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Humans, megafauna and landscape structure – Rock engravings from Namibia encourage a comparative approach to central Europe and southern Africa

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Abstract

This paper deals with reflections that arose after observing prehistoric rock engravings at different locations in Namibia. These observations stimulated comparative considerations with focus on southern Africa and central Europe. Similar to the Aurignacian rock art of European origin, the most common motifs in the Namibian rock engravings are large animals. While in Europe, the species that served as a blueprint for the illustration of Aurignacian rock art have mostly disappeared, the megafauna illustrated on the rock engravings in Namibia can still be found in the immediate vicinity of the rock art. Against this background, we discuss and further develop a comparative regional approach. We reconstruct and evaluate the suitability of African savannas and still-existing megafauna communities as an appropriate reference-frame for natural European grassland systems and extinct associated warm-adapted megafauna (Eemian Interglacial megafauna). Special attention is laid on the unique situation in Africa in the light of a global extinction wave of megafauna following increasing human activity in the Late Quaternary. This leads us to discuss the use of domesticated ungulates as surrogate taxa to fulfill ecosystem functions in Europe as part of concepts termed "rewilding" or "naturalistic grazing". After critically examining these concepts, we conclude that using domesticated forms as representatives of extinct or locally disappeared species in Europe has its justification to some extent. If, however, the naturally occurring megaherbivore community still exists (Africa), these naturally occurring species should be given priority due to their organismic abilities and limitations adapted to the harsh conditions in their specific environment. Finally, we discuss the application of (transboundary) protected areas as effective instruments to mitigate human-wildlife conflicts. A holistic approach, including nature conservation and preservation of cultural achievements (domesticated forms, grazing systems), appears promising for the effective protection of the natural African savanna ecosystems with their unique fauna elements, as illustrated in rock engravings that inspired us to write this paper.

Key words

domesticated forms, megaherbivores, prehistoric rock art, surrogate taxa, transboundary protected areas

Introduction

The ideas and considerations presented in this article arose as a result of numerous excursions and field trips conducted during the previous decades by the authors to the southern African sub-region and to Namibia in particular. One aspect, which was never the central point of these excursions, but which gave rise to ongoing reflections, is the observation of rock engravings. The motivation to publish the outcome of our considerations in this volume is that Wolfgang Maier frequently expressed his interest in the African fauna and in questions related to the African continent as the cradle of humankind (e.g. Maier 2013, 2017). Here, we look at two locations with an extraordinary richness in rock engravings in Namibia: one is the so-called Peet Alberts Koppie, a mountain ridge with more than 1000 engravings (Breunig 2014) situated only a few kilometers northeast of the town Kamanjab. The other region is known as the Mik Mountains, a hardly accessible rocky landscape on the eastern edge of the Namib Desert. The most common motifs in the rock engravings are large animals, mainly mammals (Fig. 1). In fact, the animals depicted on the rock engravings are the extant fauna-elements, the indigenous megafauna that is still occurring in southern African savannas (Fig. 2). This initial observation stimulated reflections about differences and parallels between central European and southern African ecosystems.

We have to face the point that we cannot link the engravings with an extant ethnic group (Gwasira et al. 2017). In addition, a reliable age-determination of these rock engravings is simply impossible. While rock paintings containing organic material or engravings on egg shells or other organic matter can be age-determined using the radiocarbon method, this is not the case for rock engravings (Breunig 2014). However, the degree of patination, as well as stylistic and technical differences, allow the classification of different engravings in a chronology scheme (Breunig pers. commun.). Tilmann Lenssen-Erz, for example, estimates that Namibia's hunter-gatherer rock art was created between 4,000 and 2,000 years ago (Lenssen-Erz 2015). The engravings would therefore be of much younger origin than the world-famous artifacts from the Apollo 11 cave in today's Namibia, where engravings on ostrich egg shells date back to 21.6 – 39.8 ka BP (Vogelsang et al. 2010) – a similar time horizon to the Aurignacian art in Europe (see below). However, despite this uncertain temporal determination of the prehistoric rock engravings at Peet Alberts Koppie and Mik Mountains, megafauna-elements as the predominant motif remain an obvious parallel when compared to the rock art of European origin.

The illustration of megafauna-elements and the observation that large wildlife dominates prehistoric rock art applies in a similar way to the Aurignacian rock paintings from Europe, e.g. the Chauvet-Pont-d'Arc Cave in southeastern France, where particular paintings have been dated to be older than 32,000 years (von Petzinger and Nowell 2014). As stated above, the species community illustrated on the rock engravings in Namibia can still be found in the immediate vicinity of the place of creation of the rock art. In central Europe, the situation is completely different: The species that obviously served as a blueprint for the illustration of Aurignacian rock art have mostly disappeared. Some of these species – e.g. *Equus ferus* Boddaert, 1785, *Crocuta crocuta* (Erxleben, 1777) – disappeared only from the region but others disappeared everywhere – e.g. *Ursus spelaeus* Rosenmüller, 1794, *Mammuthus primigenius* (Blumenbach, 1799), *Coelodonta antiquitatis* Blumenbach, 1799 (Bon et al. 2011; Pruvost et al. 2011; Stuart and Lister 2012, 2014).

Since these Late Quaternary extinctions on a global scale were recognized by the scientific world in the nineteenth century, there is an ongoing debate about the causes, including climatic catastrophes, gradual climate change, and overkill by humans (Grayson 1984; Koch and Barnosky 2006). In recent years, however, there has been increasing scientific evidence that the wave of extinction of the megafauna should be seen in the light of a combination of climatic changes and the global spread and increase in the activities of modern *Homo sapiens* (Lorenzen et al. 2011; Bartlett et al. 2016; Villavicencio et al. 2016; Saltré et al. 2019). Some authors go as far as to link global Late Quaternary megafauna extinctions primarily with humans but not climate change (Sandom et al. 2014b). Against this background, we have developed the concept of a comparative approach with a special focus on central Europe and southern Africa (Zeller et al. 2017; Rottstock et al. 2020); the essential aspects are presented below.

African savannas – an appropriate reference frame for natural European grassland systems

There has been an ongoing controversy about the original vegetation types in temperate Europe (Svenning 2002; Birks 2005). For many years, a densely forested landscape was regarded as the natural state of central European habitat (dense-forest hypothesis). Accordingly, this dense forest is often termed "Urwald" in German, which can be translated to "ancient forest" or "original forest". As we will see in the following, this dense forest was by far not ancient or natural but the result of human activity (Zeller et al. 2017). Paleo-botanical studies referring to the early (pre-agricultural) Holocene (10-6 ka BP) support the dense-forest hypothesis (Bradshaw et al. 2003). Regardless of these findings, Vera (2000) assumed that during the early and middle Holocene, large mammals, such as aurochs *Bos primigenius* Bojanus, 1825, European bison *Bison bonasus* (Linnaeus, 1758), red deer *Cervus elaphus* Linnaeus, 1758 and wild horse *Equus ferus*,

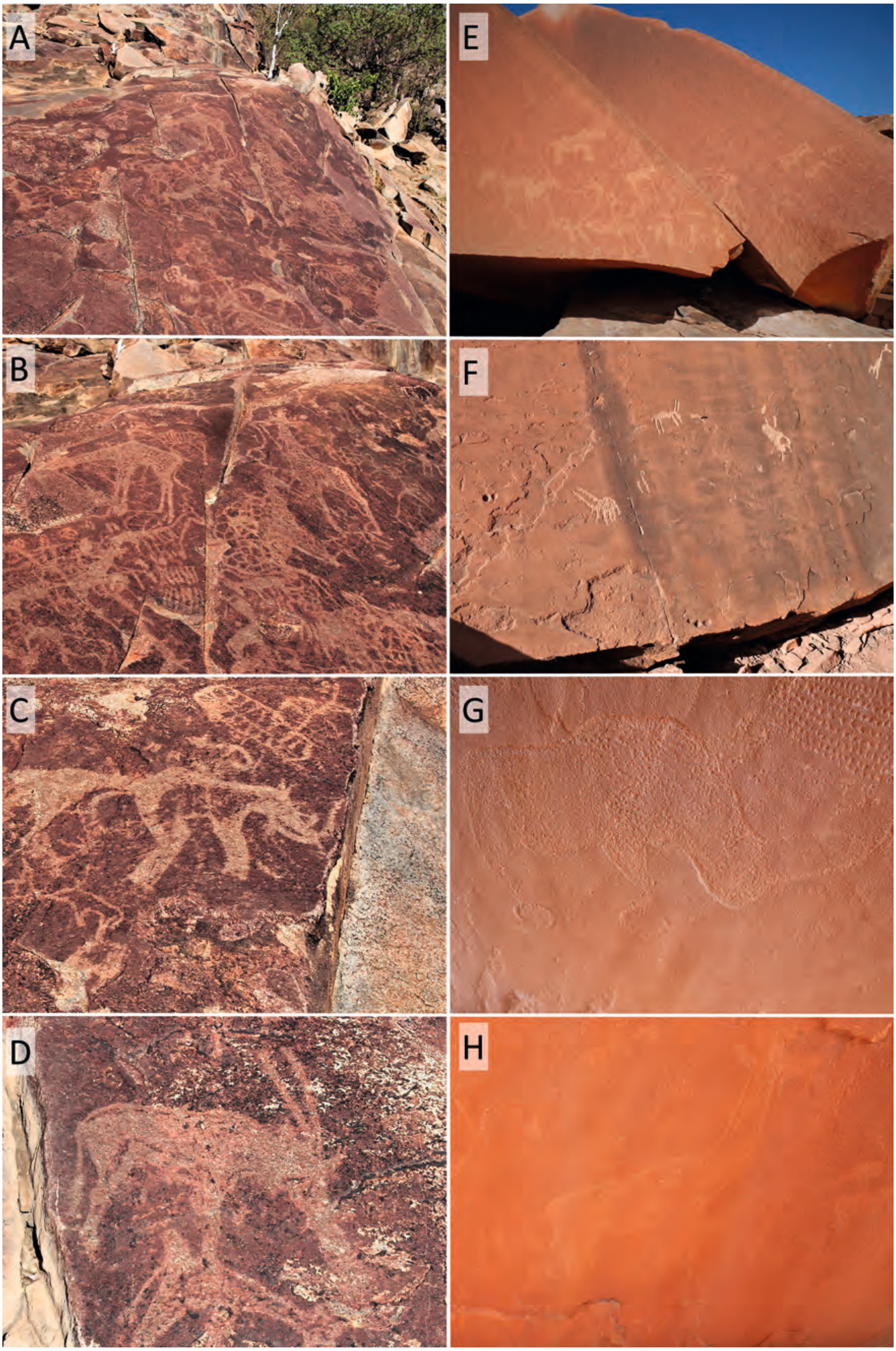

Figure 1. Rock engravings in Namibia, left side: Peet Alberts Koppie (A-D), right side: Mik Mountains (G-H). A) More than 1000 engravings can be found on rock ridges at Peet Albersts Koppie close to the town Kamanjab (Breunig 2014). B) The giraffe is the most frequently depicted animal at Peet Alberts Koppie (Breunig 2014); images also display various other animals, for example, elephant (C) or oryx antelope (D). Rock engravings at the Mik Mountains should be regarded as part of the largest concentration of ancient rock engravings in southern Africa (Breunig pers. commun.). The images of animals range from abstract, highly stylized and unpatinated (F) to realistic images of today-existing animals, such as white rhinos (G) and kudu antelopes (H). Photos: D: U. Zeller, others: T. Göttert.

Figure 2. The animals depicted at the rock engravings in Namibia are members of the extant megafauna community of the region. From top to bottom: kudu *Tragelaphus strepsiceros*, oryx *Oryx gazella*, white rhino *Ceratotherium simum* and giraffe *Giraffa camelopardalis*. Photos: oryx-engraving, oryx and giraffe: U. Zeller, others: T. Göttert.

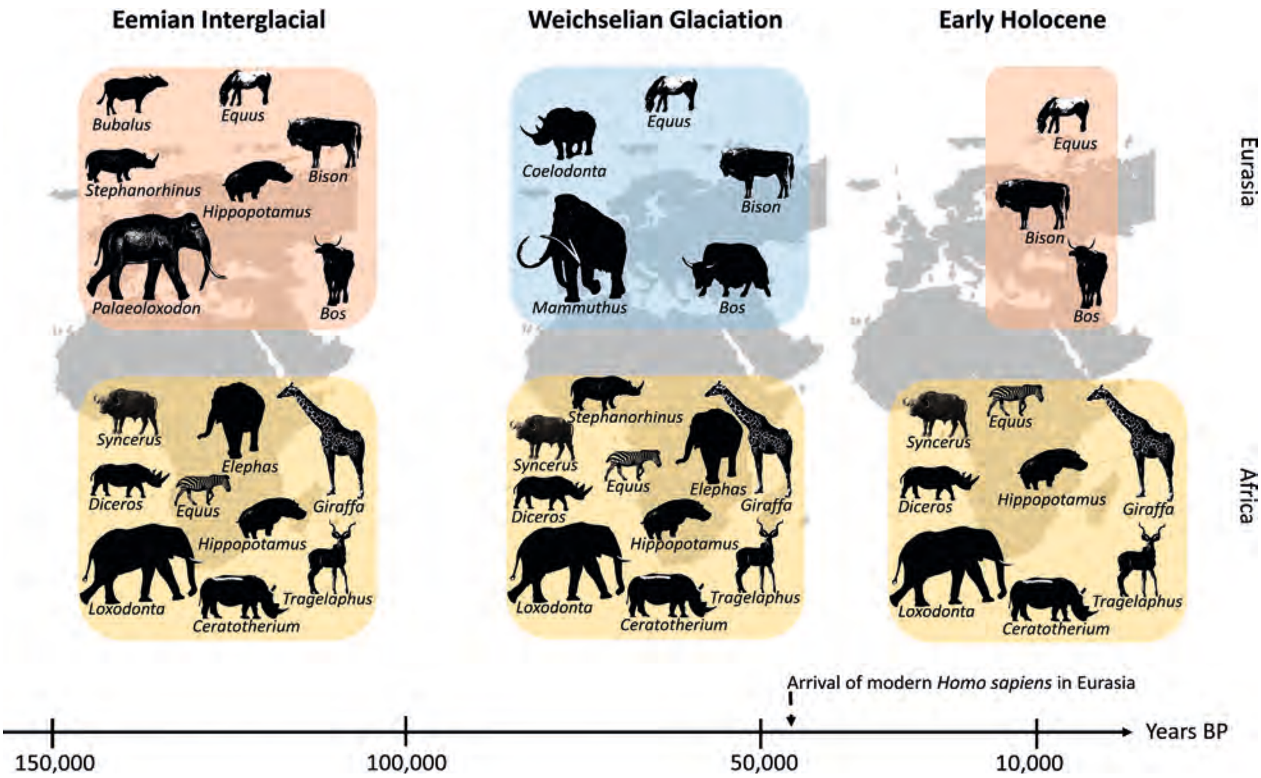

Figure 3. Comparison of central European and southern African megafauna communities at different points in time. Most species of the Pleistocene African megaherbivore guild still exist today. In central Europe, there was a change between warm-adapted and cold-adapted megafaunas. The arrival of modern humans in Europe went along with an extinction wave of the megafauna – consequently, the warm-adapted megafauna was not able to recover/return during the Early Holocene. The remaining / weakened megafauna of the Early Holocene in Europe was no longer able to create an open landscape leading to a dense forest. Since the Eemian Interglacial megafauna in central Europe largely went extinct, the extant / still existing African megafauna appears to be a good reference frame to study megafauna-ecosystem interactions that also occurred in central Europe during the Last Interglacial. Human activity but not climate was the main driver of the megafauna extinction, as Africa is the only example were the Pleistocene megafauna still exists. Animal sketches were adapted from the following sources: *Palaeoloxodon*: https://commons.wikimedia.org/wiki/File:Elephas-antiquus.jpg licence: CC BY-SA 4.0; *Stephanorhinus*: https://commons.wikimedia.org/wiki/File:Hemitoechus2011.jpg#file licence: CC BY-SA 4.0; *Mammuthus* and *Coelodonta*: Mauricio Anton in: Sedwick (2008), Creative Commons Attribution License. All other animal sketches were adopted from own photos: *Bos* (Eemian and Early Holocene): U. Zeller, all others: T. Göttert.

contributed to the establishment of a mosaic-like landscape, in which forest sections alternate with open areas. This "wood-pasture-hypothesis" is of great importance for the so-called rewilding concept (see below), although it is not supported by paleo-botanical data referring to the early and middle Holocene (Svenning 2002). To reconstruct the natural habitat of central Europe, we need to refer to a period in which a) the climatic conditions were similar to today and b) natural large herbivorous mammal communities occurred that enabled the opening of the landscape. An appealing reference frame is the Last Interglacial (132-110 ka BP), since paleo-botanical studies relating to this period support the idea of a semi-open, savanna-like landscape, in which wooded sections alternated with open grasslands (Svenning 2002; Sandom et al. 2014a). If we think about a potentially natural state of vegetation in Europe that corresponds to our current climatic conditions, we come to the following conclusion: The situation in the early (pre-agricultural) Holocene does not seem suitable, since despite similar climatic conditions as today, a large part of the megafauna was displaced or exterminated by human influence (Fig. 3). This led to a dense forest cover – a process that is currently being repeated in many regions of southern Africa under similar conditions (elimination of megafauna → bush encroachment with indigenous plant species). Neither is the time of Aurignacian rock paintings from Europe a good frame of reference for today`s situation. Although natural large mammal communities, including mammoth *Mammuthus primigenius* and woolly rhinoceros *Coelodonta antiquitatis*, existed at that time, the climatic conditions were different from today (cold-adapted large mammal fauna). The faunal conditions at the time of the Last Interglacial (Eemian Interglacial, reference value for the potentially natural situation in today's Europe), on the other hand, describe a state that is very similar to the current situation in southern Africa. This led us to the hypothesis of recognizing extant African savannas and the associated megafauna-community (as illustrated on the rock engravings in Namibia) as a "model region" or "reference-state" for the potentially natural state of central European habitat types and landscapes. Interestingly, there is evidence of cultural activity from representatives of the genus *Homo* in Europe prior to the Last Interglacial. With an age of over 300,000 years, the so-called "Schöningen spears" are the oldest preserved hunting weapons in the world (Van Kolfschoten et al. 2015). However, the large mammal community associated with the "Spear Horizon" in Schöningen, Germany corresponds to the situation of the Last Interglacial. This large mammal community included straight-tusked elephant *Palaeoloxodon antiquus* (Falconer and Cautley, 1847), narrow-nosed rhinoceros *Stephanorhinus hemitoechus* (Falconer, 1868), wild horse *Equus ferus*, European water buffalo *Bubalus murrensis* (Berckhemer, 1927), aurochs *Bos primigenius*, steppe bison *Bison priscus* Bojanus, 1825, Irish elk *Megaloceros giganteus* (Blumenbach, 1799) and European saber-toothed cat *Homotherium latidens* (Owen, 1846) among others (Serangeli and Conard 2016; Serangeli et al. 2015; van Kolfschoten et al. 2015). Similar to the situation in southern Africa today, the large herbivores of this community created a cyclic succession in Europe, as we know it from the extant African savannas. Herbivores convert tall forest into grassland, open areas are then invaded by thickets of thorny scrubs resistant to browsing. These scrubs provide refuges for palatable trees to recover. The trees shade out understory scrubs and the cycle begins again (Voysey et al. 2021.). Elaborated hunting weapons from Schöningen (Schöningen spears) are an expression of hominin activities and an early anthropogenic-induced influence on the megafauna from ca. 300,000 years ago. These findings also give us an idea of the intensity with which representatives of modern *Homo sapiens* would – at a later point in time – dramatically reduce or even completely extirpate the megafauna on almost all parts of the world. There is, however, one exception – the African continent (Bartlett et al. 2016).

Africa – an exceptional case during a global wave of megafauna-extinctions

There has been a long-lasting dispute as to whether climatic changes, human activities, or the combination of both was responsible for a global wave of megafauna-extinctions (Grayson 1984; Koch and Barnosky 2006; Sandom et al. 2014b). Climatic changes alone, however, can hardly have been crucial. We should take into account that in the northern hemisphere, there has been a constant alternation of warm and cold periods over the previous 2.6 million years (Maslin et al. 1996; Fujii and Sakai 2002; Ehlers and Gibbard 2011). Each phase was characterized by typical megafauna communities (warm-adapted vs. cold-adapted large mammal faunas), which alternated cyclically (Fig. 3). For example, the warming of the climate went hand in hand with a repression of the cold-adapted large mammal fauna and an expansion of the warm-adapted fauna. Against this background, we might consider fauna elements of today's high mountain landscapes, such as yak *Bos mutus* (Przewalski, 1883) or muskoxen *Ovibos moschatus* (Zimmermann, 1780) as typical representatives of cold periods, which in the course of warm periods, as is currently the case, are forced into increasingly smaller refuges (high alpine areas). In the course of a reduction of the temperature, however, these species would be able to re-expand their range quickly. Only the drastic expansion of modern humans interrupted this cycle, insofar as it led to the extermination of various large mammal species. In this respect, climatic changes are not problematic as long as the species that are evolutionarily adapted to the respective climates exist and can respond to climatic changes. Obviously, the disastrous process leading to the extinction of various large and very large mammal species was the combination of climatic changes and anthropogenic-induced extinction, as the weakened megafauna communities were no longer able to respond towards climatic changes.

In view of our comparative regional approach, there is an important difference between the African continent and all other parts of the world when it comes to a global wave of extinction of the megafauna as a result of the spread of modern human activity. Bartlett et al. (2016) showed that on all continents – with the exception of Africa – megafauna extinction events were directly related with the arrival / increase in modern human activities in these regions. Interestingly, the only exception was the African continent, the "cradle of mankind" and starting point of all modern human activity. This finding has been interpreted as a "co-evolutionary phenomenon" – the later the arrival of modern humans on a continent or on an island, the more fatal the impact on the megafauna of that region (Barnosky et al. 2004). Thus, the megafauna extinction rate in regions that were populated by modern humans relatively late in time (e.g. American continents, Australia, Madagascar, and New Zealand) was much higher than it was the case in regions populated by humans earlier, such as central Asia or the Indo-Malayan region (Bartlett et al. 2016).

In the light of this special situation in Africa, where most of the Pleistocene megafauna species diversity still exists today, we aim to compare response patterns of selected taxa under different ecological conditions to reach a better understanding of the common mechanisms of the interrelations between land use and biodiversity (Zeller et al. 2017). The central hypothesis is that ecosystems respond in a similar way to disturbances. The idea is that biodiversity response patterns in relatively undisturbed African ecosystems might be a valuable reference for Europe and vice versa (Rottstock et al. 2020). Knowledge about the ecological plasticity within African ecosystems could be helpful to design strategies towards increasing aridity in Europe. At the same time, response patterns of highly transformed European ecosystems could be important for the development of practices to enhance and optimize agricultural practices in Africa. Mitigation strategies towards human wildlife interactions from Africa might provide important reference for similar studies in Europe, where large predators, such as wolves *Canis lupus* Linnaeus, 1758, recolonize areas, where these species were formerly extinct. The experience from Africa, where pastoralists manage to coexist with large predators since several thousands of years, could be of great importance to address one and the same phenomenon (carnivore-livestock conflicts) under different ecological conditions.

Using domesticated ungulates as surrogate taxa to fulfill ecosystem functions

The connection between Europe and Africa can also be attributed by looking at the dispersal and distribution of cattle on a global scale (Zeller et al. 2017; Rottstock 2021). Originally domesticated in the area of the "Fertile Crescent" around 10.8 – 10.3 ka BP (Helmer et al. 2002; Zeller and Göttert 2019), the taurine form of the aurochs (*Bos primigenius* f. taurus) was brought to Europe (Epstein 1971; Edwards et al. 2007) and Africa (Felius 1995) as part of the Neolithic revolution around 8,000 years ago. At later stages, a different form of the aurochs, the indicine cattle (*Bos primigenius* f. indicus), which was developed independently from the taurine cattle on the Indian subcontinent around 7,000 years ago (Epstein 1971), was transferred to Africa and other parts of the world. Indicine cattle entered the African continent as part of several introduction events between 4 and 1.3 ka BP (Epstein 1971; Porter 1991; Marshall 1989). As both forms were derived from the same species (*Bos primigenius*), they interbreed and produce fertile offspring. Cattle breeds with special adaptations established on the African continent. The reconstruction of this crossing of the two cattle forms on the African continent is very complicated and hardly possible because of repeated and independently occurring new introductions in different epochs. In addition, there is also the theory of a third domestication center of the aurochs on the African continent (Hanotte et al. 2002). The historic distribution range of the aurochs included large parts of the Palearctic but also areas of northern Africa (van Vuure 2002). Whether and to what extent there was an independent domestication process in northern Africa that led to the establishment of the Sanga cattle group, which some also refer to as "indigenous African cattle", still remains a matter of ongoing discussions (Ajmone-Marsan et al. 2010; Decker et al. 2014). A more recent connection established during colonial times, when European cattle breeds were introduced to the southern African sub-region. Dutch settlers initiated this import in 1780; however, cattle breeds are frequently introduced to sub-Sahara Africa since the middle 19th century (Felius 1995). Given severe damages following overgrazing, such as bush encroachment, soil compaction and desertification (see below), such introductions of European high-performance breeds into the fragile ecosystems of southern Africa should be carefully considered. Another example of the undifferentiated attempt to import European concepts into the African context during colonial times is the thoughtless introduction of central European tree species into today's Tanzania with the aim of establishing a "German forest" ("Deutscher Wald"), while causing various ecological and social conflicts (Kreye 2021).

In Europe, on the other hand, the use of domesticated ungulates, whose "stem species" are already extinct (*Bos primigenius*) or nearly extinct (*Equus ferus*), can preserve ecosystem functions that could not be sustained without these domesticated ungulates. The domesticated forms act as representatives or surrogate taxa for species that have long since disappeared in their natural state. Under the heading of "rewilding" or so-called "naturalistic grazing", a nature conservation philosophy has developed in Europe that is rooted in this concept of using domesticated forms as surrogate taxa for extinct species.

"Rewilding" as a concept has had much discussion since it was introduced and means different things to different people (Lundgren et al. 2018; Pettorelli et al. 2019; Gordon et al. 2021). Some authors, e.g. Carver et al. 2021, argue that the concept emerged in North America in the 1980s and a paper by Soulé and Noss (1998) is sometimes referred to as the "original definition". The latter described the idea of rewilding as "*the scientific argument for restoring big wilderness based on the regulatory roles of large predators*" (Soulé and Noss 1998, p. 22). In fact, the idea is much older and there are roots that go back to a dark period of German history (Lorimer and Driessen 2016). Regardless of the many facets and concepts that are summarized under the umbrella of "rewilding", we do not aim to provide a review about this topic. Instead, and as stated above, we focus on the school of thought that sees "rewilding" in the sense of using domesticated forms to achieve ecosystem functions (Gordon et al. 2021).

We have already pointed out in previous publications that the concept has limitations (Zeller et al. 2017; Zeller and Göttert 2019; Rottstock et al. 2020). For example, the idea of "rewilding" in the sense of "returning" domesticated forms to a natural, ancestral or wild stage is impossible, because domestication is an irreversible process (Kruska 2005; Zeller and Göttert 2019). For centuries, if not millennia, domesticated cattle have been kept in Africa as part of agro-pastoral forms of land use (Huffman 1990). This pastoralism is oriented on natural grazing cycles of wild herbivores due to limited resource availability. Examples of this are the Maasai, who traditionally frequent the savanna landscapes of East Africa as migrant nomads with their herds of cattle and live in a functioning coexistence with the local wildlife communities. As part of our comparative approach, such interactions are examined in order to serve as a blueprint for the European context. In addition to the centuries-old pastoralist pasture management, pasture concepts were imported during the colonial period. For example, the concept of the rotational pasture was imported from Europe, where it was practiced for more than 200 years, into today's Namibia (Rothauge 2001). In the course of our comparative approach, we are interested in how these different forms of pasture management affect the corresponding wildlife communities. We compared the effects of different grazing systems on wildlife communities in Germany (permanent pasture in Lower Oder Valley National Park, ro-

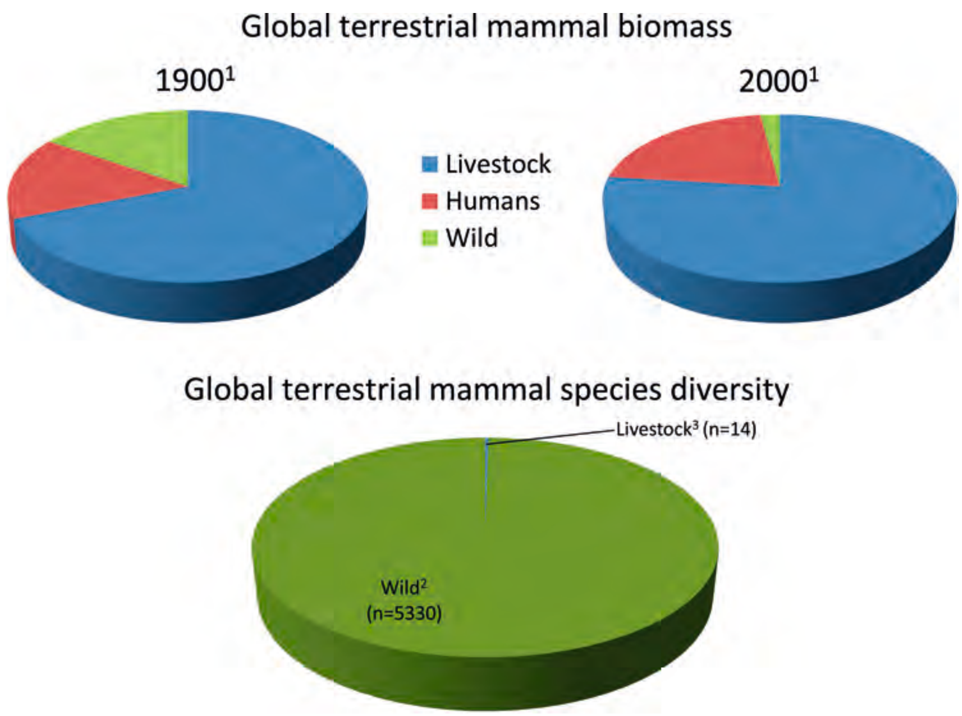

Figure 4. Estimation of the total global biomass related to humans, wild terrestrial mammals and large domesticated animals (livestock) – a comparison between the years 1900 and 2000 (upper chart). The lower chart shows the ratio of species diversity of extant terrestrial mammals (wild) as well as domesticated ungulate species (livestock). Sources: 1: Smil (2011), 2: Rondini et al. (2011), 3: Diamond (2002). The figure was adapted from Zeller et al. (2017).

tational pasture in Westhavelland Nature Park) with those in Africa (nomadic migrants in Tanzania and rotational pasture on private land in Namibia). It turned out that pastoralism in its original form no longer exists, at least in the area we examined in Tanzania (Rottstock et al. 2020). Instead, the rotational pasture system appeared to exert relatively low levels of disturbance on wildlife communities in both Germany and Namibia (Rottstock et al. 2020). Moreover, rotational pasture systems seem to be more advantageous than the so-called "naturalistic grazing" even in the European context (Rottstock et al. 2020). This is partly because "naturalistic grazing" is usually conducted on permanent pastures for technical and safety reasons. We come to the conclusion that the use of domesticated forms as representatives of extinct or locally disappeared megaherbivores in Europe has its justification to a certain extent. However, terms as "naturalistic grazing" or "rewilding" should be carefully considered. If the naturally occurring megaherbivore community still exists, as it is the case in the African context, these naturally occurring species should be given priority over domesticated forms. We should keep in mind that the organismic abilities and limitations of domesticated forms originate from their "stem species" (Zeller and Göttert 2019; Zeller et al. 2020). Thus, domesticated forms can be used as surrogate taxa as far as the organismic abilities allow – but only to the extent of the organismic limitations (Maier 2017; Zeller et al. 2018; Maier 2020). The loss of a significant proportion of a megafauna community in Europe cannot be compensated by the use of domesticated forms representing a few species only (Fig. 4). Consequently, the opening of the landscape following a uniform dense forest in Europe was not the result of grazing herbivores or livestock but active deforestation by humans to harvest wood for fuel production and create space for crop production and livestock farming – a process that started around 6,000 B.C. (Kapfer 2010) and gained momentum around 1,000 B.C. (Kaplan et al. 2009). Despite an initial increase in species diversity following a conversion of forest into open areas by humans (moderate disturbances through traditional agricultural practices) (Ostermann 1998), the intensification of agricultural practices during the previous decades puts increasing pressure on biodiversity and calls for more sustainable land use practices (Donald et al. 2001; Pretty and Bharucha 2014).

Livestock grazing in Africa – in terms of pastoralist grazing (typical in eastern Africa, Fig. 5) and even more so in terms of fenced pasture systems (typical for southern and southwestern Africa) – can lead to a number of severe problems, such as land degradation, soil compaction and bush encroachment (Starik et al. 2020). Small mammals can be used as indicators for environmental changes associated with livestock grazing as part of monitoring schemes (Hoffmann and Zeller 2005; Muck and Zeller 2006; Hoffmann et al. 2010; Starik et al. 2020). Besides the above-mentioned negative effects on the environment, livestock grazing in the African context can cause far-reaching human-wildlife conflicts. Introduced domesticated ungulates (livestock) compete with the originally occurring herbivores for resources, such as water, pasture, and shelter. These conflicts become especially pronounced in times of limited resource availability (dry periods, droughts), which are regularly recurring phenomena in the arid and semi-arid context of the savannas

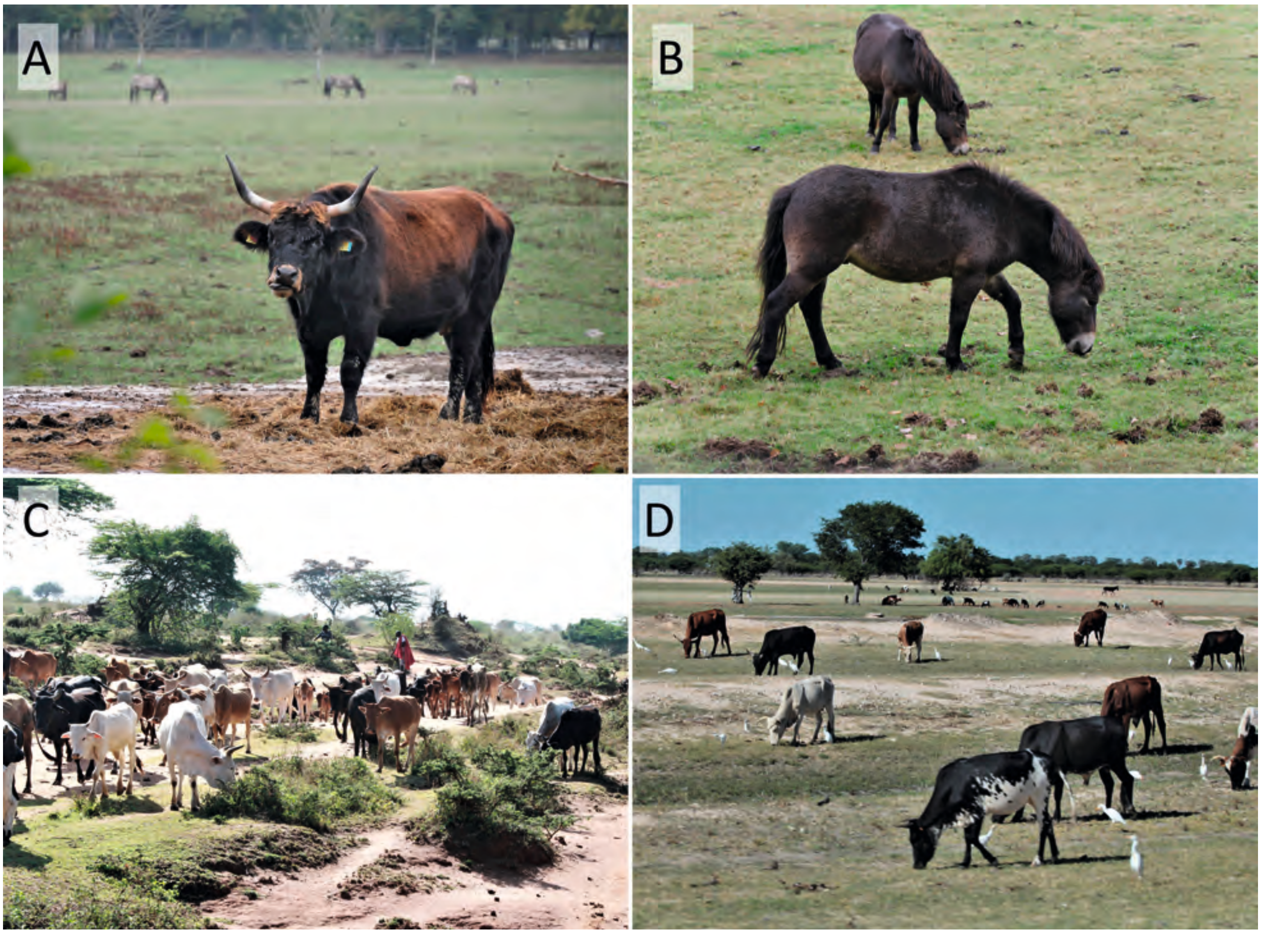

Figure 5. Naturalistic grazing in Europe makes use of domesticated ungulates, such as A: *Bos primigenius* f. taurus (Heck cattle) or B: *Equus ferus* f. caballus (Konik horse), to restore ecosystem functions. Cattle grazing systems in Africa can be conducted in the sense of herding pastoralists in Kenya (C) or by leaving the animals on their own on communal land in northern Namibia (D). Photos: A & B: U. Zeller, C & D: T. Göttert.

of sub-Sahara Africa. These conflicts are intensified by an increase in the number of domesticated ungulates, which in turn is the result of an increase in the human population, especially in regions where the herd size is positively correlated with the reputation of its owner (Doran et al. 1979; Rottstock et al. 2019). As a result, the originally occurring large ungulates, the megafauna depicted on the rock engravings, are concentrated in comparatively small and isolated protected areas, while most of the land remains reserved for livestock. This concentration of natural fauna elements in protected areas leads to density effects inside protected areas and an intensification of human-wildlife conflicts at the borders. A well-known example is the Etosha National Park in north-central Namibia, where considerable edge effects occur and put pressure on both wildlife populations inside the park and livestock herds and people outside the park (Göttert and Zeller 2008; Mannetti et al. 2017; Mannetti et al. 2019). Paradoxically, current efforts aimed at better connecting the existing network of protected areas lead to a further increase of human-wildlife conflicts. Stoldt et al. (2020) showed that despite an increase in the population size of selected large mammal species in northern Namibia, the actually available habitat for these species is constantly decreasing. This dilemma needs to be solved in order to achieve the nature conservation goals for this region. This means that the home ranges and activity areas of selected wildlife species, particularly megafauna-elements of the large mammal community, become an integral part of the land outside of the protected areas (Göttert et al. 2010). In contrast to Europe, the vast majority of African Pleistocene megafauna species still exists. Thus, reintroductions of megaherbivore species are effective instruments to restore ecosystem functions in areas where these species originally occurred but where they became extinct (Göttert and Zeller 2020; Roque et al. 2021). Reintroductions help to avoid density effects inside protected areas and enlarge the effective distribution range by including additional areas and habitat types on private land or communal conservancies (Göttert et al. 2010; Schwabe et al. 2015). Such activities support the designation of transboundary protected areas in the spirit of the Peace Park concept. In contrast to the colonial "fortress approach" (Adams and Hulme 2001) to conservation, transboundary protection approaches explicitly address the integration of socio-cultural conditions and regional-specific features. Land use scenarios and nature conservation strategies are oriented towards ecological and physio-geographic characteristics on the one hand and socio-cultural and anthropogenic factors on the other hand.

The aim is the implementation of areas whose spatial dimensions overcome national boundaries and therefore help to secure peace and political stability (Sandwith et al. 2001). In view of the spatial requirements of large and very large wildlife species, this approach of transboundary protection, while simultaneously promoting moderate forms of land use by local communities, is urgently required (West and Brechin 1991; Stoldt et al. 2020). This concept – protection through use – which also includes the preservation of cultural achievements (domesticated forms, grazing systems), appears promising for the effective protection of the natural African savanna ecosystems with their unique fauna elements, which were already stimulating the thoughts of humans in prehistoric times, as shown by rock engravings that inspired us to write this paper.

We can conclude that – despite all obvious differences between ecosystems in temperate Europe and in southern Africa – there are strong natural connections between both regions. To address the global impact of land use and climate change on biodiversity and ecosystem stability, holistic approaches on a trans-national scale are needed. By comparing ecological responses of selected and meaningful taxa in different regions, we want to differentiate between region-specific characteristics and universally applicable rules. We believe that such data leads to a better understanding of the complex interrelations between biodiversity and land use.

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