The nature of the Old World savannah palaeobiome

Mikael Fortelius[1*], Faysal Bibi[2], Hui Tang[3], Indrė Žliobaitė[4], Jussi T. Eronen[5,6], Ferhat Kaya[1]

[1]Department of Geosciences and Geography, PO Box 64 (Gustaf Hällströminkatu 2), FI-00014 University of Helsinki, Finland
[2]Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstrasse 43, Berlin, Germany
[3]Department of Geosciences, University of Oslo, PO Box 1047 Blindern, Oslo, Norway
[4]Department of Computer Science, PO Box 68 (Pietari Kalmin katu 5) FI-00014 University of Helsinki, Finland
[5]Ecosystem and Environment Research Programme, University of Helsinki, Finland
[6]BIOS Independent Research Unit, Kalliolanrinne 4, Helsinki, Finland

Corresponding author: Mikael Fortelius, Department of Geosciences and Geography, PO Box 64 (Gustaf Hällströminkatu 2) FI-00014 University of Helsinki, Finland
Email: mikael.fortelius@helsinki.fi

Writing in Nature Ecology & Evolution in 2018, we argued that there existed during the later Miocene of the Old World (ca 15-5 million years ago) "a single cohesive Old-World savannah palaeobiome of which the modern African savannah fauna is the surviving branch"[1]. Subsequently, Denk et al have taken issue with this interpretation and argued, using palaeobotanical data, that no such cohesive biome existed, and that a more compelling reconstruction sees mixed trees and shrublands dominant at that time[2]. In addition to defending our original interpretation we would like here to clarify some terms used in our paper, as we feel that much of the apparent discrepancy may actually reflect differences in terminology.

We used the term savannah in a broad sense, common in Neogene and Quaternary palaeoecology[3], meaning a woodland to grassland biome characterised by co-dominance of trees and grasses[4], the "mixed grass–tree biome" of Ref 5. In contrast, Denk et al, approaching the matter from a botanical perspective, adhere to a more restricted definition of savannah as grasslands. We formulated the term Old World Savannah Paleobiome (OWSP) to describe localities showing high similarity to our selected reference localities representing open-adapted large mammal communities: Lower Nawata, Pikermi, and Baode. These localities have all been previously identified as representing woodland-dominated, or mixed woodland-grassland ecosystems[6-9] through methods independent of mean ordinated hypsodonty. The evidence includes microwear, mesowear, stable isotope, phytolith, sedimentological, and functional morphological approaches, and covers Late Miocene sites from Turkey, Hungary, Bulgaria, Greece, Iran, and China[6-16]. Denk and colleagues' critique of our interpretations therefore stands against a wide, multiproxy literature repeatedly confirming the dominance of woodland and grassy woodland environments across a wide swath of Eurasia and Africa during the late Miocene.

We used the term cohesive, to which Denk et al[2] object, to imply interconnectedness of the faunal assemblages rather than uniformity of vegetation cover, which we should have made more explicit. The genus-level similarity analysis of large mammal faunas was used to trace the origin and dispersal of mammals within the OWSP as it expanded and contracted, in sync with the environment as approximated by mean hypsodonty (our figures 2 and 3)[1]. It was cohesive in the sense of connectedness of internal dispersal, not in the sense of being at all times and in all places a uniform system. We propose that in the OWSP, the diverse habitat of the Hipparion fauna[17], increasing overall and seasonal aridity created a world in which herbivores were progressively adapting to similar limiting conditions over vast areas.

It is not unexpected for phytological and zoological proxies to result in differing reconstructions. Even present-day mammal zoogeography (e.g., Ref. 18, Fig. 3c) does not exactly match

terrestrial vegetation biomes (e.g., Ref. 19, Fig. 4.3). Within a zoogeographic region, the terrestrial vegetation biomes may vary from semi-desert to forest. It has also been suggested that vertebrate fossils and macrofossils/palynomorph floras may reflect different environmental conditions and climatic cycles[9] though space prohibits further discussion here.

In principle, the existence of vegetational differentiation – including forests – within the large area covered by the OWSP is of course inevitable and we never doubted it. Indeed, such heterogeneity is also suggested by our own results, e.g., our Figs 2-3[1]. We deliberately used the robust but coarse metric of mean ordinated hypsodonty as a proxy for environmental harshness in general[20]. We did so because we expected that, while the local details would vary, the overall effect would be one of lowered ecosystem productivity, increased seasonality, and other factors contributing to harshness. Although more detailed ecometric models of climate or vegetation were available, we accordingly selected mean hypsodonty as the appropriate metric[21-25].

Denk and colleagues' paper[2] is a welcome opening towards the holistic survey of evidence and we look forward to discovering what exactly the floristic patterns mean in terms of habitats and ecosystems, and whether there is any actual disagreement in the reconstructions or interpretations of either of the methodologies.

References

1. Kaya, F. et al. The rise and fall of the Old World savannah fauna and the origins of the African savannah biome. *Nature Ecol. Evol.* **2**, 241–246 (2018).
2. Denk, T. et al. Plant fossils reveal major biomes occupied by the late Miocene Old-World Pikermian fauna. *Nature Ecol. Evol.* **2**, 1864–1870 (2018).
3. Sankaran, M. et al. Determinants of woody cover in African savannas. *Nature* **438**, 846–849 (2005).
4. Reed, K. et al. in Early hominin paleoecology (eds Sponheimer, M., Lee-Thorp, J.A., Reed, K. & Ungar, P.), 3-34 (University Press of Colorado, Boulder, 2013).
5. Berling DJ, Osborn CP. The origin of the savanna biome. Global Change Biology 12:2023–2031 (2006)
6. Passey, B.H. et al. Strengthened East Asian summer monsoons during a period of high-latitude warmth? Isotopic evidence from Mio-Pliocene fossil mammals and soil carbonates from northern China. Earth and Planetary Science Letters 277:443-452 (2008).
7. Solounias, N. et al. Dietary interpretation and paleoecology of herbivores from Pikermi and Samos (late Miocene of Greece). *Paleobiology* **36**, 113–136 (2010).
8. Cerling, T.E. et al. in Lothagam: The Dawn of Humanity in Eastern Africa (eds Leakey M.G. and Harris J.H.), 605-624 (Columbia University Press, New York, 2003).
9. Uno, K.T. et al. Late Miocene to Pliocene carbon isotope record of differential diet change among East African herbivores. *Proc. Natl. Acad. Sci. USA* 108, 6509–6514 (2011).
10. Strömberg, C.A.E. et al. The spread of grass-dominated habitats in Turkey and surrounding areas during the Cenozoic: Phytolith evidence. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **250**, 18–49 (2007).
11. Bernor, R.L. et al. Maragheh Ungulate Mesowear: Interpreting paleodiet and paleoecology from a diverse fauna with restricted sample sizes. Annal. Zool. Fenn. 51, 1–2 (2014).
12. Solounias, N. et al. in *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology* (eds Wang, X., Fortelius, M. & Flynn, L.) 676–692 (Columbia Univ. Press, New York, 2013)
13. Merceron, G. et al. Bovid paleoecology and paleoenvironments from the late Miocene Bulgaria: Evidence from dental microwear and stable isotopes. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* **241**, 637–654 (2006).
14. Merceron, G. et al. Paleoenvironmanet of *Dryopithecus brancoi* at Rudabanya, Hungary: Evidence from dental meso- and micro-wear analyses of large vegetarian mammals. *J. Hum. Evol.* 53, 331–349 (2007).
15. Kaya, F. et al. Magnetostratigraphy and paleoecology of the hominid-bearing locality Corakyerler. Tuglu formation (Cankiri Basin, Central Anatolia). *J. Vert. Paleont.* 36, e1071710 (12 pages) (2016).
16. Böhme, M. et al. Messinian age and savannah environment of the possible hominin *Graecopithecus* from Europe. PLoS ONE 12, e0177347 (2017).
17. Kurtén, B. The Chinese Hipparion fauna. *Commentationes Biologicae Soietatis Scientiarum Fennicae* **13**, 1–52 (1952).
18. Holt, B.G. et al. An update of Wallace's zoogeographic regions of the world. *Science* 339 (6115), 74–78 (2013).
19. Millennium Ecosystem Assessment. Ecosystem and Human Well-Being: Biodiversity Synthesis, World Resources Institute, DC. (2005).
20. Fortelius, M., et al. Evolution of Neogene mammals in Eurasia: environmental forcing and biotic interactions. *Annu. Rev. Earth Planet. Sci.* 42:579–604 (2014).
21. Liu, L. et al. Dental functional traits of mammals resolve productivity in terrestrial ecosystems past and present. *Proc. R. Soc. B* 279, 2793–2799 (2012).
22. Fortelius, M. et al. An ecometric analysis of the fossil mammal record of the Turkana Basin. *Philos. Trans. Royal Soc. B.* 371, 1698. (2016).
23. Galbrun, E. et al. Computational biomes: The ecometrics of large mammal teeth. *Palaeont. Eelectr.* 21.1. 3A 1–31. (2017).
24. Žliobaitė, I. et al. Dental ecometrics of tropical Africa: Linking vegetation types and communities of large plant-eating mammals. *Evol. Eco. Res.* 19, 127–147 (2018).
25. Žliobaitė, I. et al. Herbivore teeth predict climatic limits in Kenyan ecosystems. *Proc. Natl. Acad. Sci. USA* 113, 12751–12756 (2016).