

Dental ecometrics of tropical Africa: linking vegetation types and communities of large plant-eating mammals

Indrė Žliobaitė¹, Hui Tang², Juha Saarinen³, Mikael Fortelius³,
Janne Rinne⁴ and Janina Rannikko³

¹*Department of Computer Science, University of Helsinki, Helsinki, Finland,*

²*Department of Geosciences, University of Oslo, Oslo, Norway,*

³*Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland and*

⁴*Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden*

ABSTRACT

Background: The dental characteristics of large plant-eating mammals, such as hypsodonty, quite accurately describe present and past climatic conditions worldwide. However, several peculiar regions give systematically higher predictions of primary productivity than the local average environmental conditions should support. We call these ‘anomalies’. Anomalies are prominent in areas dominated by pastoralism, such as the Sahel in Africa, suggesting human-competitive pressure against the wild animal communities.

Question: What might explain such dental ecometric anomalies?

Data: Occurrence of large, plant-eating mammals worldwide; quantitative characteristics of their teeth; global net primary productivity derived from temperature and precipitation relationships.

Analyses: We analyse dental ecometrics of present-day Africa, with the aim to understand the ecology behind such anomalies. By identifying dental traits that are differentially sensitive to human activities, we can develop tailored models for accurate reconstruction of tropical habitats while taking human activities into account.

Results: A combination of dental crown height and reinforcement of cusps helps to distinguish continuous, moist forests from patchy forest fragments within arid grasslands. We demonstrate how dental traits that have different sensitivity to competition with livestock can capture anthropogenic effects on wild animal communities in climatically sensitive zones. We produce a methodology for understanding the present and guiding the future of terrestrial ecosystems.

Keywords: ecometrics, grasslands, mammalian teeth, pastoralism, Sahel, vegetation types.

INTRODUCTION

Since plant-eating animals are adapted to process the vegetation available in their habitats, morphological features of teeth reflect the properties of available foods. Therefore, the

Correspondence: I. Žliobaitė, Department of Computer Science, University of Helsinki, PO Box 68, 00014 Helsinki, Finland. email: indre.zliobaite@helsinki.fi

Consult the copyright statement on the inside front cover for non-commercial copying policies.

morphological traits of animal communities can be used to characterize the vegetation cover and climatic conditions of their habitats (Fortelius *et al.*, 2002; L. Liu *et al.*, 2012; Žliobaitė *et al.*, 2016). Such functional approaches have become known as ‘ecometrics’. Ecometric models allow one to deduce the habitats of species, the productivities of those habitats, and local climate (Eronen *et al.*, 2010a; Polly *et al.*, 2011; L. Liu *et al.*, 2012; Žliobaitė *et al.*, 2016; Galbrun *et al.*, 2018). Applying ecometric models to fossil data provides a means to reconstruct climatic conditions and habitats of the past at fine temporal and spatial scales (Eronen *et al.*, 2010b; Fortelius *et al.*, 2016).

Dental ecometric modelling usually relies on two types of dental traits – the durability of teeth (such as hypsodonty) and characteristics of the occlusal surface (such as lophedness) (L. Liu *et al.*, 2012; Fortelius *et al.*, 2016). Those functional traits are pervasive, and exist across different body sizes and taxonomic lineages (Žliobaitė *et al.*, 2016). Dental traits carry predictive signals about local climate, as follows. High productivity commonly signifies woodlands whereas low productivity is consonant with grasslands or barren lands. Meanwhile feeding in woodlands generally requires different dental traits from those in grasslands because grass contains abrasive particles, requiring durable high-crowned teeth that preserve their functionality as they wear down during the lifetime of an animal (Janis and Fortelius, 1988).

Since there are varying ecological niches within most environments, the presence or absence of any particular dental trait does not carry enough information to specify the environment. However, the distribution of dental traits within a community (i.e. the proportion of species having some or other dental traits) captures environmental characteristics quite precisely, even at spatial scales below 1000 km (Žliobaitė *et al.*, 2016).

Prevailing global-scale dental ecometric models (L. Liu *et al.*, 2012) predict precipitation, temperature, and net primary productivity based on mean hypsodonty and mean longitudinal loph counts of animal communities. These linear models are designed for analysis at the global scale. At that scale, higher mean hypsodonty and longitudinal loph count indicate lower precipitation and more arid, less productive environments. However, estimates provided by these models show some local systematic overprediction of productivity and rainfall, particularly in certain arid tropical zones. Systematic overpredictions are intriguing from the biological perspective, since the most common teeth found within animal communities suggest more rainfall than there actually is in an area. How do animal communities dominated by such teeth survive in those areas?

Such anomalies are possible if communities are somehow incomplete, with some species missing for reasons other than climatic incompatibility. Climate and productivity estimates based on the remaining communities would be distorted. Indeed, it would appear that areas with major overpredictions can be explained by the absence of large wild grazers in open near-desert habitats dominated by grasslands. In such habitats, browsers occupy marginal forest patches, typically close to streams. In the absence of large wild grazers, the overall signal is being driven by the browsers in these marginal forest patches, and such sites resemble ecometrically moist forests.

The most pronounced cases of overprediction occur in modern-day Africa. To address, explain, and resolve cases, we develop tailored, fine-resolution, ecometric models for tropical habitats. We design these models to distinguish between woody or less woody savanna, grasslands, shrublands, and semi-deserts. Overpredictions are pronounced in areas dominated by pastoralism such as the Sahel in Africa, suggesting competitive pressure on the wild animal communities there. Our analysis is aimed at understanding the ecology behind such anomalies.

The present study consists of three stages and the paper is organized accordingly. First, we revisit global ecometric models, and identify and analyse dental ecometric anomalies captured by those models. We then analyse the most prominent anomaly – the Sahel region of tropical Africa – and discuss its ecometrics in the context of the whole of tropical Africa. Having identified a lack of large grazers as a potential explanation, we then run a simulation of ecometrics as if large grazers had returned, which largely removes the anomalies. Having demonstrated that such anomalies indicate incomplete communities of large grazers, we then identify dental traits that could potentially signal incompleteness of communities and, with them, build tailored predictive models for more accurate land cover prediction in tropical habitats.

GLOBAL DENTAL ECOMETRIC ANOMALIES

The prevailing global dental ecometric model for estimating net primary productivity (NPP) (L. Liu *et al.*, 2012) is perhaps the most generic and straightforward model to summarize global dental ecometric patterns. The model takes two input variables – mean hypsodonty and mean longitudinal loph count over animal communities – in a form of a linear regression.¹ The model is consistent with the theoretical understanding that aridity of the environment is strongly associated with hypsodonty (Fortelius *et al.*, 2002; Damuth and Janis, 2011; Stromberg, 2011); thus, the higher the mean hypsodonty, the lower the NPP prediction. Mean longitudinal loph count is strongly correlated with mean hypsodonty, since lack of lophs primarily occurs in teeth which also lack hypsodonty, and therefore the relationship of loph count with NPP has the same directionality as mean hypsodonty in the model.

Globally, mean hypsodonty and longitudinal loph count are correlated (the global linear correlation is around 0.8), but they are not fully exchangeable. The global distribution of hypsodonty values has a bit more spread than loph count, and therefore is more sensitive as a proxy. Yet a model of hypsodonty alone would not succeed in South America today, since hypsodont species are almost completely missing there. A model based on loph count alone would hardly distinguish harsh tropical environments from harsh temperate forests in the north. Therefore, we consider this two-variable model as the simplest reasonable approximation of present-day global ecometric patterns.

Overpredictions by this global model occur when the climate is dry but mean hypsodonty and longitudinal loph count of the animal community are low. Figure 1a plots major overpredictions exceeding $800 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$, colour-coded by observed vegetation types in those areas. This magnitude of overprediction is roughly equivalent to mistaking a desert for a woody savanna, or mistaking an arid grassland for a tropical forest. Such mistakes suggest that animal communities in those low-precipitation locations on average have teeth the morphology of which would be appropriate for feeding in moist forest environments. Let us now look closer at these environments.

¹ Net primary productivity = $2958 - (304 \times \text{mean hypsodonty}) - 1044 \times \text{mean longitudinal loph count}$. Net primary productivity is measured in grams carbon per m^2 per year. Species occurrences for fitting this model have been based on global ecoregions, where each ecoregion contains a set of species. This is a crude approximation, since in reality species often have individual ranges. As a contingency check, we have fitted an alternative regression model on individual species ranges obtained from Lawing *et al.* (2017). The model coefficients turned out to be close to those of L. Liu *et al.* (2012). For consistency and continuity in this study, we use the published model of L. Liu *et al.* (2012).

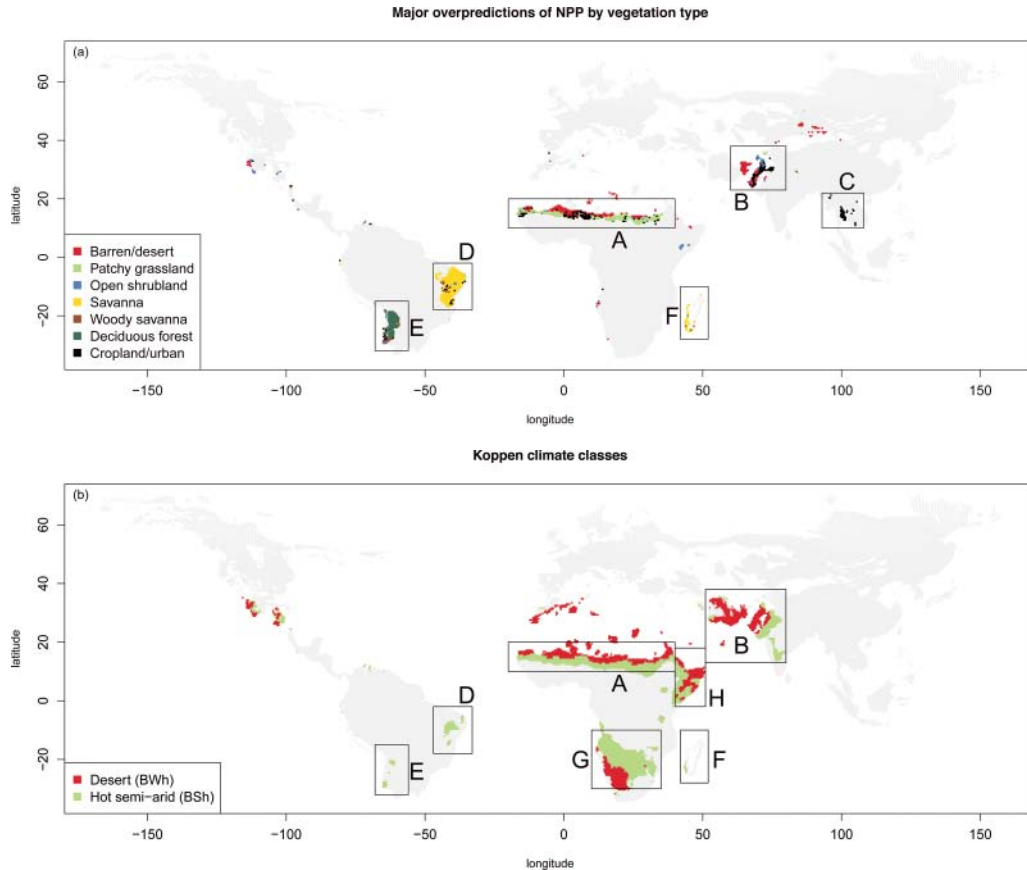


Fig. 1. Major overpredictions of net primary productivity and their climatic context. Sites with at least two wild, large, plant-eating mammal species are shown. Australia is not considered. (a) Major overprediction areas by the global model (L. Liu *et al.*, 2012), coloured areas denote overpredictions exceeding $800 \text{ g C} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ (dry matter). Letters refer to the areas under discussion in the text. The areas are coloured by their dominant vegetation type according to MODIS satellite data. (b) Global coverage of two main Köppen climate classes denoting hot semi-arid and arid environments (Friedl *et al.*, 2010). This plot depicts all the areas covered by these climatic zones without any filtering in relation to overpredictions.

Figure 1a identifies six zones of major overpredictions denoted by letters. The first two zones (A and B) are covered with a mixture of desert, hot steppe, and shrubland vegetation, which implies very modest vegetation and thus very harsh conditions for plant-eating animals. In addition, those zones include extended areas of pasture land (see evolutionary-ecology.com/data/3135Appendix.pdf, wherein Fig. A1 is a detailed map of agricultural activities). Notably, C in South Asia is exclusively agricultural and highly urbanized (surroundings of Bangkok), where only a few wild animal species remain, almost exclusively brachyodont primates.

Large grazers are mostly absent from faunal lists perhaps not least due to competition with domestic animals in all those areas heavily dominated by pastoralism (Hempson *et al.*, 2017).

Indeed, a historical account of zone A suggests that the Sahel was formerly home to large populations of grazing mammals which disappeared due to overhunting and competition with livestock (Beudels *et al.*, 2005; Brito *et al.*, 2014; <https://en.wikipedia.org/wiki/Sahel>). Similarly, an informal historical account for zone B recalls abundant wildlife, including rhinos (https://en.wikipedia.org/wiki/Indus_River). But these disappeared from the area due to severe deforestation and human interference. Faunal lists of zones A and B are short (typically 3–5 species), dominated by primates, sometimes including a gazelle or a pig (in Asia). Primates in those zones primarily inhabit riparian or gallery forests near seasonal rivers or streams, which, given the absence of large grazers in the open, generate a forest-like ecometric signal.

The circumstances are slightly different in the other three major areas of overprediction: D, E, and F. Sahel faunal lists are slightly longer (typically 5–7 species) and vegetation is more woody, as land cover types in Fig. 1a suggest. South America used to have large grazing mammals, but today these niches are occupied mostly by small mammals, which are not accounted for in global dental ecometric models. [Small mammals are not accounted for in the ecometric models considered here because even though their dental mechanics, in principle, are the same as for large mammals, dependence on climate is not the same due to the possibility to sleep or hide (Liow *et al.*, 2009).] The Late Pleistocene mass extinction of large mammals was particularly harsh in South America where 83% of the genera died out, including most large, hypsodont taxa such as notoungulates, South American horses, and many large xenarthrans (Koch and Barnosky, 2006). The remaining, dramatically impoverished large herbivorous mammal fauna is heavily dominated by deer and tapirs, which have brachyodont dentitions, with only lamine camels being hypsodont.

Since hypsodonty is largely absent among large mammals in South America, the model predicts rather constant productivity across the whole continent. Meanwhile, in reality, zones D and E happen to be the driest in the continent and therefore appear to be the most marked anomalies. Zone F in Madagascar contains some woody cover as well, yet lacks large grazing mammals. But as in South America, small mammals occupy those niches. Again, the small mammals are not accounted for in the ecometric models considered here because even though their dental mechanics, in principle, are the same as for large mammals, dependence on climate is not the same owing to the possibility to sleep or hide (Liow *et al.*, 2009).

The difference between Madagascar and other areas may be that Madagascar is a separate zoological region (Sclater, 1858; Rosenzweig *et al.*, 2012; Samonds *et al.*, 2012). That means it displays a very high level of endemism (Goodman and Benstead, 2005). In particular, it lacks large grazers except for hippopotamids, the only group of large African grazers to colonize Madagascar.

Most of the major overpredictions in Fig. 1a correspond to, or are nearby, two climatic zones – hot semi-arid zones and desert zones, as illustrated in Fig. 1b. Yet, even in such arid environments, small forest patches exist, for example as riparian or gallery forests along rivers or streams. When grazing species are absent from those climatic zones, the ecometric variables mainly reflect species in the patchy woody habitats, and the global ecometric model predicts a forest-like environment.

Can we distinguish areas covered with patchy forests from those with full forest cover by noting the absence of the grazing part of the community? In the next sections, we look at how to address this question from an ecometric standpoint.

Modern-day Africa is a good place to study tropical habitats because of its geographic continuity and continuing diverse native wildlife. It also has the most prominent over-

prediction (zone A), as well as two interesting zones, G and H (see Fig. 1b), which are in the pre-desert climatic zone (BSh). Curiously, in Africa, these two zones do not show any major overpredictions, although they have the same climate as those where most global overpredictions occur.

DENTAL ECOMETRICS OF TROPICAL AFRICA

Our study area covers tropical Africa from -25° to 25° latitude, excluding high-elevation, high-precipitation sites and sites of high industrial or agricultural activities. We excluded Madagascar as well because it is its own zoological region – its species are mostly endemic: different from those in any other region, including mainland Africa (Goodman and Benstead, 2005; Rosenzweig *et al.*, 2012).

Figure 2a shows NPP derived from annual rainfall and temperature measurements (Lieth, 1975 as cited in L. Liu *et al.*, 2012). The figure shows a rather monotonic gradient of NPP change. The highest NPP is at the equator and the lowest is at the northern and southern tips of tropical Africa.

Figures 2c and 2d show the corresponding maps for mean hypsodonty and mean longitudinal loph count. These show similar trends of change, quite monotonic from the equator to the south, yet not quite monotonic from the equator to the north. In fact, the highest mean hypsodonty and loph count appear at quite moderate NPP, around $1200\text{--}1500\text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$, as highlighted by the black rectangles. The dental ecometric traits recede again before the Sahara desert. The mean hypsodonty values there resemble moist tropical forest values near the equator, and mean longitudinal loph count falls even lower than in the equatorial forest. This happens where NPP is at its minimum, and therefore generates massive overpredictions in the Sahel area, as can be seen from Fig. 2b. In the southern part of Africa, the global model makes predictions that are quite accurate (Fig. 2b), with no major overprediction.

The north and the south (southwest) have similar values of NPP, and quite similar climatic conditions according to the Köppen classification system (Kottek *et al.*, 2006), as illustrated in Fig. 2e. Both north and south are dominated by a hot semi-arid climate (BSh) which end in deserts (BWh). Yet, the actual vegetation differs in those areas, as depicted in Fig. 2f. These land cover types are derived from MODIS land cover data MCD12C1 (https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/med12c1; Friedl *et al.*, 2010) that directly reflect the major vegetation types growing there at present (2001–2012). The gradient of land types from the equator towards the north and south accommodates steadily decreasing amounts of woody cover, as can be inferred from Fig. 2f and Table 1.

Table 1. Woody cover fraction for each type of vegetation used in Fig. 2f (Friedl *et al.*, 2010)

Habitat class	Vegetation type	Woody cover
Barren, partially covered by vegetation	Barren/desert	Vegetation cover <10%
	Open shrublands	Shrubs 10–40%, no trees
Open grasslands mixed with ‘gallery forests’	Patchy grasslands	Tree/shrub canopy <10%
	Savanna	Forest canopy 10–40%
Woody, dominated by forest canopy	Woody savanna	Forest canopy 40–60%
	Evergreen forest	Forest canopy >60%

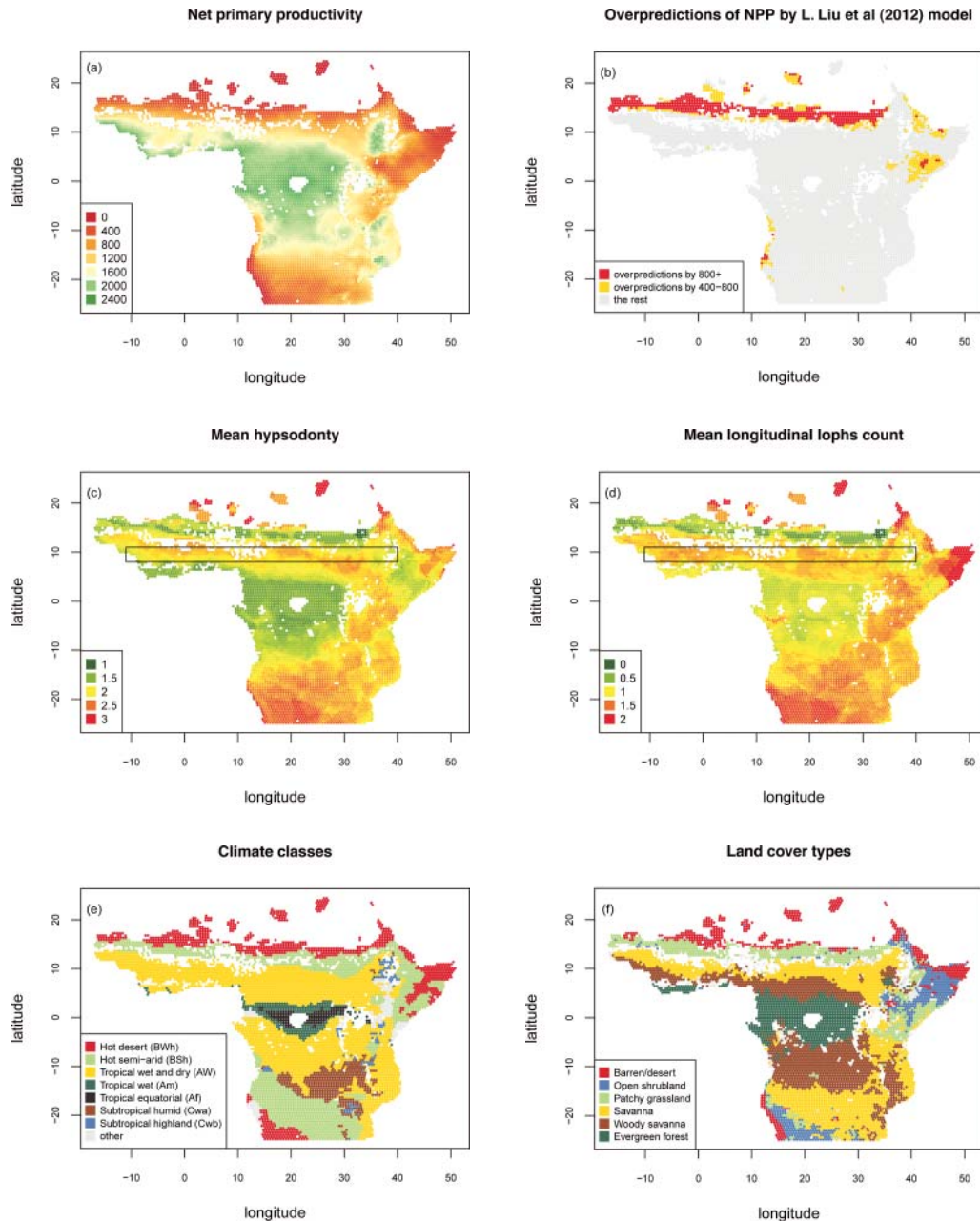


Fig. 2. Climate, vegetation, and dental ecometrics in modern-day tropical Africa. (a) Net primary productivity ($\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$), estimated from annual precipitation and mean annual temperature from Worldclim2 (Fick *et al.*, 2017). (b) Overpredictions of net primary productivity by the global model (L. Liu *et al.*, 2012) as compared to values plotted in (a). (c) Mean hypsodonty scores. (d) Mean longitudinal loph counts [hypsodonty and loph scores for species are from data reported by Žliobaitė *et al.* (2016) and Galbrun *et al.* (2018)]. (e) Köppen climate classes (Kottek *et al.*, 2006). (f) Vegetation types (data based on Channan *et al.*, 2014); the maximum land cover types per grid cell are reported.

The transition from the equator towards the subtropics is quite steady in both directions, starting from evergreen forests, through woody savannas to savannas, then patchy grasslands in the northern hemisphere and shrublands towards desert areas. Woody savanna, savanna, and patchy grassland cover the regions that are influenced predominantly by an African monsoon climate (J. Liu *et al.*, 2012; Wang *et al.*, 2012). Precipitation in those regions is highly seasonal due to seasonal movement of the intertropical convergence zone. In the main, shrublands are found at higher elevations, which are in the northeast and southwest, while at low elevations barren areas are preceded by patchy grasslands. The Sahel, which is the main zone of overpredicted productivity, is typically of low elevation with patchy grassland.

Southern Africa is narrower longitudinally than northern Africa. Moisture from the ocean can be transported into the continent more easily in the south. In addition, southern Africa is also higher in elevation, thus surface temperatures are lower than in northern Africa given the same distance from the equator, indicating less evaporation in southern Africa. As a result, southern African latitudes are more moist than equivalent latitudes in northern Africa even though the precipitation values are very similar (a map of precipitation minus potential evaporation is available in the [Appendix](#), Fig. A2), and more woody cover (savanna instead of grassland) exists in southern Africa (at 10–15°S) compared with northern Africa (at 10–15°N).

The patchy forests we aim to account for ecometrically are not necessarily gallery forests with a fully closed canopy over a river. They are forests in the sense that woody vegetation is concentrated in clusters, rather than distributed as isolated trees, providing forest-like habitats. Such forests are generally too small for large herbivores, but they can accommodate primates. Primates, indeed, dominate the modest faunal lists of the Sahel, whereas antelopes are almost completely absent. Modern primates are brachyodont and they rarely have lophs, depressing both mean hypsodonty and mean longitudinal loph count in the area. The other natural communities of the Sahel are mainly communities of patchy forests. That is why the global ecometric model predicts their productivity as if it were all forest. Thus, lack of community representatives from the open part of grasslands leads to severe overpredictions of NPP.

Patchy grasslands are dominated by herbaceous vegetation with trees distributed as clusters. Maximum woody cover has been shown to have a direct linear relationship with mean annual precipitation (Sankaran *et al.*, 2005). Based on the assumption that precipitation is the limiting factor for NPP in those areas, this relationship of woody cover with precipitation translates to a near linear monotonic relationship with NPP, applying Lieth's (1975) formula.

Even though the overall tree cover in the patchy grassland zone is less than 10%, trees are typically concentrated in patches (hence the name patchy grasslands), often along streams. Gallery forests are one common type of forest patches. Gallery forests are patches of forests along rivers or wetlands. They exist in landscapes that otherwise do not support forests, such as savannas, grasslands, or deserts. Gallery forests exist there because of locally higher fertility, better soil drainage, a better water supply, and less risk of fire in the riparian zones (Biddulph and Kellman, 1998).

The Sahel today is the most extensive pasture-dominated area in Africa. For example, Fig. 3a shows very high concentrations of cattle in the Sahel area (Robinson *et al.*, 2014). Apart from the Sahel, there is a notable concentration of livestock in East Africa (around Ethiopia, Somalia, and Kenya), as well as in the south, of which the southwest (near the Angola–Namibia border) is covered by our study area. Figure 3b shows that there are

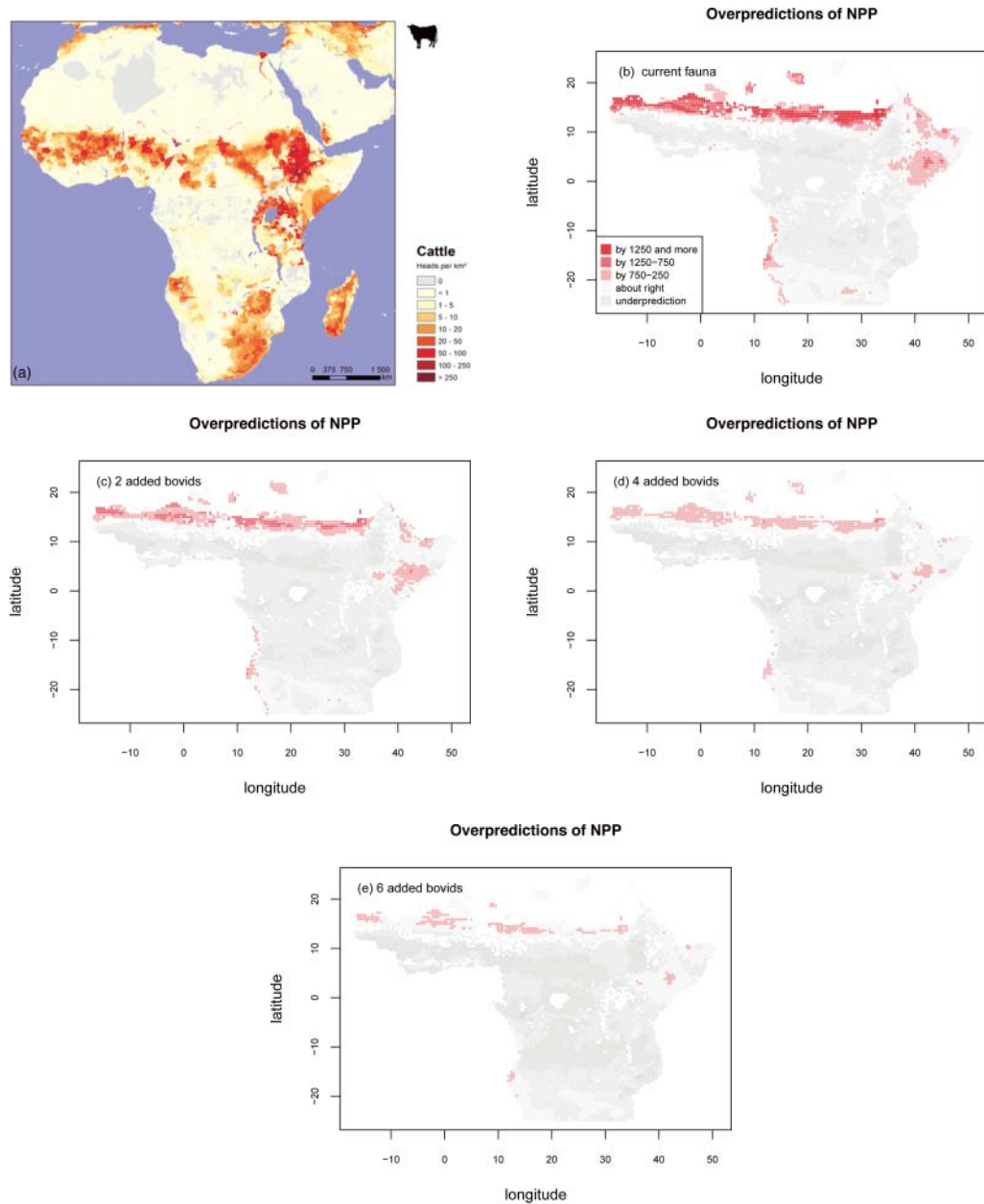


Fig. 3. Livestock and ecometric anomalies. (a) Heads of cattle per km² in Africa. Source: <https://livestock.geo-wiki.org/graphics/> (Robinson *et al.*, 2014). (b) Ecometric anomalies with current wild fauna. (c) Ecometric anomalies if two extra bovids are added throughout the whole of Africa. (d) Ecometric anomalies if four extra bovids are added. (e) Ecometric anomalies if six extra bovids are added. The most likely reason why we observe incomplete communities in those areas is competition for grazing with livestock. This is supported by evidence from the fossil record in East Africa, which suggests that large grazing bovids have shifted their diet from grazing towards mixed feeding during the Holocene, especially from the mid-Holocene towards the present (Rowan *et al.*, 2015).

corresponding areas of ecometric overprediction in the east and in the southwest. Although these are less severe, they closely match the intensive concentrations of cattle in Fig. 3a. The Sahel overprediction is the most pronounced in Africa probably a result of the largest continuous area of intensive pastoralism. The livestock of the other areas – east and southwest – is intensive, but it is patchy. Perhaps this allows wildlife to exist in between, thus overpredictions are not that pronounced. Indeed, there are many natural parks in East Africa, providing refugia for wildlife.

Once, vast populations of large wild herbivores inhabited the Sahel region (https://en.wikipedia.org/wiki/Sahel#Flora_and_fauna; see also Walther, 2016), including scimitar-horned oryx, dama gazelle, dorcas gazelle, red-fronted gazelle, giant prehistoric buffalo, and Bubal hartebeest. While we do not know with certainty the exact ranges of these herbivores in the past, we can do an approximate analysis of how ecometric estimates would look if the current communities had one, three, or five such wild animals added. All the above large bovids have hypsodont teeth with two lophs, thus dental crown type values will be the same no matter which of the animals are added to the current communities for the whole study domain. Figures 3c, 3d, and 3e show remaining overpredictions of NPP if two, four, or six bovids are added to the current faunal communities. We can see that even with two bovids added (Fig. 3c), overpredictions become much less pronounced, and with six bovids added all major overpredictions disappear, and only a few relatively mild overpredictions remain. This demonstrates that if those large grazers that are reported to have been present in the Sahel in the past were still present, we would see few ecometric anomalies in Africa.

A DENTAL ECOMETRIC MODEL FOR IDENTIFYING TROPICAL HABITATS

Even though animal communities are incomplete in the Sahel, we would like to be able to distinguish by ecometric means tropical habitats from Sahel communities as they are, with the aim to distinguish between patchy gallery forests and full tropical forests. One approach today, where we know complete faunal lists, would be to look at the number of species. Full tropical forests have many more species, as can be seen from Fig. 4a. However, the number of fossil species at a locality varies considerably depending on taphonomic processes and collection efforts – which, to a variable extent, often make community lists incomplete. So we cannot rely on the raw number of species. But we can develop ecometric models that work on incomplete communities of both the past and present.

A dental trait called ‘structural fortification of cusps’ (Žliobaitė *et al.*, 2016) helps. Structural fortification is a morphological feature of molars amplifying cusp basins as teeth wear. Structural fortification is achieved by differential thickening of enamel ridges. It typically appears along with hypsodont or mesodont teeth. Figure 5 provides examples of fortified and non-fortified bovid teeth. Differential thickening of enamel is a necessary but not sufficient condition for fortification. *Tragelaphus* (Fig. 5a) has thicker enamel of the second ridge, but the enamel is folded in an angled structure, which forms an acute loph as the tooth wears. In contrast, structural fortification of cusps can be seen in *Redunca* (Fig. 5b); a round structure has formed from the inner enamel and this maintains a cusp during tooth wear rather than allowing the tooth to wear into a blade-like loph (as in Fig. 5a). Therefore, a rounded enamel structure is the second necessary condition for fortification. Without enamel thickening, tooth wear would erase the relief, flattening the occlusal surface, as seen in *Alcelaphus* (Fig. 5c). The biomechanical function of maintaining a cusp

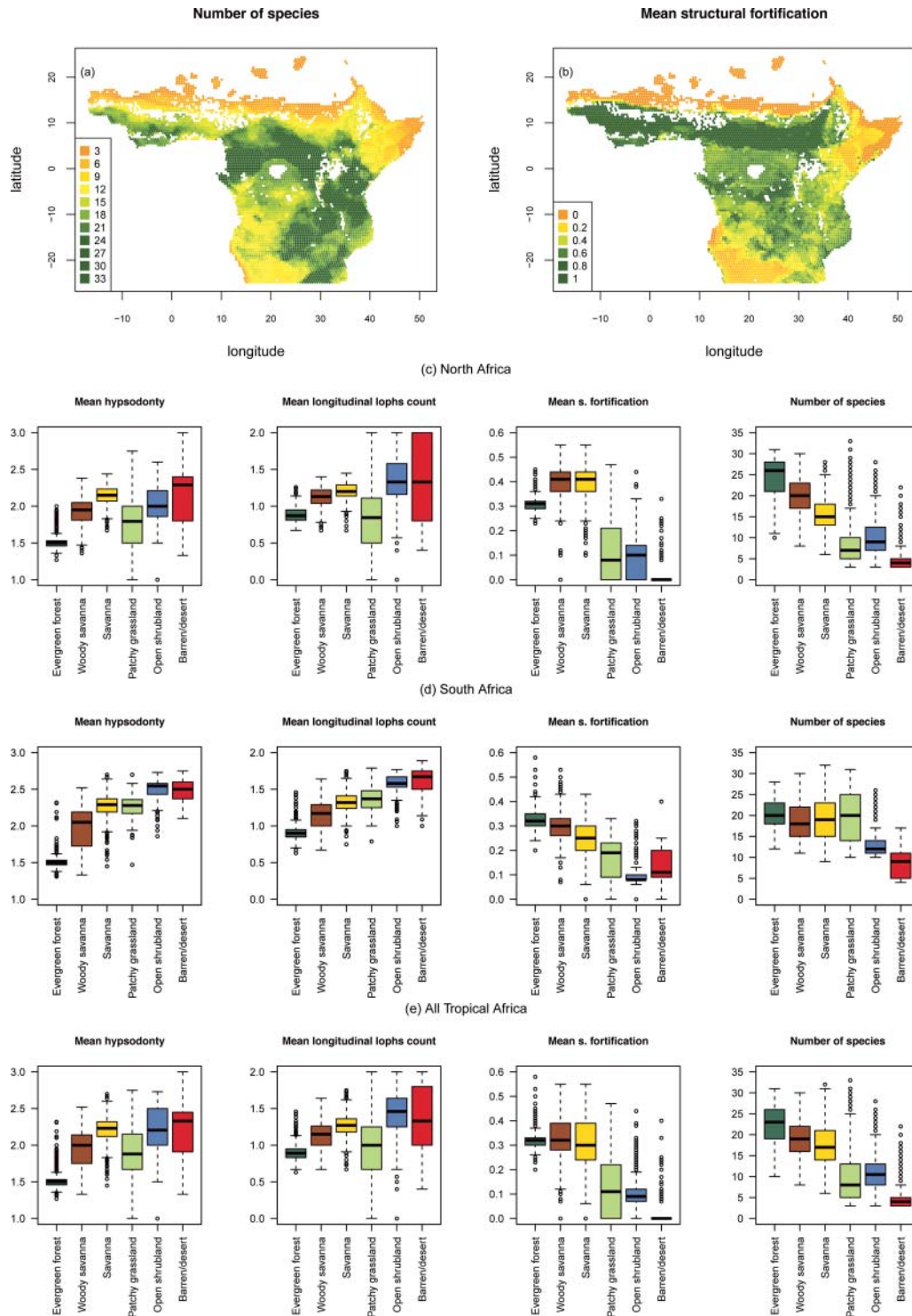


Fig. 4. Distribution of dental traits and number of species in the northern and southern parts of Africa. (a) Number of species; (b) mean structural fortification; (c) distribution of dental traits and number of species in the northern part of Africa; (d) distribution of dental traits and number of species in southern Africa; (e) distribution of dental traits and number of species in the whole of tropical Africa.

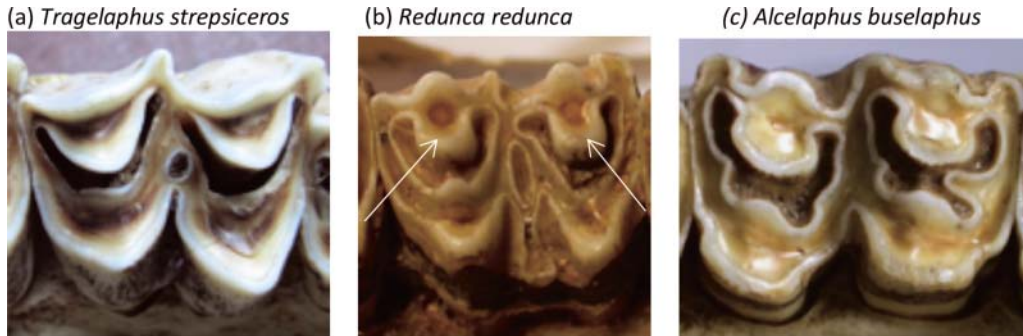


Fig. 5. Illustration of structural fortification on the second upper molars of three bovid species. (a) Non-fortified and non-flat tooth; (b) structural fortification is present (the arrows highlight prominence of cusps); (c) non-fortified but flat tooth. Photo credit: Liu Liping.

(b) versus a loph (a) when a tooth wears is not yet fully clear, but our current understanding is that it is a specialization for chewing on tall grasses (such as wetland grasses), which have three-dimensional structures and therefore require a three-dimensional arrangement of otherwise plagiolophodont-like teeth.

Structural fortification in selenodont teeth usually corresponds to high-relief, rounded mesowear patterns, which are observed with mixed-feeding diets (Fortelius and Solounias, 2000). Indeed, most species having fortified teeth tend to be grass-dominated mixed-feeders, typically switching their diet seasonally from fresh grass to fruits and browse. Table 2 provides a more detailed description of the diets and habitats of species with structural fortification. They tend to live in wooded habitats, wetlands, or montane areas. Since they are grazers in forest habitats, the grass they consume is softer and fresher than the harsh dusty grass of open areas.

Closed tropical forest habitat and open habitat with patchy woody cover have different values of mean structural fortification. Figure 4b shows the distribution of mean structural fortification in tropical Africa. The gradient of structural fortification is rather monotonic, steadily declining from the equator towards both north and south. Comparison with Fig. 2a shows that this trait is closely correlated with the number of species. Closed-canopy forests tend to have a greater number of structurally fortified species, and this number steadily decreases towards the deserts.

Many of the fortified species depend on the regular availability of drinking water. For example, Heywood (2010) lists two species of cervids (*Elaphurus davidianus* and *Rucervus duvaucelli*) that ‘display grazing in near water habitats or of fresh grass, and never show diets that are entirely formed of this component’. They are ecologically analogous to reduncine bovids. Both species of cervids have fortified molars (Galbrun et al., 2018). Thus, a common denominator of the fortified species seems to be woody habitats, often associated with wetlands or permanent water sources. Fortified species are commonly graze-dominated mixed-feeders in closed habitats. They are not often present in patchy-forest fragments with seasonal streams within otherwise semi-desert environments. This would explain why the mean structural fortification can distinguish closed forests from forest patches within generally open habitats.

Figures 4c–e show distributions of dental traits separately in the north of Africa (above the equator), in the south of Africa (below the equator), and in the north and south combined. Recall that northern Africa has pronounced overpredictions but, by and large, southern Africa does not. We can see from Figs. 4c–e that, in all parts of Africa, mean structural fortification follows similar trends. Therefore, even though the animal community in the north is incomplete, if there were large grazers there, grazers adapted to those arid habitats would not have structural fortification.

The same reasoning does not hold for mean hypsodonty and mean longitudinal loph count (also depicted in Figs. 4c–e). We can see that the more arid habitats (patchy grasslands, open shrublands, and barren/deserts) have high loph counts and hypsodonty in the south, but much lower values in the north. This is particularly true for patchy grasslands, which have hypsodonty values and loph counts almost as low as evergreen forests. This reflects the fact that those communities lack large grazers whereas forest patches within those grasslands do have browsers or mixed-feeders.

In summary, mean hypsodonty (and/or loph count) promises to distinguish grass-dominated from browse-dominated communities; and fortification, as inferred from Fig. 4, promises to reveal the share of woody cover in the environment that is necessary to accommodate closed-habitat mixed-feeders.

Since the plots suggest non-linear relationships between productivity and mean hypsodonty, we consider non-linear models for predicting ecometrically the type of habitat. We build a decision-tree model (Quinlan, 1986) that can capture non-linear relationships in a non-parametric way. Because it is non-parametric, the model does not assume any specific data distribution. Moreover, decision tree models are easy to interpret, allowing one explicitly to trace and analyse the resulting decision rules. For details on how we form the dataset for model fitting and how we fit the actual model, see evolutionary-ecology.com/data/3135Appendix.pdf.

Figure 6a shows our predictive model for habitat estimation. The model uses two input variables: mean ordinated hypsodonty (HYP) and mean structural fortification (SF) for a given locality. Beginning at the top of the tree, the rules are sequentially evaluated until a node specifying the habitat is reached. That habitat is the prediction.

Decision trees are flexible models. They can match the underlying data very closely, building decision rules not only for sets of observations but following data even up to single data points. Such precision is often undesired, since it may capture too much noise in addition to generic underlying patterns. This is called ‘overfitting’. To avoid overfitting, we restrict the depth of the decision tree to a maximum of three levels – in accord with the expectation that we use up to three dental traits.

A discussion of the resulting model structure is presented in the Appendix. Hypsodonty distinguishes forest from open habitats. Structural fortification then helps one to make a finer distinction as to whether the habitat has extensive woody cover, has only patches of woodland, or is open.

The accuracy of classification of the model fit is 64%, which is very good given that the model is not particularly complex. The overall fit appears very good too. The major misclassifications are: missing grasslands in east central Africa; too much desert cover in the Somalian peninsula; missing woody savanna in the southeast; and missing desert in the southwest. The Sahel is also estimated to be more desert-like than it is. These effects may be further related to human activities (Figs. 6b, c).

Table 2. A list of species with structural fortification in the tropical Africa dataset that occur in at least ten localities

Taxon	Family	Diet	Habitat
<i>Cephalophus callipygus</i>	Bovidae	Primarily fruit, but also leaves, flowers, and fungi	Dense undergrowth rainforests
<i>Cephalophus dorsalis</i>	Bovidae	Primarily fruits and seeds, but also leaves, fungi, flowers, and animal matter	Old-growth of primary forests
<i>Cephalophus leucogaster</i>	Bovidae	Primarily seeds and both unripe and ripe fruits (fallen), with small amounts of foliage, fungi, and animal matter	Mature forests
<i>Cephalophus natalensis</i>	Bovidae	Primarily fallen leaves, as well as fruits, seeds, and flowers	Coastal and riverine forests, mixture of open understory and dense thickets
<i>Cephalophus niger</i>	Bovidae	Mostly fruit, but also leaves and shoots, roots, fungi, and animal matter	Lowland rainforest
<i>Cephalophus nigrifrons</i>	Bovidae	Fruits and seeds, foliage, mosses, lichens, fungi, and invertebrates	Montane, lowland, and swamp forests, marshes, margins of rivers and streams
<i>Cephalophus ogilbyi</i>	Bovidae	Fallen fruits and seeds, flowers, and leaves	High-altitude rainforests
<i>Cephalophus rufilatus</i>	Bovidae	Primarily leaves, fallen fruits, flowers, seeds, and twigs	Open savanna woodlands
<i>Cephalophus silvicultor</i>	Bovidae	Primarily fruit, seed pods, seeds, but also leaves, stems, and some animal matter	Semi-deciduous forests, rainforests, riparian forests, and montane forests
<i>Cephalophus weynsi</i>	Bovidae	Mostly fruit (ripe, unripe, and seeds), but also foliage, flowers, and fungi	Lowlands and montane rainforests
<i>Cephalophus zebra</i>	Bovidae	Mostly fruits and seeds, but also leaves and some animal matter	Lowland primary rainforests, particularly by clearings and along forest margins
<i>Hippotragus equinus</i>	Bovidae	Medium high grasses, rarely leaves	Woodland and grassland savanna, from forest with a grassy understory to grasslands dotted with a few trees
<i>Hippotragus niger</i>	Bovidae	Medium high grasses, leaves	Wooded savanna
<i>Kobus ellipsiprymnus</i>	Bovidae	Grasses, reeds, and leaves	Scrub and savanna areas along rivers, lakes, and valleys

<i>Kobus kob</i>	Bovidae	Fresh grasses	Wet areas, such as floodplains
<i>Kobus leche</i>	Bovidae	Succulent grasses, water plants, and rice	Wetlands, marshy areas
<i>Kobus megaceros</i>	Bovidae	Brasses and other marsh vegetation	Swamps, marshy areas
<i>Kobus vardonii</i>	Bovidae	Grasses (especially perennials) and some forbs	Marshy grasslands
<i>Oryx beisa</i>	Bovidae	Grasses, leaves, buds, and fruit	Semi-desert and steppe
<i>Oryx gazelle</i>	Bovidae	General grazer but browser during dry season, also roots and tubers	Arid regions
<i>Ourebia ourebi</i>	Bovidae	Fresh grasses (90%), browse, and flowers	Savanna, floodplains, and tropical grasslands
<i>Redunca arundinum</i>	Bovidae	Grasses, herbs, and reeds	Woodlands, moist grasslands with tall grasses, reeds, sufficient cover, and water nearby, such as floodplains and pastures
<i>Redunca fulvorufula</i>	Bovidae	Grasses (selective)	Montane areas, near water
<i>Redunca redunca</i>	Bovidae	Grasses and tender reed shoots	Grasslands, swamplands, and woodlands (near water)
<i>Syncerus caffer</i>	Bovidae	Grasses, leaves, sedge, and browse	Savanna, rainforest, habitat with permanent water and grass
<i>Hylochoerus meinertzhageni</i>	Suidae	Primarily grasses, but also leaves, fruits, eggs, and animal matter; forest hogs tend not to root up the soil when feeding	Wooded habitats
<i>Potamochoerus larvatus</i>	Suidae	Grasses, water plants, roots, bulbs, fruit, carrion, and small animals	Forests, woodlands, riverine vegetation, and reedbeds
<i>Potamochoerus porcus</i>	Suidae	Grasses, water plants, roots, bulbs, fruit, carrion, and small animals	Rainforests, areas near rivers or swamps
<i>Hippopotamus amphibius</i>	Hippopotamidae	Grasses, sometimes aquatic plants	Rivers, lakes, and mangrove swamps
<i>Theropithecus gelada</i>	Cercopithecidae	Seeds (preferred) and blades of grass, rarely flowers, rhizomes and roots, herbs, small plants, fruits, creepers, bushes, and thistles	Montane grasslands

Note: Diet items and habitat information gathered from public descriptions of species. Information collected from various sources (ultimateungulate.com, Wikipedia).

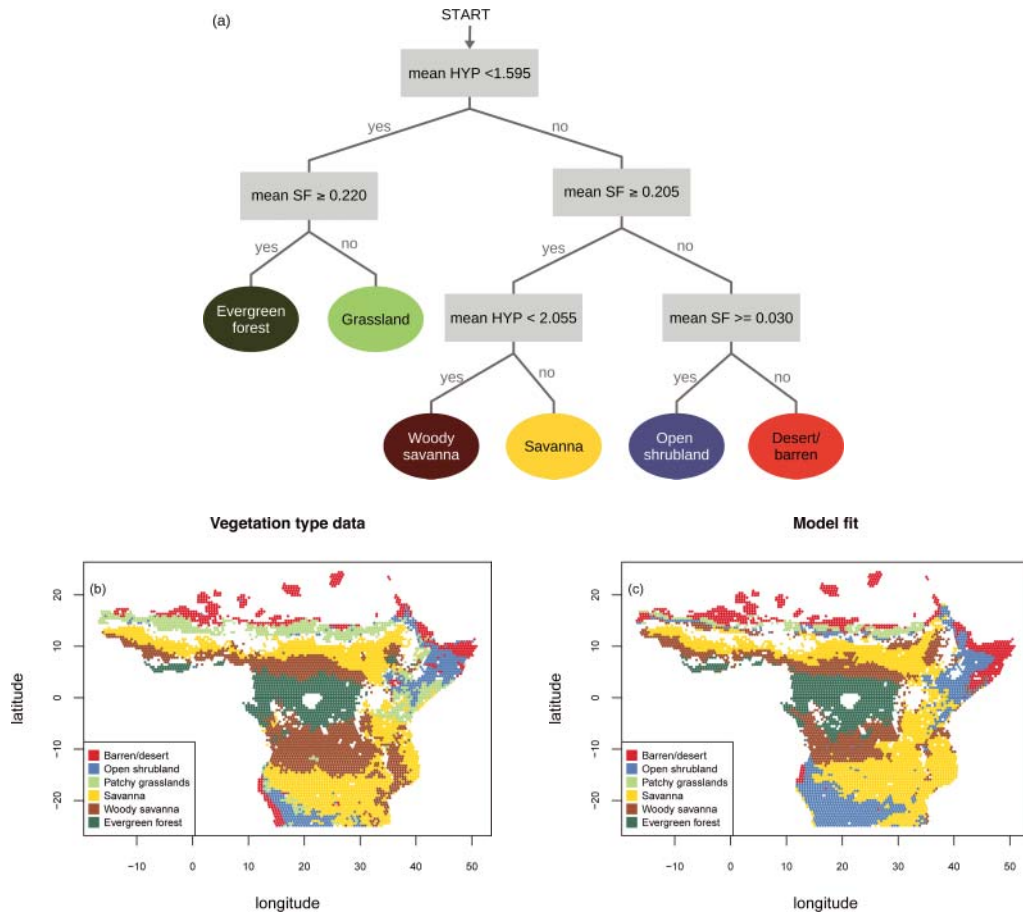


Fig. 6. (a) Decision tree for estimation of vegetation type in tropical areas. The model is fitted to modern-day African data. Inputs: mean hypsodonty and mean structural fortification for a locality. Usage: start at the top, check the condition, if the condition is satisfied – go left, otherwise go right down the tree until a vegetation type is reached, which gives the estimate. (b) Modelling dataset and (c) estimates produced by the model fit the data presented in a training fit.

Patchy grasslands are correctly identified in the Sahel, where they are the most extensive. In the south, where only small fragments of patchy grasslands are available, they are misclassified as shrublands, which are adjacent to them. This happens because of higher hypsodonty in patchy grasslands in the south, where, as discussed, large grazers are not facing severe competition from livestock. In the east, patchy grasslands are mostly classified as savanna since they are very closely intermixed with savanna there and, perhaps, animal occurrence ranges do not end precisely at the transition of one to the other.

The model is tailored to modern-day Africa. Therefore, it considers possibly incomplete communities with lower hypsodonty in patchy grasslands. The model demonstrates that even if the hypsodonty signal from dental traits of communities is forest-like, we can distinguish true forest from forest patches through structural fortification – a trait

that is largely insensitive to incompleteness of communities, since there would be limited fortification in the patchy grasslands anyway, even if large grazers were present there.

DISCUSSION AND CONCLUSION

In the Introduction, we referred to ‘overpredictions’ as anomalies. But ecometric estimates are not anomalous – it is the faunal communities that are, which can be seen from historical accounts and comparison with areas having less intensive livestock presence. The global model predicts forest habitats where distribution of dental traits of the faunal community suggests forest. An incomplete faunal community, likely due to anthropogenic activities, is the anomaly, not the model. Yet this anomaly presents an interesting natural experiment for ecometric modelling: to what extent can ecometrics distinguish between grassland and forest in a mixed-habitat mosaic, even when faunal communities are incomplete and represent one end of the spectrum more than the other. We find that complementing ecometric models with a dental trait describing structural fortification of cusps makes such models more reliable in incomplete faunal communities, and, at least in modern-day Africa, able accurately to estimate vegetation types.

Structural fortification is a relatively recent trait in the history of life. It seems to have first appeared during the Miocene in Asia along with grasslands – not open, arid grasslands but grasslands in woody environments. Looking at the fossil record, we find a broad presence of fortification in the classic late Miocene assemblages from Pikermi and Samos in western Asia and the Siwaliks in southern Asia [including the curious case of the giraffid, *Samotherium*, a grass-dominated mixed-feeder or even grazer (Solounias *et al.*, 1988)]. Nowadays, fortification is primarily observed in bovids, cervids, and hippos, more rarely in pigs and monkeys (Gelada). We have even observed several species of fortified hipparions from Pikermi and Samos. While the trait predominates in selenodont teeth, it is not exclusive to them and it seems to have developed independently for different groups in the same environments.

We are not aware of any Miocene or Pliocene fossil fauna in the Americas showing clearly fortified teeth. One reason could be a lack of mosaic-vegetation patterns and more widely spaced trees in arid habitats, at least in North America, as compared with the Old World (Janis, 1982). More sparse and less patchy tree cover would not provide the soft grass and forest fruit resources for selective feeders, which dominate fortified fauna. Structural fortification is a way to retain the three-dimensional occlusal structure while teeth are worn down, and in most cases it is seen in combination with hypsodont or mesodont teeth and is primarily associated with grass-dominated, selective mixed-feeding in woody tropical habitats.

Our model for predicting habitat types is tailored to Africa and builds on vegetation types that are found only in tropical environments. We focused our analysis on Africa to understand why the most pronounced overpredictions of NPP by the global model occur there (L. Liu *et al.*, 2012). Yet, a common denominator for overpredictions worldwide, highlighted in Fig. 1, seems to be human activities in vulnerable ecoregions. The grasslands of the Sahel (zone A in Fig. 1), ‘although not particularly rich biologically, [are] savannas [that] once supported a large and diverse ungulate community. The first European explorers to visit the region found vast herds of game, even larger in number than those of eastern and southern Africa. Sadly, these herds have been reduced to mere remnants due to nearly a century of unregulated over-hunting with modern firearms and vehicles, coupled with habitat loss’ (World Wildlife Fund, 2017). The scimitar-horned oryx, now presumed to be extinct in the wild, dama gazelle, dorcas gazelle, and red-fronted gazelle used to be abundant and widespread,

as was the now extinct sub-species of the common hartebeest, the bubal hartebeest (East, 1999, as cited in World Wildlife Fund, 2017). Climatic desiccation poses another long-term threat to this ecoregion, where excessive land use can result in the total loss of vegetation and perhaps conversion into desert or near-desert (Gonzalez, 2001). The density of livestock (especially cattle) in the area is very high, especially when compared with the corresponding latitude ranges in southern Africa (Robinson *et al.*, 2014). The area is among the earliest zones of civilization and agriculture since the Middle Holocene (Larson *et al.*, 2014).

Interestingly, the surroundings of the Kalahari desert in the south have a climate similar to the Sahel. Yet this area does not emerge as an anomaly (zone G in Fig. 1). Notably, it has less pastoral activity (Fig. A1). Pastoral activities and agriculture spread to Africa from the Fertile Crescent, and reached southern Africa relatively late on. Since there were no recent mass extinctions of megafauna in Africa, perhaps local hunter-gatherers were not under strong pressure to change their ways of life. Even today the Kalahari desert hosts one of the last remaining hunter-gatherer communities. Therefore, the pressure that livestock put on large wild grazers was much less than in the northern part of Africa, as can be seen from the modern pastoralism and livestock maps (Fig. A1, Fig. 3). That would explain why we see no dental ecometric anomalies in the Kalahari area.

The surroundings of the Thar desert (zone B in Fig. 1) present a similar story. The ecoregion is classified as thorn scrub forest, which represents a state of tropical dry forests. ‘Grazing of livestock, mostly sheep and goats, is intensive, affecting soil fertility and destroying native vegetation’ (World Wildlife Fund, 2017). The area has supported one of the earliest civilizations; domestication and agricultural activities started in the Middle Holocene, *c.* 5000 years ago (Larson *et al.*, 2014). Similarly, south China and Caatinga and the central Andes in South America (zones C, D, and E in Fig. 1) have hosted early civilizations, centred around agricultural activities. The earliest agricultural area, the Fertile Crescent, is not part of our analysis because it has fewer than two wild large plant-eating mammals left.

By identifying dental traits that are differentially sensitive to human activities, we are able to develop advanced tailored models for the accurate reconstruction of tropical habitats whether or not human activities were present. A combination of dental crown height and reinforcement of cusps has different sensitivity to competition with livestock in tropical Africa, since that part of the wild, large-mammal community that most directly competes with livestock for habitat tends to be hypsodont, while that part of the community that inhabits forest patches is not. Therefore, when the hypsodont part of the community is outcompeted, the average hypsodonty for the area changes markedly. On the other hand, structural fortification in the area is expected to be mostly absent from both the large grazer communities that compete with livestock and the communities that inhabit patchy forest. Therefore, when large grazers are outcompeted, the average structural fortification for the area will be little affected.

Dental traits that have different sensitivity to competition with livestock can capture anthropogenic effects on wild animal communities in climatically sensitive zones. Our study focused on predicting vegetation type while accurately adjusting for competition with livestock. The same modelling principles can potentially be used to identify the intensity of competition with livestock and thus to identify pastoral activities and adjust for them by pointing to anthropogenic anomalies in nature. With those same models, furthermore, we can go back to the fossil record and characterize early human environments (Fortelius *et al.*, 2016). From such a characterization, we should be able to infer early human influences on the environment.

The present study also provides a methodological means as well as a case study for merging paleobiology with conservation biology, a direction recommended in a recent position paper (Barnosky *et al.*, 2017) for guiding the future of terrestrial ecosystems.

DATA ACCESSIBILITY

All data are taken from published sources. We have made several updates and plugged some gaps in the dental trait data since Galbrun *et al.* (2018). The traits dataset is given in full in evolutionary-ecology.com/data/3135Appendix.pdf. Version 11 was used here. The latest electronic version of the trait data is available at <http://www.helsinki.fi/science/now/ecometrics.html>.

ACKNOWLEDGEMENTS

We thank M. Lawing and J.T. Eronen for consultations about species distribution data and for sharing that data (Lawing *et al.*, 2017), and Mar Cabeza for consultations about the status of decline of large African fauna. The work of H.T. is supported by Land-Atmosphere Interactions in Cold Environments (LATICE), which is a strategic research area funded by the Faculty of Mathematics and Natural Sciences at the University of Oslo. Juha Saarinen, Mikael Fortelius, Janina Rannikko, and Indrė Žliobaitė acknowledge funding from the Academy of Finland (ECHOES project). This is a contribution from the Valio Armas Korvenkontio Unit of Dental Anatomy in Relation to Evolutionary Theory.

REFERENCES

- Barnosky, A.D., Hadly, E.A., Gonzalez, P., Head, J., Polly, J.P., Lawing, A.M. *et al.* 2017. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science*, **355**: eaah4787.
- Beudels, R.C., Devillers, P., Lafontaine, R.-M., Devillers-Terschuren, J. and Beudels, M.-O. 2005. *Sahelo-Saharan Antelopes. Status and Perspectives*. Report on the Conservation Status of the Six Sahelo-Saharan Antelopes. CMS SSA Concerted Action, 2nd edn. CMS Technical Series Publication #10. Bonn: UNEP/CMS Secretariat.
- Biddulph, J. and Kellman, M. 1998. Fuels and fire at savanna-gallery forest boundaries in south-eastern Venezuela. *J. Trop. Ecol.*, **14**: 445–461.
- Brito, J.C., Godinho, R., Martínez-Freiria, F., Pleguezuelos, J.M., Rebelo, H., Santos, X. *et al.* 2014. Unravelling biodiversity, evolution and threats to conservation in the Sahara-Sahel. *Biol. Rev. Camb. Phil. Soc.*, **89**: 215–231.
- Channan, S., Collins, K. and Emanuel, W.R. 2014. *Global Mosaics of the Standard MODIS Land Cover Type Data*. College Park, MD: University of Maryland and the Pacific Northwest National Laboratory.
- Damuth, J. and Janis, C. 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. *Biol. Rev.*, **86**: 733–758.
- Diallo, I., Giorgi, F. and Stordal, F. 2018. Influence of Lake Malawi on regional climate from a double-nested regional climate model experiment. *Clim. Dyn.*, **50**: 3397–3411.
- East, R., compiler. 1999. *African Antelope Database 1998*. IUCN/SSC Antelope Specialist Group. Gland, Switzerland/Cambridge, UK: IUCN.
- Eronen, J.T., Puolamäki, K., Liu, L., Lintulaakso, K., Damuth, J., Janis, C. *et al.* 2010a. Precipitation and large herbivorous mammals, part I: Estimates from present-day communities. *Evol. Ecol. Res.*, **12**: 217–233.

- Eronen, J.T., Puolamäki, K., Liu, L., Lintulaakso, K., Damuth, J., Janis, C. et al. 2010b. Precipitation and large herbivorous mammals, part II: Application to fossil data. *Evol. Ecol. Res.*, **12**: 235–248.
- Fick, S.E. and Hijmans, R.J. 2017. Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.*, **37**: 4302–4315.
- Fortelius, M. and Solounias, N. 2000. Functional characterization of ungulate molars using the abrasion–attrition wear gradient: a new method for reconstructing paleodiets. *Am. Mus. Novitates*, **3301**: 1–36.
- Fortelius, M., Eronen, J., Jernvall, J., Liu, L., Pushkina, D., Rinne, J. et al. 2002. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evol. Ecol. Res.*, **4**: 1005–1006.
- Fortelius, M., Žliobaitė, I., Kaya, F., Bibi, F., Bobe, R., Leakey, L. et al. 2016. An ecometric analysis of the fossil mammal record of the Turkana Basin. *Phil. Trans. R. Soc. Lond. B: Biol. Sci.*, **371**: 20150232.
- Friedl, M.A., Sulla-Menashe, D., Tan, B., Schneider, A., Ramankutty, N., Sibley, A. et al. 2010. MODIS Collection 5 global land cover: algorithm refinements and characterization of new datasets. *Remote Sens. Environ.*, **114**: 168–182.
- Galbrun, E., Tang, H., Fortelius, M. and Žliobaitė, I. 2018. Computational biomes: the ecometrics of large mammal teeth. *Paleontol. Electron.*, article 21.1.3A [<https://doi.org/10.26879/786>].
- Gonzalez, P. 2001. Desertification and a shift of forest species in the West African Sahel. *Clim. Res.*, **17**: 217–228.
- Goodman, S.M. and Benstead, J.P. 2005. Updated estimates of biotic diversity and endemism in Madagascar. *Oryx*, **39**: 73–77.
- Harris, J.M. 1975. Evolution of feeding mechanisms in the family Deinotheriidae (Mammalia: Proboscidea). *Zool. J. Linn. Soc.*, **56**: 331–362.
- Hempson, G.P., Archibald, S. and Bond, W.J. 2017. The consequences of replacing wildlife with livestock in Africa. *Sci. Rep.*, **7**: 17196.
- Heywood, J. 2010. Explaining patterns in modern ruminant diversity: contingency or constraint? *Biol. J. Linn. Soc.*, **99**: 657–672.
- Janis, C. 1982. Evolution of horns in ungulates: ecology and paleoecology. *Biol. Rev.*, **57**: 261–318.
- Janis, C.M. and Fortelius, M. 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biol. Rev.*, **63**: 197–230.
- Jung, G., Prange, M. and Schulz, M. 2016. Influence of topography on tropical African vegetation coverage. *Clim. Dyn.*, **46**: 2535–2549.
- Koch, P.L. and Barnosky, A.D. 2006. Late Quaternary extinctions: state of the debate. *Annu. Rev. Ecol. Evol. Syst.*, **37**: 215–250.
- Kottek, M., Grieser, J., Beck, C., Rudolf, B. and Rubel, F. 2006. World map of the Köppen-Geiger climate classification updated. *Meteorol. Z.*, **15**: 259–263.
- Larson, G., Piperno, D.R., Allaby, R.G., Purugganan, M.D., Andersson, L., Arroyo-Kalin, M. et al. 2014. Current perspectives and the future of domestication studies. *Proc. Natl. Acad. Sci. USA*, **111**: 6139–6146.
- Lawing, A.M., Eronen, J.T., Blois, J.L., Graham, C.H. and Polly, P.D. 2017. Community functional trait composition at the continental scale: the effects of non-ecological processes. *Ecography*, **40**: 651–663.
- Lieth, H. 1975. Modelling the primary productivity of the world. In *Primary Productivity of the Biosphere* (H. Lieth and R.H. Whittaker, eds.), pp. 237–263. New York: Springer.
- Liow, L.H., Fortelius, M., Lintulaakso, K., Mannila, H. and Stenseth, N.C. 2009. Lower extinction risk in sleep-or-hide mammals. *Am. Nat.*, **178**: 264–272.
- Liu, J., Wang, B., Yim, S.Y., Lee, J.Y., Jhun, J.G. and Ha, K.J. 2012. What drives the global summer monsoon over the past millennium? *Clim. Dyn.*, **39**: 1063–1072.

- Liu, L., Puolamäki, K., Eronen, J.T., Mirzaie Ataabadi, M., Hernesniemi, E. and Fortelius, M. 2012. Dental functional traits of mammals resolve productivity in terrestrial ecosystems past and present. *Proc. R. Soc. Lond. B: Biol. Sci.*, **279**: 2793–2799.
- Polly, P.D., Eronen, J.T., Fred, M., Dietl, G.P., Mosbrugger, V., Scheidegger, C. *et al.* 2011. History matters: ecometrics and integrative climate change biology. *Proc. R. Soc. Lond. B: Biol. Sci.*, **278**: 1131–1140.
- Quinlan, J.R. 1986. Induction of decision trees. *Mach. Learn.*, **1**: 81–106.
- Robinson, T.P., Wint, G.R.W., Conchedda, G., Van Boeckel, T.P., Ercoli, V., Palamara, E. *et al.* 2014. Mapping the global distribution of livestock. *PLoS One*, **9** (5): e96084.
- Rosenzweig, M., Drumlevitch, F., Borgmann, K.L., Flesch, A.D., Grajeda, S.M., Johnson, G. *et al.* 2012. An ecological telescope to view future terrestrial vertebrate diversity. *Evol. Ecol. Res.*, **14**: 247–268.
- Rowan, J., Faith, J.T., Gebru, Y. and Fleagle, J.G. 2015. Taxonomy and paleoecology of fossil Bovidae (Mammalia, Artiodactyla) from the Kibish Formation, southern Ethiopia: implications for dietary change, biogeography, and the structure of the living bovid faunas of East Africa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **420**: 210–222.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S. *et al.* 2005. Determinants of woody cover in African savannas. *Nature*, **438**: 846–849.
- Sclater, P.L. 1858. On the general geographical distribution of the members of the class Aves. *J. Proc. Linn. Soc. Zool.*, **2**: 130–145 [<http://people.wku.edu/charles.smith/biogeog/>].
- Solounias, N., Teaford, M. and Walker, A. 1988. Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid. *Paleobiology*, **14**: 287–300.
- Stromberg, C. 2011. Evolution of grasses and grassland ecosystems. *Annu. Rev. Earth Planet. Sci.*, **39**: 517–544.
- Walther, B. 2016. A review of recent ecological changes in the Sahel, with particular reference to land-use change, plants, birds and mammals. *Afr. J. Ecol.*, **54**: 268–280.
- Wang, B., Liu, J., Kim, H.J., Webster, P.J. and Yim, S.Y. 2012. Recent change of the global monsoon precipitation (1979–2008). *Clim. Dyn.*, **39**: 1123–1135.
- World Wildlife Fund. 2017. *Terrestrial Ecoregions*. Washington, DC: WWF [<http://www.worldwildlife.org/biome-categories/terrestrial-ecoregions>].
- Žliobaitė, I., Rinne, J., Toth, A., Mechenich, M., Liu, L., Behrensmeyer, A.K. *et al.* 2016. Herbivore teeth predict climatic limits in Kenyan ecosystems. *Proc. Natl. Acad. Sci. USA*, **113**: 12751–12756.

