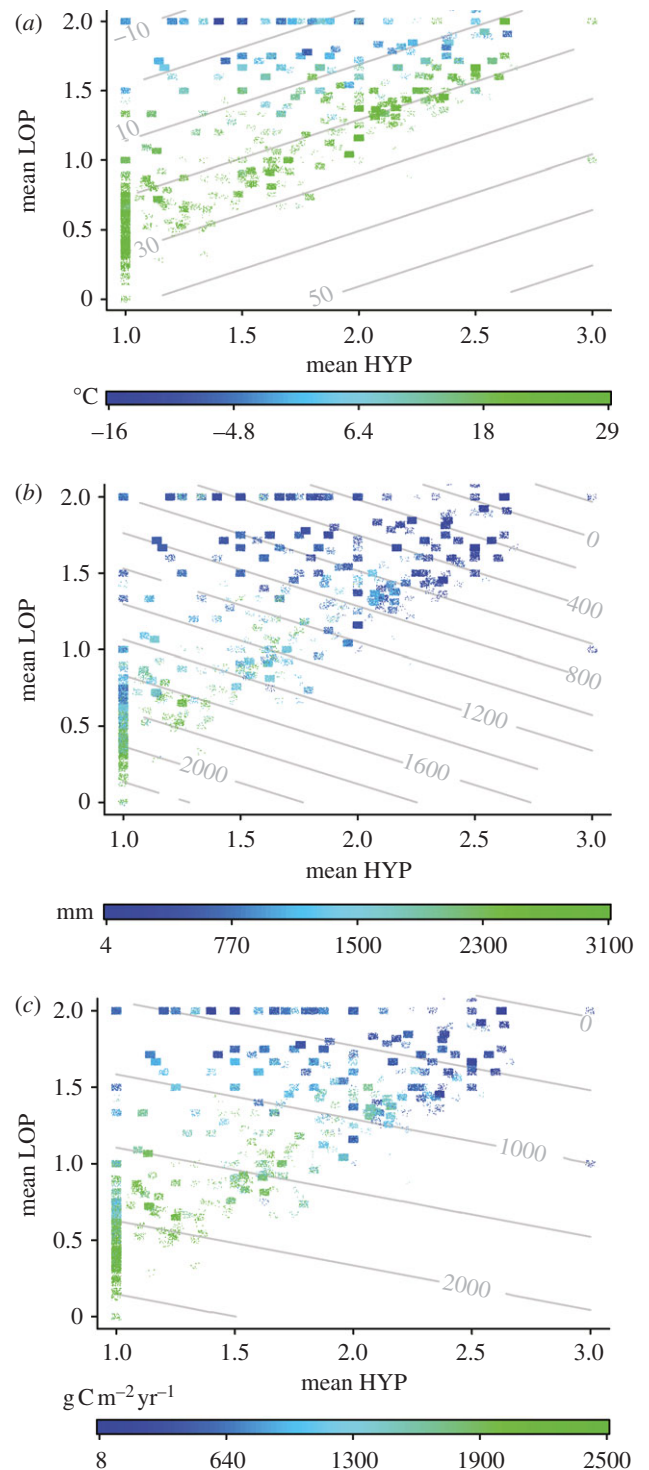


Figure 1. Bivariate plots of mean LOP versus mean HYP for estimating (a) MAT, (b) MAP and (c) NPP. The areas in the empty lower right corner of the plot are ecophysiolegically improbable combinations of high food quality and lack of water.

Plotting mean LOP against mean HYP according to biome shows that the main biomes are separated in the bivariate space in a consistent manner (figure 2). They are also highly similar to the results from simulation models where climate space was represented by MAT and a water balance coefficient [12]. The warmest biomes (tropical forest—grasslands—desert) form a continuum from high productivity near the origin to increasingly lower values along an oblique trajectory of increasing aridity, with biomes representing colder conditions transposed

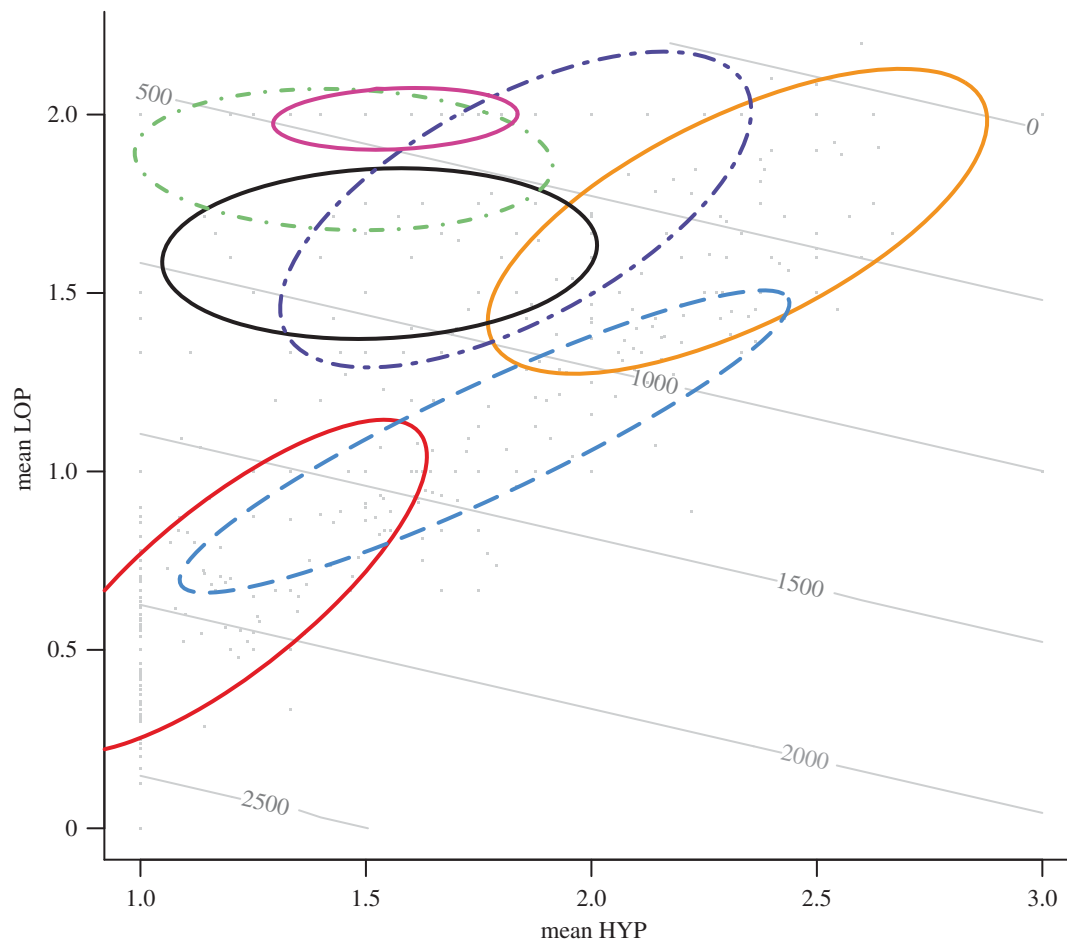


Figure 2. Bivariate plot of mean LOP versus mean HYP for biomes along the NPP gradient. The biomes in the bivariate plots are shown with 1σ confidence ellipses. The biomes shown in the figure cover 88% of the grid cells. Red line, tropical and subtropical moist broadleaf forests; orange line, deserts and xeric shrublands; black line, temperate broadleaf and mixed forests; green dashed line, boreal forests/taiga; blue dashed line, tropical and subtropical grasslands, savannahs and shrublands; violet dashed line, temperate grasslands, savannahs and shrublands; pink line, tundra.

vertically from this baseline. The forest sequence from evergreen broad-leaf forest over deciduous forest to taiga is all within a relatively humid range, while temperate grasslands and tundra are displaced towards the drier end of the range. The lowest productivity is implied for environments limited by low precipitation (high HYP), low temperatures (high LOP), or a combination of both.

(f) *Past ecosystems*

We apply the method to two cases from the mammalian fossil record of western Eurasia: the Sansanian and the Pikermian chronofaunas. Although these chronofaunas are technically defined on taxonomic similarity [16], the Sansanian chronofauna can roughly be taken to represent conditions prior to and at the beginning of the mid-Miocene global cooling at about 14 Ma [29], while the Pikermian chronofauna can be taken to represent the full expression of mid-latitude drying of the late-Miocene, with a peak development at about 8 Ma. In the plots, the Sansanian chronofauna is located close to today's tropical and subtropical moist broadleaf forest (figure 3a). This supports the independent result from the botanic evidence of this fauna [30]. Parts of the Sansanian chronofauna plot higher on the LOP axis, suggesting that habitats were cooler than present-day tropical and sub-tropical forest, but warmer than temperate deciduous forests. In comparison,

the Pikermian chronofauna is shifted towards a drier range, and plots in the dry part of temperate broadleaf and mixed forests biome and in the humid part of temperate grasslands, savannahs and shrublands biome (figure 3b). The mixed forest mosaics with savannahs are concordant with the evidence from a palaeodiet study [31]. The placement of the fossil chronofaunas in biome space suggests that they most probably represent multiple palaeobiomes, at least some of which do not correspond directly to any biomes of today's world.

(g) *Dental functional traits and climate variables*

While precipitation is strong correlated with both HYP and LOP (table 1), only LOP contains a significant temperature signal. However, the temperature signal of LOP and HYP together is much stronger than the sum of their individual temperature signals, suggesting the existence of a strong, temperature-dependent interaction. This interaction probably arises mainly from the fact that LOP alone cannot distinguish between warm and cool low-productivity biomes, but HYP, being lower in cool (and therefore moist) biomes, does resolve them (figure 4).

The surprisingly strong association of dental traits with temperature as well as precipitation may to some extent be understood in terms of short-term versus long-term functional demands. The topography of the chewing

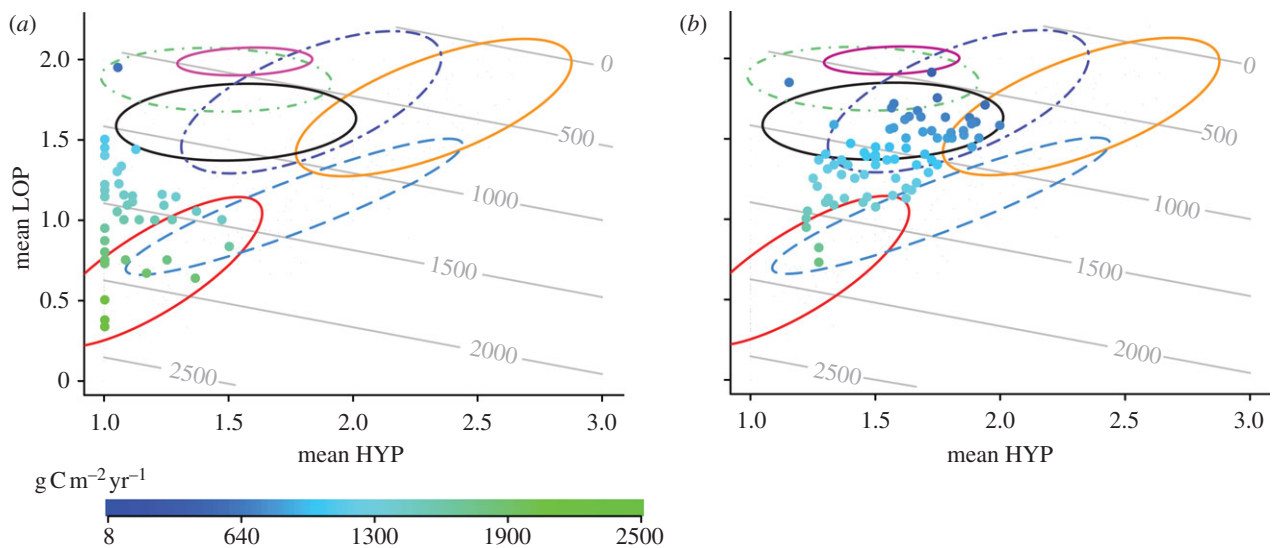


Figure 3. Bivariate plots (colour dots) of mean LOP versus mean HYP for (a) Sansan chronofauna and (b) Pikermi chronofauna and the comparisons with known biomes. Red line, tropical and subtropical moist broadleaf forests; orange line, deserts and xeric shrublands; black line, temperate broadleaf and mixed forests; green dashed line, boreal forests/taiga; blue dashed line, tropical and subtropical grasslands, savannahs and shrublands; violet dashed line, temperate grasslands, savannahs and shrublands; pink line, tundra.

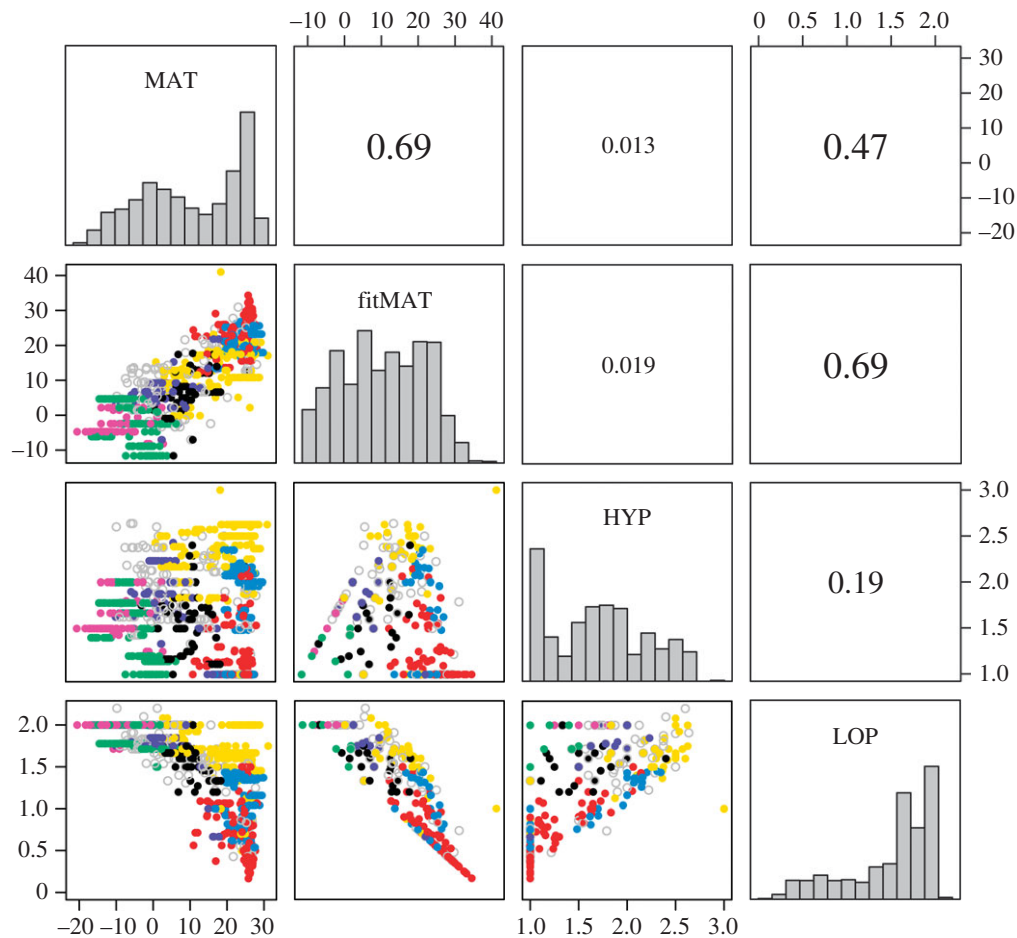


Figure 4. Scatterplots between the mean LOP, mean HYP, the fitted value of MAT and the MAT (lower triangle). The axis labels are shown on the diagonal. For visual clarity only 1000 randomly sampled grid cells are shown in the scatterplots. The biomes are shown by different colours with the colour coding as in figure 2, hollow grey spheres indicating biomes not coloured in figure 2. The upper triangle shows the squared Pearson correlation coefficients between the variables. Notice that the squared Pearson correlation among the fitted values and the MAT is, by definition, the r^2 value of the model used to estimate the MAT.

surface reflects the tooth's cutting capacity per unit action, i.e. the power stroke of the chewing cycle [32]. The required cutting capacity depends on the ratio between a food quality factor, determined mainly by the food's mechanical properties and energy-content, and the metabolic needs of the animal. Typical challenges would be to survive until the next day or until new growth becomes available. HYP in contrast, measures the tooth's ability to remain functional in the face of dental wear [4]. The degree of durability required depends on the ratio between the food-induced dental wear and the life history of the animal. A typical challenge would be surviving until sufficient offspring has been produced. The combination of low cutting capacity and low HYP represents general lack of stress, such as herbivores may encounter in warm and humid conditions with a rich range of edible plant parts available through the year. A high cutting capacity in combination with high HYP is typically found in habitats where both short-term and long-term demands on tooth function are high because a season without fresh vegetation is combined with the presence of extrinsic and intrinsic abrasives [1]. A high cutting capacity in combination with low HYP implies high functional demand without increased tooth wear, mainly found in cool and vegetated habitats, offering herbivores little to eat except structural plant parts during the cold season, but with a low presence of abrasives. A low cutting capacity in combination with high HYP conversely would imply easy-to-break but highly abrasive plant foods, a combination rarely if ever encountered in existing terrestrial habitats.

Consistent with the explanatory scenario-offered above, a recently published global study of leaf mechanical properties [33] found a strong association of leaf properties to life history and growth form but only a weak association with climate variables. The climate variable most consistently associated with leaf properties was MAP, which was found to explain only 4–6% of global variation of leaf structural resistance. Thus, although the link between climate and tooth function involves the properties of the ingested plant matter, it appears to be formed by the availability and condition of edible plant parts rather than by the properties of the plant parts themselves.

4. CONCLUSIONS

Molar height and LOP together explain 73 per cent of the recent global variation in terrestrial NPP and resolve today's main terrestrial biomes in bivariate temperature–precipitation space. The NPP estimates (electronic supplementary material, table S2) show that the results derived using dental traits are comparable to estimates derived from other sources. The quantitative nature of these estimates allows them to be used as an input for climate models as well as a proxy source for validating model results. The method has the additional advantage of being based on known functional relationships that could themselves, in principle, be modelled. Estimating NPP for the past in this straightforward manner, using the rich and well-resolved fossil mammal record holds considerable promise for integrative research connecting the present with the geological past. Our method does not rely on estimates of biodiversity, and should therefore be

robust in the face of sampling intensity, which notoriously creates problems for palaeobiological analyses.

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