LETTER

Species richness and composition are not sufficient for determining the functionality of ancient ecosystems

Tom Weihmann[a,1]

Taking into account the effect of climatic changes over the last few millions of years on fauna both worldwide and in eastern Africa, hardly anyone would challenge the ecosystem shift addressed recently by Faith et al. (1). In eastern Africa, diminishing precipitation triggered the expansion of C4 grassland; reduced net production and the appearance of large grazers increased the relative impact of megaherbivore consumption, eventually facilitating and stabilizing the development of more open landscapes.

Whereas some of the emerging grazing genera had already preadapted their masticatory apparatus, others, like proboscides, did not evolve highly hypsodont grazing teeth until the late Pleistocene period (2). The switch to grass-dominated diets occurred in parallel in several proboscidean genera. At the end of this development, however, in Africa one genus of proboscides replaced all others: the only extant genus, *Loxodonta*. Although one might interpret the apparent loss in species richness as resulting in decidedly functionally non-analog modern ecosystems throughout Africa (1), the enormous ecological range of African elephants is striking. Currently, there are desert-dwelling groups of *Loxodonta africana* in southern and western Africa, those grazing and browsing savanna, and the forest-dwelling sister species *Loxodonta cyclotis*, apparently covering at least parts of the ecological niches previously occupied by a number of proboscidean species (1–3). Similarly, black and white rhinos, African buffalo, and other large herbivores have taken over the ecological roles of ancient species or even species groups, to which the often high degree of ecological flexibility in the absence of competition certainly contributes (4). This flexibility, however, is an asset that likely enabled the extant species to be successful also in troubled times. Their decline all the more highlights the vexations imposed by present-day developments.

Moreover, high numbers of very large herbivore species do not necessarily have to coincide with increased consumption and overgrazing as suggested in ref. 1. Taking natural scaling laws into consideration, it is clear that communities dominated by very large species do not have to consume more than those dominated by smaller ones. On the contrary, it is well documented that resting metabolism and minimum cost of locomotion per unit body mass decline with body size (5), as expressed in Kleiber's law of metabolic scaling or the metabolic theory of ecology, respectively (6).

Thus, a herd of smaller herbivores can reduce plant cover as efficiently as a community of large herbivores with the same collective mass even if timescales and spatial patterns may vary (7). This notion also contradicts the authors' assumption of significant changes in fire regimes potentially caused by the evident changes in megaherbivore community compositions (1, 8).

However, at least some present-day African areas do come close to ancient environmental conditions and provide habitat for rich megafaunas. As such, these areas can be regarded as functionally equivalent. In order to obtain reliable pictures of past ecosystem functionality, deeper information on the species' ecological ranges, adaptability, and biomass proportions as well as energy demands is needed (9, 10).

Acknowledgments

I would like to thank Emily Pycroft for proofreading and Adrian Lister for helpful and encouraging comments.

1 J. T. Faith, J. Rowan, A. Du, Early hominins evolved within non-analog ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 21478–21483 (2019).

2 A. M. Lister, The role of behaviour in adaptive morphological evolution of African proboscideans. *Nature* **500**, 331–334 (2013).

[a]Department of Animal Physiology, Institute of Zoology, University of Cologne, 50674 Cologne, Germany

Author contributions: T.W. performed research and wrote the paper.

The author declares no competing interest.

Published under the PNAS license.

[1]Email: tom.weihmann@uni-koeln.de.

First published February 4, 2020.

3 J. Soberón, M. Nakamura, Niches and distributional areas: Concepts, methods, and assumptions. *Proc. Natl. Acad. Sci. U.S.A.* **106** (suppl. 2), 19644–19650 (2009).
4 J.-C. Svenning *et al.*, Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 898–906 (2016).
5 C. R. Taylor, K. Schmidt-Nielsen, J. L. Raab, Scaling of energetic cost of running to body size in mammals. *Am. J. Physiol.* **219**, 1104–1107 (1970).
6 J. van der Meer, Metabolic theories in ecology. *Trends Ecol. Evol. (Amst.)* **21**, 136–140 (2006).
7 R. M. Pringle, T. M. Palmer, J. R. Goheen, D. J. McCauley, F. Keesing, Ecological importance of large herbivores in the Ewaso ecosystem. *Smithson. Contrib. Zool.* **2011**, 43–53 (2011).
8 N. Owen-Smith, "The interaction of humans, megaherbivores, and habitats in the late Pleistocene extinction event" in *Extinctions in Near Time*, R. D. E. MacPhee, Ed. (Springer, 1999), pp. 57–69.
9 A. Sinclair, The role of mammals as ecosystem landscapers. *Alces* **39**, 161–176 (2003).
10 B. J. McGill, B. J. Enquist, E. Weiher, M. Westoby, Rebuilding community ecology from functional traits. *Trends Ecol. Evol. (Amst.)* **21**, 178–185 (2006).