



Late Pleistocene and Holocene History of Mammals in Europe **5**

Robert S. Sommer

Contents

Introduction	84
Synopsis of Late Quaternary Environmental History	84
Pleistocene and Holocene Distribution Dynamics of Mammals in Europe	88
Ungulates and Other Large Herbivores	88
Carnivorans	91
Rodents and Small Mammals	92
Concluding Remarks	94
References	95

Abstract

This chapter describes the history of mammal species and their zoogeographical patterns during the Late Pleistocene and Holocene. The scientific results of the past 20 years on biogeography, phylogeny, and population history of mammals in combination with information on the development of climate and environment yield a complex picture of the dynamics of species in the past and offer a better understanding of the Quaternary biogeography of Europe. Overviews of the individual pattern

of the different species and the differences among the species are presented. In addition to the extinction pattern of typical Ice Age species like mammoth and cave lion and colonization history of temperate species from glacial refugia like roe deer or beaver, the chapter highlights how successful the different species were during a relatively short period of fundamental climate change. Apart from the extinct species, this is of high relevance for extant species which underwent significant changes of their distribution range during the Pleistocene to Holocene shift like reindeer, saiga antelope, pika, spotted hyena, or arctic fox.

R. S. Sommer (✉)
Department of Landscape Sciences and Geomatics,
Neubrandenburg University of Applied Sciences, Rostock,
Germany

Department of Zoology, Institute of Biosciences,
University of Rostock, Rostock, Germany
e-mail: robert.sommer@uni-rostock.de

Keywords

Post-glacial · Climate change · Environmental change · Extinction · Recolonization · Glacial refugia · Last Glacial Maximum · Faunal history · Mammals · Palaeoecology · Population history

Introduction

The past 50,000 years of the Late Quaternary (Fig. 1) are characterized by several climatic oscillations and environmental changes (Dansgaard et al. 1993; Huntley et al. 2003; Wohlfarth et al. 2008). The consequences of these environmental dynamics on mammals in Europe over time are documented by a complex spatiotemporal pattern of extirpation, extinction, and (re-)colonization for many species in Europe (Hewitt 2000; Sommer and Nadachowski 2006; Stewart and Cooper 2008; Sommer and Zachos 2009; Stuart and Lister 2012; Crees 2013; Crees et al. 2016; Stuart 2015).

From a biogeographical point of view, the faunal dynamics of mammals in Europe are generally characterized by different main patterns during the Pleistocene/Holocene change:

1. Several typical mammal species of the Ice Age fauna, which were adapted to the steppe-tundra biome, the so-called “mammoth steppe,” for example, cave lion *Panthera spelaea* or wholly rhino *Coelodonta antiquitatis*, became extinct in Holarctic regions several 1000 years before or directly at the end of the Pleistocene (Stuart and Lister 2012; Stuart 2015; Cooper et al. 2015).
2. Many extant species, distributed in the Pleistocene landscape and adapted to steppe or tundra environments, such as the arctic fox *Vulpes lagopus*, reindeer *Rangifer tarandus*, saiga *Saiga saiga*, or spotted hyena *Crocuta crocuta*, experienced a local extirpation from Central Europe during the end of the Pleistocene or Early Holocene but were able to maintain their distribution in either recent steppe or tundra biomes in Eurasia or Africa (Nadachowski

et al. 2016; Rohland et al. 2005; Sommer et al. 2014).

3. The majority of extant mammal species, adapted to temperate environments (mixed woodlands or open mixed woodlands), such as west-European hedgehog *Erinaceus europaeus*, red deer *Cervus elaphus*, beaver *Castor fiber*, or brown bear *Ursus arctos*, recolonized Central and northern European regions from glacial refugia in southern European regions or adjacent areas (Sommer and Nadachowski 2006; Sommer and Zachos 2009).
4. Species adapted to different habitats like stoat *Mustela erminea* and wolf *Canis lupus* were distributed continuously in Europe throughout the Pleistocene and Holocene. However, these species underwent a considerable population turnover/demographic change triggered by the Last Glacial Maximum or Pleistocene/Holocene change (McDevitt et al. 2012; Pilot et al. 2010; Sommer and Benecke 2005b).

Since the Late Holocene, human influence has had an increasing effect on species, which led to extinction (*Equus ferus*, *Bos primigenius*) or loss of large parts of the natural distribution range in large ungulates (*Alces alces*, *Bison bonasus*) or large carnivores (Crees et al. 2016).

This chapter describes the Late Quaternary history of mammal species in Europe with a focus on species of the extant fauna. Subfossil records of the species from archaeological sites, pattern of DNA or stable isotopes of the species along with records of climate and vegetation dynamics inform our understanding of development of past patterns of mammalian biodiversity in Europe.

Synopsis of Late Quaternary Environmental History

The climate and vegetation history of Europe for the Late Pleistocene and Holocene is relatively well documented (e.g., Dansgaard et al. 1993; Björck et al. 1998; Hubberten et al. 1998; Litt et al. 2001, 2003; Barron et al. 2003; Davis et al.

2003; Huntley and Allen 2003; Renssen et al. 2009). In this chapter, the European environmental history of the last 60,000 years is briefly summarized in order to provide a temporal framework for understanding the colonization history of mammals.

From 60,000 to 27,000 years ago (ka), during the Marine Isotope Stage 3 of the Quaternary, the northern hemisphere was characterized by a generally cold environment punctuated by regular warm intervals, the Greenland Interstadials, which lasted from several 100 years to around 3000 years (Fig. 1). The landscape of Europe north of the glacial refuge areas (Fig. 2b) was characterized by open steppe-tundra (so-called mammoth steppe) with an annual mean temperature of -4°C to -8°C (Hubberten et al. 1998). The steppe-tundra contained a mix of plant species of today's steppe as well as tundra biomes and was a unique biome during the Pleistocene with no extant analogue. During warmer Interstadial periods the mean temperature rose abruptly (within a few years) to around 10 – 16°C and led to a spread of animal and plant species from the southern refuge areas (e.g., Balkans or Iberia) to at least 50° latitude, significantly changing regional biotic assemblages. During the warmer Interstadial periods (Fig. 1) the European Lowland was characterized by a shrub tundra with occurrence of willow and juniper. South of 50° northern latitude there was an open coniferous park-like landscape.

The Last Glacial Maximum (LGM) from 27 to 18 ka was characterized by the maximum advance of the ice sheets, and all regions of Central Europe were affected by discontinuous permafrost. During this period of cooling, when annual mean temperatures in Greenland were about 21°C lower than today, cold-adapted species and open landscapes reached their most southerly extent and temperate species became isolated in southern glacial refugia (Sommer and Nadachowski 2006; Sommer et al. 2014), although the degree of range isolation differed depending on their adaptation to certain biomes such as mixed deciduous forests. During the LGM the sea level was about 120 m lower than today because of the large amount of water bound in glaciers (Lambeck et al. 2002).

The onset of the last deglaciation of the northern hemisphere in the Early Late Glacial (18–14.7 ka) began around 18 ka, and by 14 ka most northern parts of what are now Germany and Poland, as well as the Baltic States, were deglaciated. Mean temperatures during the Late Glacial (14.7–11.7 ka) rose by about 12°C from the beginning of the Greenland Interstadial 1, also known as Bølling/Allerød Interstadial (Fig. 2c), and led to environmental change across the whole northern hemisphere. In Central Europe, the warming induced the expansion of birch *Betula* sp., willow *Salix* sp., and poplar *Populus* sp., and during the Greenland Interstadial 1c–a (Allerød) pine *Pinus* sp. also increased its range

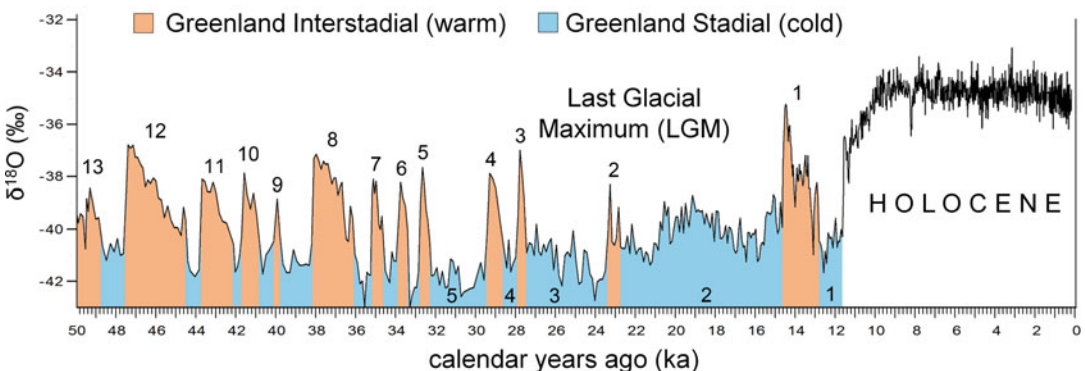


Fig. 1 Climate history of the last 50,000 years based on oxygen isotope ratios $\delta^{18}\text{O}$ in ‰ from the GISP2 ice core record (using CalPal, Weninger et al. 2008) and ice core event stratigraphy after Blockley et al. (2012)

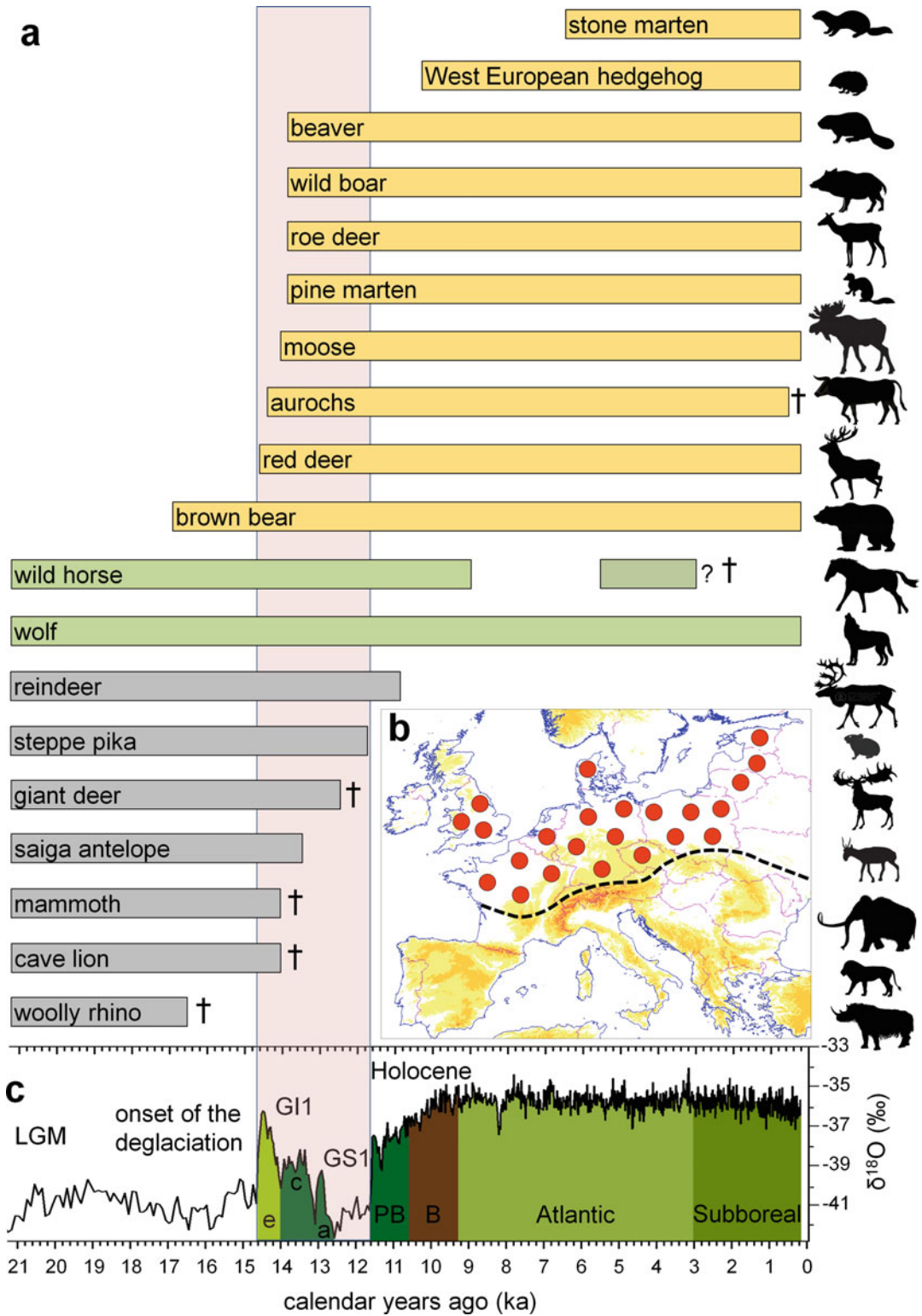


Fig. 2 Chronological comparison of the colonization history of Europe by different mammal species on the basis of the subfossil vertebrate record from archaeological or palaeontological sites since the Last Glacial

(Litt et al. 2001, 2003). However, Europe then experienced a brief cool snap, the Younger Dryas, that lasted for 1000 years and caused the forests which had established during the Greenland Interstadial 1c–a to vanish from northern Central Europe (Theuerkauf and Joosten 2012). The ice core records from Northern Europe (which correspond with temperature changes) unequivocally reflect a rapid rise in temperature at the onset of the Holocene (Fig. 1), which was followed by a slower rise during the Preboreal (PB) and Boreal (Bo) periods (Fig. 2b). This early Holocene warming was associated with a major biome change in Central Europe and the rapid spread of birch and pine, later followed by

warm-adapted tree taxa such as hazel *Corylus* sp., oak *Quercus* sp., and elm *Ulmus* sp. During the Holocene Thermal Maximum within the Atlantic climatic period, about 9–5 ka (Fig. 2c and Table 1), when annual mean temperatures were up to 2–3 °C higher than today (Renssen et al. 2009), Central Europe was largely forested, with oak, elm, lime *Tilia* sp., and pine dominating in the lowlands and spruce *Picea* sp., beech *Fagus* sp., and fir *Abies* sp. predominant at higher altitudes. South of 50° northern latitude, open forest steppe communities existed. Since 7 ka ago, the vegetation in Europe has been increasingly influenced by human activities.

Table 1 Event chronology of climatic epochs and environmental change during the Weichselian Glacial and Holocene in Europe

Chronology of Weichselian Glacial and Holocene	Features of environmental change and climate events	Time interval (years ago)
Marine Isotope Stage 4 (MIS 4), Pleniglacial	First maximum cooling of the Weichselian Glacial about 60,000 years ago	75,000–60,000
Isotope Stage 3 (MIS 3), Pleniglacial	Rapid stadial and interstadial oscillations (cf. Fig. 1)	60,000–27,000
Last Glacial Maximum (LGM)	Second maximum cooling of the Weichselian Glacial and maximum and maximal expansion of ice sheets	27,000–18,000
Early Late Glacial	Onset of the last deglaciation	18,000–14,700
Late Glacial Interstadial 1 (Bølling/Allerød warming)	Rapid warming and local return of forests in northern European regions	14,700–12,700
Late Glacial Stadial 1 (younger Dryas)	Cooling oscillation, decline of local woodlands, and subarctic environments in northern Central Europe	12,700–11,700
Early Holocene	Appearance of birch/pine forests, later also hazelnut, in northern Central European regions	11,700–9100
Middle Holocene	Appearance of deciduous woodlands (dominated by oak and lime tree) in northern Central European regions; Holocene Thermal Maximum (HTM) about ca. 9000–4000 years ago; first opening of woodlands by Neolithic settlers about 7000 years ago	9100–5800
Late Holocene	Increasing influence of humans on landscape and environment	5800–present



Fig. 2 (continued) Maximum (LGM). Presence of a species over time is indicated by bars (a) from the areas north of the typical refugial regions (b) along the climate and environmental history of northern Central European regions. The curve in (c) indicates the oxygen isotope ratios $\delta^{18}\text{O}$ in ‰ from the GISP2 ice core record (using CalPal, Weninger et al. 2008) and ice core event stratigraphy after Björck et al. (1998). *GII* Greenland Interstadial 1 (Bølling/Allerød warming epoch), *GS1* Greenland Stadial 1 (Younger Dryas cooling), *PB* Preboreal, *B* Boreal. (a) Gray bars: extinct Pleistocene megafauna species or

species that underwent substantial range shifts after the Pleistocene; green bars: species that were able to adapt to Pleistocene and Holocene biomes in Europe; yellow bars: temperate species that recolonized Central Europe at the end of the Pleistocene from glacial refugia. The vertical pink bar in (a, c) between ca. 14.7 and 11.7 ka ago indicates the time of the Greenland Interstadial 1 warming (GII) and the Greenland Stadial 1 (GS1). The bars in (a) show that the majority of faunal shifts took place during this epoch at the end of the Weichselian Glacial

Pleistocene and Holocene Distribution Dynamics of Mammals in Europe

Ungulates and Other Large Herbivores

With respect to the reconstruction of spatiotemporal dynamics of mammals, ungulates are the most representative species, because they were the main prey of Neanderthals and modern humans in prehistoric times and thus represent the main part of vertebrate bones as food remains of Stone Age hunters at archaeological sites.

The history of the woolly mammoth *Mammuthus primigenius* and the woolly rhino *Coelodonta antiquitatis*, most prominent and dominant members of the Ice Age fauna in Eurasia, has been studied in great detail, most of all in the framework of radiocarbon-based chronologies and population history (Stuart et al. 2004; Stuart and Lister 2012; Palkopoulou et al. 2013; Lister and Sher 2015; Stuart 2015; Kahlke 2015; Chang et al. 2017). The mammoth always occurred in the ice-free parts of Europe during the Weichselian Glacial until 14 ka ago, when it experienced a global collapse caused by environmental change during the Greenland Interstadial 1 and survived only in restricted areas of Northern Siberia and in some parts of the northern Russian Plain until the Early Holocene. On the Wrangel Island in Northeastern Siberia, the mammoth survived until about 4 ka ago (Stuart et al. 2004; Stuart 2015). The endemic European mammoth population of the Weichselian Glacial became extinct after 24 ka ago and was replaced by mammoths of a Siberian genetic clade, which had been colonizing Europe since 34 ka ago (Palkopoulou et al. 2013).

The woolly rhino experienced a local extinction in Europe about 17 ka ago and died out globally about 14 ka ago. Another typical megafauna species of the Ice Age, the giant deer or “Irish elk” *Megaloceros giganteus*, disappeared from Europe during the terminating glacial but persisted until at least 8 ka ago in Western Siberia and European Russia (Stuart et al. 2004; Stuart 2015).

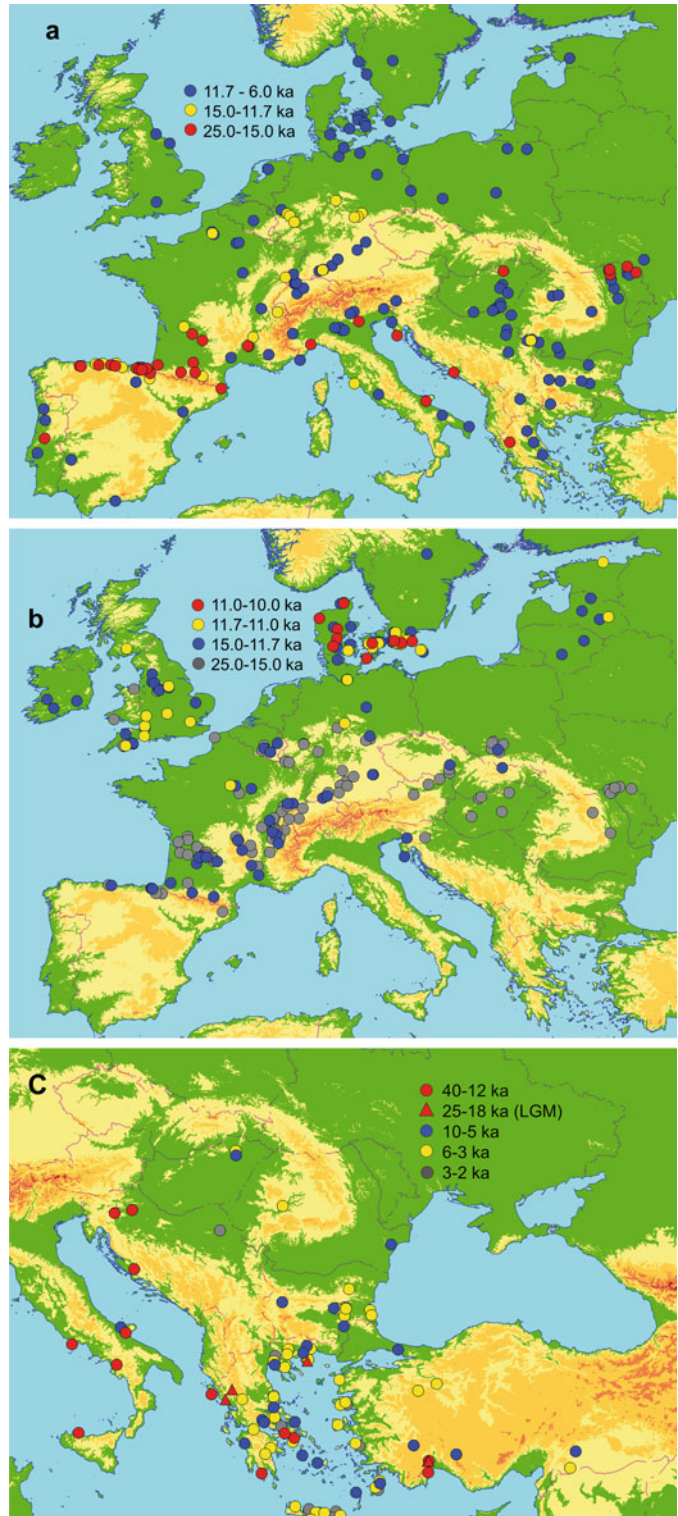
The range of the saiga antelope, an extant steppe dweller of Ponto-Caspian and Asian steppe

regions, was restricted to large parts of North Asia and steppe areas north of the Black Sea during the Late Quaternary (Kahlke 2014). It colonized Central and Western Europe only at irregular intervals since the Last Glacial Maximum between 24 and 13 ka ago (Nadachowski et al. 2016; Yalden 1999) and occupied a separate ecological niche compared with other ungulate species of the mammoth steppe (Jürgensen et al. 2017).

The reindeer *Rangifer tarandus*, a key species of the Pleistocene megafauna of the northern hemisphere (Kahlke 2014; Stuart and Lister 2012) and characteristic faunal element of extant European taiga and tundra biomes, was distributed throughout the continent during the Last Glacial, with the exception of the Mediterranean peninsulas, some glaciated parts of Scandinavia, and the northern Caspian region (Kahlke 2014). In contrast to other megafauna species like mammoth or woolly rhino, which died out in most parts of the distribution area after the collapse of the steppe-tundra about 14 ka ago (Stuart and Lister 2012), it showed a much weaker reaction to the loss of the Pleistocene steppe-tundra after the GI1 warming event with a continuous local presence in the northern European Lowlands (Sommer et al. 2014). It survived into the early Holocene until about ca. 11 ka ago and in southern Scandinavia until ca. 10.3 ka ago (Sommer et al. 2014) (Fig. 2a). In southeastern Central Europe, *Rangifer tarandus* quickly became extinct after the LGM, and in Southwestern Europe, its last occurrence was during cold spells of the Younger Dryas period at the end of the Ice Age (Sommer et al. 2014) (Fig. 3b).

Among the extant deer species, the fallow deer *Dama dama* colonized Central Europe only during the Eemian Interglacial (126–115 ka ago). During the Weichselian Glacial it was restricted to Asia Minor, the Balkans (mainly today’s Greece), and today’s Italy (Yannouli and Trantalidou 1999; Masseti 1996, 1999). Only archaeological sites of Greece and Turkey show a continuous presence from the Late Pleistocene into the Holocene, as displayed in Fig. 3c, which suggests a glacial refugium and thus a natural post-glacial origin of *Dama dama* also in the

Fig. 3 Pleistocene and Holocene distribution of subfossil remains of different ungulate species in Europe showing different spatiotemporal dynamics and range shifts as a reaction to the Pleistocene/Holocene climate change. **(a)** Roe deer *Capreolus capreolus* as a typical temperate species with a restriction to southern glacial refugia during the LGM, a colonization of southern Central Europe during the Late Glacial, and a Holocene range shift to northern regions. **(b)** Reindeer *Rangifer tarandus* as a species adapted to Pleistocene landscapes that underwent a significant range shift from southern to northern regions at the end of the Pleistocene. **(c)** Fallow deer *Dama dama* as a Ponto-Mediterranean species with glacial refugia in Anatolia and the Balkans. During the Holocene, *Dama dama* was not able to colonize Central Europe out of its glacial refugia. Its present distribution range is largely due to human translocations since Roman Times



Balkans, as discussed in Baker et al. (2017). Bulgaria was colonized by fallow deer since the Mid-Holocene at least 10 ka ago (Fig. 3c). Fallow deer never recolonized Central Europe during the early to Mid-Holocene by natural dispersal. Its presence outside of Ponto-Mediterranean regions is the result of repeated (re-)introductions and translocations by humans since Roman Times (Fig. 3c).

During the Weichselian Glacial temperate species like European roe deer *Capreolus capreolus* (Fig. 3a), red deer *Cervus elaphus*, and moose *Alces alces*, but also wild boar *Sus scrofa* and aurochs *Bos primigenius*, were restricted to glacial refugia in southern European regions (Sommer and Nadachowski 2006; Sommer and Zachos 2009). Among these temperate large mammal species (typical elements of the Holocene fauna of Europe), the red deer was more tolerant of Pleistocene environmental conditions. As a consequence, in warmer Interstadial periods during the Weichselian Glacial, it co-occurred with typical Pleistocene species like mammoth, reindeer, wild horse, spotted hyena, or cave bear in northern regions of Western Europe (Sommer et al. 2008) and Central Europe (Sommer et al. 2008; Musil 2003).

The recolonization process of Central and Northern Europe by the abovementioned temperate artiodactyls began already in the Late Glacial during Greenland Interstadial 1, which started 14.7 ka ago (Fig. 2a). During this warmer epoch of about 2000 years, the northern hemisphere was characterized by fundamental environmental changes which led to the collapse of the steppe-tundra biome and global extinction of woolly rhino and cave lion as well as local extinction of woolly mammoth in Europe (a contribution of humans to the decline of the mammoth in Western Europe may be possible, cf. Lorenzen et al. 2011).

In contrast to the other aforementioned species, the red deer recolonized the western northern European Lowland regions and the British Isles already during the very early stage of this warming during Greenland Interstadial 1e between 14.7 and 14.0 ka ago in the wake of the first occurrence of birch (Sommer et al. 2008). The recolonization of the northern parts of Central Europe by the other species after the LGM took

place during the Greenland Interstadial 1a–c (also known as Allerød-warming), in line with a further spread of birch and pine in northern European regions. The moose colonized the British Isles already during the very early Late Glacial stage GI1e (Yalden 1999). While in Central Europe and Britain the red deer shows a similar presence as the moose, i.e., already during the early Late Glacial, the expansion to southern Scandinavia took place only during the Early Holocene (Aaris-Sørensen 2009).

During the Younger Dryas cooling period, the last 1000 years before the beginning of the Holocene, the transformation of the northern regions of the European Lowland from light birch/pine forests to open park-like tundra caused a new dominance of reindeer as well as the last appearance in Southwestern Europe (Sommer et al. 2014) and local extirpation of temperate species.

Temperate ungulate species, for example, represented by the roe deer, survived in light birch/pine forests south of 50° northern latitude (Sommer et al. 2009). The moose, however, showed a more resilient reaction to the Younger Dryas environments in Northern Europe because it appeared in the European Lowlands together with the reindeer, and both species show comparable economic importance in an archaeological site of stone age hunters (Gramsch et al. 2013; Sommer pers. data) and occurred also in Denmark (Schmölcke and Zachos 2005).

During the Early Holocene, also other temperate artiodactyls (re-)colonized southern Scandinavia and the British Isles which were connected by land bridges with the continent since about 10 ka ago. The spatiotemporal complexity of this process is shown, for instance, by red and roe deer (Sommer et al. 2008, 2009). While the aurochs *Bos primigenius* seems to represent a similar temporal recolonization pattern of Central and Northern Europe after the LGM as typically represented by roe deer, the European bison *Bison bonasus* has a more enigmatic faunal history in Europe. Since it has been hypothesized that *Bison bonasus* is the product of a natural hybridization of the extinct steppe bison *Bison priscus* and the aurochs *Bos primigenius* during the Eemian Interglacial c. 120 ka ago (Soubrier et al. 2016), the faunal origin

for its Holocene distribution is probably Europe. Although it is recorded since the terminating Late Glacial or Early Holocene in Central and Northern Europe (Benecke 2004, 2005; Aaris-Sørensen 2009), its presence in the vertebrate faunal record from archaeological sites of the early to Mid-Holocene is extremely rare. This, however, might partly be an artifact caused by the fact that fragmented bone remains of aurochs and European bison are difficult to discriminate, and it is likely that an unknown part of bones of the European bison was identified as aurochs in the Holocene Vertebrate faunal record from archaeological sites in Europe (Benecke 2005). Higher frequencies as prey species for humans are recorded only during the Late Holocene in Northeastern Europe, for example, the Baltic States or Belarus (Benecke 2005), which coincides with the core area of the later Holocene distribution area of *Bos bonasus* in eastern Central Europe on the basis of geographic modeling (Kuemmerle et al. 2012).

The biogeographical history of the wild horse *Equus ferus* stands in clear contrast to most other ungulate species in Europe. During the Pleistocene, it was a typical element of the cold-adapted faunal community of the steppe-tundra and experienced a decline in Northern Europe in the course of forest growth and expansion of deciduous forests and a loss of open landscape in the Mid-Holocene (Sommer et al. 2011; Leonardi et al. 2018). In southern European and southern Central European regions, it survived in the open forests and even adapted to open woodlands, as evidenced by the development of a black coat color (Sandoval-Castellanos et al. 2017). After the opening of the primeval forests by Neolithic farmers, *Equus ferus* could recolonize the European Lowland to a certain extent and was replaced by the domestic horse from the Bronze Age onward (Sommer et al. 2011, 2018).

Carnivorans

Among the carnivorans, very prominent members of the Ice Age megafauna were distributed in Europe. The spotted hyena *Crocota crocuta* was distributed in Pleistocene faunal communities in

Eurasia. The traditional view that it was a separate Pleistocene hyena on species or subspecies level was rejected by Rohland et al. (2005), who show that cave hyenas are a genetic clade of African spotted hyenas, arisen through dispersal and separation in Eurasian environments during the Late Pleistocene. Interestingly, it represents the earliest extirpation event among the megafauna carnivorans during the Last Glacial in Eurasia; the latest record is dated about 30 ka ago in Italy (Stuart and Lister 2014; Stuart 2015).

The cave bear *Ursus spelaeus*, well known from numerous Pleistocene fossil bone assemblages in European cave systems (Münzel et al. 2011), became extinct in Europe (and globally) about 28 ka ago (Pacher and Stuart 2009). Interestingly, long before this event, a different species of cave bear, *Ursus ingressus*, hypothesized to be a separate cave bear species in Eastern Europe only on the basis of ancient DNA (Knapp et al. 2009), appeared in the Alpine region and coexisted with the cave bear at least for 4500 years (Münzel et al. 2011). *Ursus ingressus* replaced *Ursus spelaeus* in the Alpine region about 30 ka ago but outlived *Ursus spelaeus* only by about 2000 years (Münzel et al. 2011). Genetic data from cave bears in Northern Spain (Fortes et al. 2016) show that each cave was colonized by a unique genetic lineage of *Ursus spelaeus* suggesting an extreme fidelity of cave bears to their birth sites (homing behavior). Brown bears *Ursus arctos*, which also occurred in the same region during the Weichselian Glacial and the LGM (Sommer and Benecke 2005a), do not show this strong association of genetic lineage and cave locality; thus, in times of increasing competition between humans and brown bears, it is very likely that this could have contributed to cave bear extinction (Fortes et al. 2016). The brown bear was the earliest colonizer of the regions north of potential glacial refugia and reached today's British Isles during the Early Late Glacial following the onset of the deglaciation (Sommer and Benecke 2005a; Fig. 2a). *Ursus arctos* colonized Northwestern Europe sporadically for probably shorter periods during warmer interstadials, several 1000 years before the LGM (Sommer and Benecke 2005a). The polar bear

Ursus maritimus was distributed to an unknown extent in the periglacial landscape of the Weichselian Glacial, probably where northern ice shields met open waters of the Atlantic. The youngest record is from the Late Glacial in Denmark about 12.4–12.9 ka ago (Aaris-Sørensen 2009).

Among the mustelids, the stoat *Mustela erminea* and the least weasel *M. nivalis* were distributed in both full glacial and forested Holocene landscapes of Europe (Sommer and Benecke 2004). The temperate mustelid species, isolated into glacial refugia in Southern Europe during the Weichselian Glacial like the forest-dependent pine marten *Martes martes*, colonized Central Europe and southern Scandinavia during the Allerød-warming in the Late Glacial when these regions were increasingly covered by open birch-pine woods (Sommer and Benecke 2004). However, it is unclear to what extent these species underwent local extinction during the unfavorable environmental conditions of the Younger Dryas.

The biogeographical pattern of the stone marten *Martes foina* is in strong contrast to *M. martes*, because the colonization of the stone marten during the Mid-Holocene followed the spread of agriculture and farming with an assumed origin in Asia Minor; thus, the adaptation of *M. foina* to human settlements has its origin already in the Neolithic (Sommer and Benecke 2004). In contrast to most other carnivoran species the Eurasian otter *Lutra lutra* only recolonized Central Europe during the Holocene about 10 ka ago (Sommer and Benecke 2004; Aaris-Sørensen 2009), perhaps because it was only present in a single glacial refuge in the Apennine peninsula. The Alps would have been a migration barrier during this recolonization process (Sommer and Benecke 2004). The relatively low genetic diversity of otter populations in Europe (Mucci et al. 2010; Honnen et al. 2011) may be a consequence of this. The Pleistocene and Holocene distribution dynamics of canids are described by Sommer and Benecke (2005b).

The cave lion *Panthera spelaea*, which was a classical faunal element and very widespread in Eurasia during the Late Pleistocene (Stuart and Lister 2011), became extinct about 14 ka ago

(like the woolly rhino), caused by the collapse of the steppe-tundra, their typical biome (Stuart and Lister 2011, 2012). After global extinction of the cave lion, the modern lion (*Panthera leo*) reached Eastern Europe about 8000 years ago and colonized today's Greece, Bulgaria, and the Pannonian Basin during the Mid-Holocene (Sommer and Benecke 2006; Masseti and Mazza 2013). The latest presence of *Panthera leo* in Europe in Bulgaria and Greece is dated to the Bronze and Iron Ages (Ninov 1999; Sommer and Benecke 2006). The Eurasian Lynx *Lynx lynx* was climatically less specialized and was regularly present in Central Europe in the Weichselian Pleniglacial before the LGM (Sommer and Benecke 2006). During the Late Glacial it was one of the earliest carnivorans to colonize the northern regions, and its distribution included Northern Iberia where it occurred sympatrically with the Iberian lynx *Lynx pardinus* during this period. From a zoogeographical point of view, the Iberian lynx shows an interesting palaeoendemism, because during the LGM it was distributed also in Northern Italy together with *L. lynx* (Rodríguez-Varela et al. 2015), and its Holocene range included parts of Southern France until about 2000 years ago (Sommer and Benecke 2006; Rodríguez-Varela et al. 2015). Since the Late Holocene, the range of *L. pardinus* has been restricted to Iberia (Sommer and Benecke 2006). The wildcat *Felis silvestris* reached Central Europe out of southern refugia during the Late Glacial Allerød-warming in the wake of the returning forests. It is unknown to what extent the species survived the Younger Dryas cooling period north of the Alps (Sommer and Benecke 2006). During the Holocene Thermal Maximum (HTM) the wildcat was also distributed in Scandinavia but vanished again due to the cold climate after the HTM (Sommer and Benecke 2006).

Rodents and Small Mammals

In contrast to carnivorans and ungulates, the biogeographic pattern of Pleistocene and Holocene distribution dynamics of smaller mammals like

rodents or bats in Europe has been studied much less. One very good scientific reference is the unpublished PhD thesis of J. Fahlke (2009). The occurrence of subfossil bones of small mammals in Pleistocene and Holocene layers often does not indicate a clear climatic preference, which is also caused by the fact that small and lightweight mammal bones may be frequently relocated in sediment layers over time (von Koenigswald 1974, 1977, 1984a, b). However, when assessing (and re-evaluating) large numbers of subfossil records of a species, the spatiotemporal dynamics in reaction to past climate change can be understood much better (Sommer 2007).

Among the Pleistocene small mammal fauna of Central Europe, the Norwegian lemming *Lemmus lemmus* and the collared lemmings *Dicrostonyx* spp. were typical cold-adapted species which disappeared from Central Europe and survived in recent northern Eurasian boreal and tundra regions. However, there is no detailed information about the exact time of local extinction (whether at the end of the Pleistocene or the beginning of the Holocene). Prost et al. (2010a) showed that previous climate warming events had a strong influence on genetic diversity and population size of collared lemmings *D. torquatus* in arctic ecosystems. An interesting zoogeographical case is the narrow-headed vole *Microtus gregalis*. Presently distributed in both tundra and steppe environments of Asia, it was considered to be an indicator of cold climate in Central European faunal history (von Koenigswald 2002) and already reached northern European regions during the Weichselian Glacial (Fahlke 2009). One of the most prominent representatives of past Pleistocene faunal communities in Europe is the steppe pika *Ochotona pusilla*. As a steppe dweller, it is presently restricted to steppe regions of Kazakhstan and Russia but colonized large parts of the European steppe-tundra, including parts of Northern Europe (Fahlke 2009). *Ochotona pusilla* was a frequent small mammal species in colder stages of the Pleistocene in Europe and disappeared from today's Germany and the British Isles at the end of the Younger Dryas Stadial (Street and Baales 1999; Fahlke 2009; Yalden 1999). Whereas the steppe pika underwent a postglacial contraction of

its range, the mountain hare *Lepus timidus*, which was continuously distributed throughout Central Europe during the Weichselian Glacial, experienced a separation which resulted in a disjunct arctic-alpine distribution (plus the British Isles). Assuming that the discrimination of numerous Pleistocene and Holocene subfossil bone remains of hares is correct, they reveal a clear pattern of an exclusive presence of mountain hares in Pleniglacial and Late Glacial epochs in Central Europe and southern Scandinavia. During the Early Holocene, it was then replaced by the brown hare *Lepus europaeus*. Southern Scandinavia was first colonized during the Neolithic, possibly in the wake of the opening of woodlands by Stone Age farmers.

The common hamster was part of both Pleistocene and Holocene faunal communities in Europe (Fahlke 2009). As a steppe dweller, it may have benefited, similarly to the wild horse, from opening of woodlands by Neolithic farmers since the end of the Mid-Holocene.

It is interesting that the Russian Desman *Desmana moschata*, presently restricted to semi-aquatic habitats mainly at the riverbanks of the Volga, Don, and Ural in Russia, colonized the northern European Lowland and southern Scandinavia during the whole Late Glacial period and disappeared with the beginning of the Holocene. In contrast to that, the European Mole *Talpa europaea* was present during Pleni- and Late Glacial stages of the Pleistocene north of the Alps (Fahlke 2009) but is first recorded from the European Lowland and Scandinavia during the Holocene (Fahlke 2009; Aaris-Sørensen 2009).

Among the temperate species, the beaver *Castor fiber* shows an interesting recolonization pattern very similar to temperate ungulate species like moose, red deer, and roe deer. At first, a post-LGM recolonization of parts of the European Lowlands (including southern Scandinavia) during the Greenland Interstadial 1 took place following the sudden climate warming and increase in forests and appearance of typical food plants like birch and willow. Moreover, subfossil wood with visible cut marks from beavers from Northeastern Germany has been dated to the Greenland Interstadial 1c-a (Lampe et al. 2016). During the

Younger Dryas cooling period there is a gap in the beaver subfossil record in northern regions of Central Europe (Fahlke 2009; Aaris-Sørensen 2009) which may indicate local extinction caused by unfavorable climatic conditions. However, since the early Holocene the beaver has continuously been documented in the subfossil vertebrate record of northern European regions (Benecke 1999; Aaris-Sørensen 2009).

The bank vole *Myodes glareolus* is known as a typical Holocene small mammal species in Europe. Today the species is mainly associated with woodlands. The species shows a remarkable flexibility in climatic preferences in its post-LGM distribution history and colonized the lower mountain ranges of today's Germany from the Early Late Glacial onward (Fahlke 2009). The phylogeographic pattern clearly suggests a post-LGM colonization out of a Carpathian refuge (Kotlík et al. 2006). The survival of the LGM in the Carpathian region was also discovered in brown bear (Sommer and Benecke 2005a) and numerous temperate mammals such as red fox, pine marten, red deer, roe deer, and moose (Sommer and Nadachowski 2006). The strongly forest-dependent edible dormouse *Glis glis* was restricted to deciduous forest refugia in the Mediterranean/Pontomediterranean regions of Southern Europe during the LGM and first colonized the area north of the Alps during the Boreal period in the wake of the northward spread of deciduous forests (Hürner et al. 2010). The Eurasian red squirrel *Sciurus vulgaris*, ecologically more flexible than the edible dormouse due to its adaptation to mixed wood and taiga biomes, was also an exclusive Holocene colonizer of Central Europe (Fahlke 2009), and it can be assumed that the colonization process took place very rapidly during the Preboreal period. However, the species is underrepresented in the vertebrate faunal record and thus it is questionable if the first record in southern Scandinavia with an age of 9.5 ka ago really represents its first appearance in Northern Europe.

The west-European hedgehog *Erinaceus europaeus* is an example of a Holocene immigrant (Fig. 2a) that colonized Central Europe and southern Scandinavia first during the Early Holocene about 11–10 ka ago and shows (in contrast to other smaller

mammal species) a clear preference of warmer Inter-glacial climate (Sommer 2007). The white-breasted hedgehog *Erinaceus roumanicus*, which recolonized eastern parts of Central Europe out of a glacial refuge from the Balkans, is only rarely found in the vertebrate record, but a similar temporal pattern as in *E. europaeus* has been suggested (Sommer 2007).

The common shrew *Sorex araneus* as well as the Eurasian Pygmy Shrew *Sorex minutus* show no strong climatic preference and appear frequently in Pleistocene as well as Holocene faunal communities. The common shrew developed a large ecomorph in Alpine regions during the Late Glacial which led to the assumption of a separate species *Sorex macrognathus*. However, the populations of this large morph of *S. araneus* were replaced by other populations after the Pleistocene/Holocene change (Prost et al. 2013). This example demonstrates the high morphological plasticity and the dynamics of population turnover in a small mammal species during climate change at the end of the Pleistocene. A similar case is the suggested extinction of the Don-hare *Lepus tanaiticus* at the end of the Pleistocene in the Russian Plains, which has genetically been identified as a morphotype of *L. timidus* (Prost et al. 2010b). In light of Prost et al., it would be interesting to check if the large Pleistocene hamster species *Cricetus major*, extinct in Europe by the beginning of the Greenland Interstadial 1 (Fahlke 2009), may rather be an ecomorph of *Cricetus cricetus* than a separate hamster species.

Concluding Remarks

Increasingly, research activities and the development of new methods pertaining to ancient DNA over the last decades have led to a “revolution” of our understanding of species dynamics and faunal development, yielding new results on species origins, dynamics of species at the population level, morphology, and even behavior of species.

The Pleistocene and Holocene history of mammals in Europe in light of modern research increasingly suggests individualistic dynamics of

species in response to the climatic and environmental change at the end of the Pleistocene or the Pleistocene/Holocene shift.

Without doubt, the Last Glacial Maximum with its impact on phylogeography and as a driver of speciation processes shaped the roots of our extant European fauna. Apart from the Last Glacial Maximum and the beginning of the Holocene, the Greenland Interstadial 1 (Bølling/Allerød warming) was the most important climatic event for the timing of the faunal shifts about 10,000 years after the culmination point of the Last Glacial Maximum. Fundamental changes in the faunal history of extant temperate European mammal species and basic features of the extant distribution patterns of these species (like the colonization of Central European regions north of the Alps from glacial refugia) took place during the Bølling/Allerød warming. The intensive and detailed analysis of subfossil records of mammals, mainly from archaeological and palaeontological sites, indicates that only few species like hedgehogs, otter, or the forest-dependent edible dormouse are “real” Holocene colonizers. The majority of species, for example, most of the carnivorans and ungulates, recolonized important Central European regions already during the Greenland Interstadial 1 (Fig. 2), about 2000 years before the start of the Holocene. Thus, the impact of this climatic event, which caused the local extinction of the mammoth in Western Europe, the recolonization of Central Europe by temperate species and the global extinction of the cave lion and the woolly rhino during the Late Glacial, warrants further research efforts in Quaternary zoogeography and palaeoecology. Together with the dynamics of vegetation and Stone Age humans this will yield a much more detailed picture of the multifaceted connections and interactions of mammals, climate, landscape change, and humans in the past.

The striking combination of the spatiotemporal distribution pattern on the basis of subfossil records (at species level) and information from ancient DNA (at population or species level) has led, and is still leading, to a much better understanding of European biogeography, and it may also be key to

our understanding of how the reconstruction of past biogeography might inform us on future developments in the face of global change.

Acknowledgments I am grateful to Frank Zachos for helpful suggestions and comments on an earlier version of the text.

References

- Aaris-Sørensen K (2009) Diversity and dynamics of the mammalian fauna in Denmark throughout the last glacial–interglacial cycle, 115–0 kyr BP. *Fossils Strata* 57:1–59
- Baker KH, Gray HWI, Ramovs V, Mertzaniidou D, Akın Pekşen Ç, Bilgin CC, Sykes N, Hoelzel AR (2017) Strong population structure in a species manipulated by humans since the Neolithic: the European fallow deer (*Dama dama dama*). *Heredity* 119:16–26
- Barron E, van Andel TH, Pollard D (2003) Glacial environments II. Reconstructing the climate of Europe in the last glaciation. In: van Andel TH, Davies W (eds) Neanderthals and modern humans in the European landscape during the last glaciation: archaeological results of the Stage 3 Project. McDonald Institute Monographs, Cambridge
- Benecke N (1999) Die Jungpleistozäne und holozäne Tierwelt Mecklenburg-Vorpommerns – Faunenhistorische und kulturgeschichtliche Befunde. *Documenta Naturae* 124:1–198
- Benecke N (2004) Faunal succession in the lowlands of northern Central Europe at the Pleistocene–Holocene transition. In: Terberger T, Eriksen BV (eds) Hunters in a changing world. Environment and archaeology of the Pleistocene–Holocene transition (ca. 11,000–9000 BC) in northern Central Europe. Marie Leidorf Publisher, Rahden
- Benecke N (2005) The Holocene distribution of European bison: the archaeozoological record. *Munibe* 57:421–428
- Björck S, Walker MJC, Cwynar LC, Johnsen S, Knudsen K-L, Lowe JJ, Wohlfarth B (1998) An event stratigraphy for the Last Termination in the North Atlantic region based on the Greenland ice core record: a proposal by the INTIMATE group. *J Quat Sci* 13:283–292
- Blockley SPE, Lane CS, Hardiman M, Rasmussen SO, Seierstad IK, Steffensen JP, Svensson A, Lotter AF, Turney C, Ramsey C, INTIMATE Members (2012) Synchronisation of palaeoenvironmental records over the last 60,000 years, and an extended INTIMATE event stratigraphy to 48,000 b2k. *Quat Sci Rev* 36:2–10
- Chang D, Knapp M, Enk J, Lippold S, Kircher M, Lister A, MacPhee RDE, Widga C, Czechowski P, Sommer RS, Hodges E, Stümpel N, Barnes I, Dalén L, Derevianko A, Germonpré M, Hillebrand-Voiculescu A, Constantin S, Kuznetsova T, Mol D, Rathgeber T, Rosendahl W,

- Tikhonov AN, Willerslev E, Hannon G, Lalueza-Fox C, Joger U, Poinar H, Hofreiter M, Shapiro B (2017) The evolutionary and phylogeographic history of woolly mammoths: a comprehensive mitogenomic analysis. *Sci Rep* 7:44585
- Cooper A, Turney C, Hugueny KA, Brook BW, McDonald HG, Bradshaw CJA (2015) Abrupt warming events drove Late Pleistocene Holarctic megafaunal turnover. *Science* 349:602–606
- Crees JJ (2013) Dynamics of large mammal range shifts and extinction: evidence from the Holocene of Europe. PhD thesis, Imperial College London and Institute of Zoology, ZSL
- Crees JJ, Carbon C, Sommer RS, Benecke N, Turvey S (2016) Millennial-scale faunal record reveals differential resilience of European large mammals to human impacts across the Holocene. *Proc R Soc B* 283:1–9
- Dansgaard W, Johnsen SJ, Clausen HB, Dahl-Jensen D, Gundestrup NS, Hammer CU, Hvidberg CS, Steffensen JP, Sveinbjörnsdóttir AE, Jouzel J, Bond G (1993) Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature* 364:218–220
- Davis BAS, Brewer S, Stevenson AC, Guiot J (2003) The temperature of Europe during the Holocene reconstructed from pollen data. *Quat Sci Rev* 22:1701–1716
- Fahlke JM (2009) Der Austausch der terrestrischen Säugetierfauna an der Pleistozän/Holozän-Grenze in Mitteleuropa. Unpublished PhD thesis, University of Bonn, pp 279
- Fortes GG, Grandal-d'Anglade A, Kolbe B, Fernandes D, Meleg IN, GarciaVazquez A, Pinto-Llona AC, Constantin S, de Torres TJ, Ortiz JE, Frischauf C, Rabeder G, Hofreiter M, Barlow A (2016) Ancient DNA reveals differences in behaviour and sociality between brown bears and extinct cave bears. *Mol Ecol* 25:4907–4918
- Gramsch B, Beran J, Hanik S, Sommer RS (2013) A Palaeolithic fishhook made of ivory and the earliest fishhook tradition in Europe. *J Archaeol Sci* 40:2458–2463
- Hewitt GM (2000) The genetic legacy of the Quaternary ice ages. *Nature* 405:907–913
- Honnen A-C, Petersen B, Kaßler L, Elmeros M, Roos A, Sommer RS, Zachos FE (2011) Genetic structure of Eurasian otter (*Lutra lutra*, Carnivora: Mustelidae) populations from the western Baltic Sea region and its implications for the recolonisation of Northwestern Germany. *J Zool Syst Evol Res* 48:169–175
- Hubberten HW, Andreu A, Astakhov VI, Demikov I, Dowdeswell JA, Henriksen M, Hjort C, Houmark-Nielsen M, Jakobsson M, Kuzmina S, Larsen E, Lunkka JP, Lysa A, Mangerud J, Moller P, Saarnisto M, Schirmermeister L, Sher AV, Siegert C, Siegert MJ, Huijzer B, Vandenberghe J (1998) Climatic reconstruction of the Weichselian Pleniglacial in Northwestern and Central Europe. *J Quat Sci* 13:391–417
- Huntley B, Allen JRM (2003) Glacial environments III: palaeo-vegetation patterns in Late Glacial Europe. In: van Andel TH, Davies W (eds) Neanderthals and modern humans in the European landscape during the last glaciation: archaeological results of the Stage 3 Project. McDonald Institute Monographs, Cambridge
- Huntley B, Alfano MJ, Allen JRM, Pollard D, Tzedakis PC, de Beaulieu JL, Grüger E, Watts B (2003) European vegetation during Marine Oxygen Isotope Stage-3. *Quat Res* 59:159–212
- Hürner H, Krystufek B, Sara M, Ribas A, Ruch T, Sommer RS, Ivashkina V, Michaux J (2010) Mitochondrial phylogeography of the edible dormouse (*Glis glis*) in the western Palearctic region. *J Mammal* 91:233–242
- Jürgensen J, Drucker DG, Stuart AJ, Schneider M, Buuveibaatar B, Bocherens H (2017) Diet and habitat of the saiga antelope during the late Quaternary using stable carbon and nitrogen isotope ratios. *Quat Sci Rev* 160:150–161
- Kahlke RD (2014) The origin of Eurasian mammoth faunas (Mammuthus–Coelodonta Faunal Complex). *Quat Sci Rev* 96:32–49
- Kahlke RD (2015) The maximum geographic extension of Late Pleistocene *Mammuthus primigenius* (Proboscidea, Mammalia) and its limiting factors. *Quat Int* 379:147–154
- Knapp M, Rohland N, Weinstock J, Baryshnikov G, Sher A, Nagel D, Rabeder G, Pinhasi R, Schmidt HA, Hofreiter M (2009) First DNA sequences from Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. *Mol Ecol* 18:1225–1238
- Kotlík P, Deffontaine V, Mascheretti S, Zima J, Michaux JR, Searle JB (2006) A northern glacial refugium for bank voles (*Clethrionomys glareolus*). *Proc Natl Acad Sci U S A* 103:14860–14864
- Kuëmmerle T, Hickler T, Olofsson J, Schurgers G, Radeloff VC (2012) Reconstructing range dynamics and range fragmentation of European bison for the last 8000 years. *Divers Distrib* 18:47–59
- Lambeck K, Esat MT, Potter E-K (2002) Links between climate and sea levels for the past three million years. *Nature* 419:199–206
- Lampe R, Jahnke W, Schuldt M, Meng S, Lampe M (2016) Multiproxy-Untersuchungen zur Paläoökologie und -hydrologie in spätglazial- bis frühholozänen Flachsees im nordostdeutschen Küstengebiet (Glowe-Paläosee/Insel Rügen). *E&G Quat Sci J* 65:41–75
- Leonardi M, Boschin F, Giampoudakis K, Beyer RM, Krapp M, Bendrey R, Sommer RS, Boscato P, Manica A, Noguez-Bravo D, Orlando L (2018) Late Quaternary horses in Eurasia in the face of climate and vegetation change. *Sci Adv* 4:1–11
- Lister AM, Sher AV (2015) Evolution and dispersal of mammoths across the Northern Hemisphere. *Sci* 350 (6262):805–809
- Litt T, Brauer A, Goslar T, Merkt J, Balaga K, Müller H, Ralska-Jasiewiczowa M, Stebich M, Negendank JFW (2001) Correlation and synchronisation of Lateglacial continental sequences in northern Central Europe based on annually laminated lacustrine sediments. *Quat Sci Rev* 20:1233–1249

- Litt T, Schminke HU, Kromer B (2003) Environmental response to climatic and volcanic events in Central Europe during the Weichselian Lateglacial. *Quat Sci Rev* 22:7–32
- Lorenzen ED, Noguès-Bravo D, Orlando L, Weinstock J, Binladen J, Marske KA, Haile J, Borregaard MK, Ugan A, Yoccoz NG, Coissac E, Gussarova G, Brochmann C, Taberlet P, Gilbert MTP, Nielsen R, Ho SYW, Goebel T, Graf KE, Byers D, Stenderup JT, Rasmussen M, Campos P, Leonard J, Koepfli K-P, Froese D, Zazula G, Stafford T, Higham T, Munch K, Aaris-Sørensen K, Baryshnikov G, Batra P, Burns JA, Conard N, Davydov SP, van Geel B, Gravendeel B, Hockett B, Jenkins D, Kosintsev P, Kuznetsova T, Xulong L, Martin L, Mol D, Meldgaard M, Stephan E, Sablin M, Sommer RS, Sipko T, Scott E, Tikhonov A, Telka A, Willerslev R, Wayne RK, Cooper A, Hofreiter M, Sher A, Shapiro B, Rahbek C, Willerslev E (2011) Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature* 479:359–364
- Masseti M (1996) The postglacial diffusion of the genus *Dama* Frisch, 1775, in the Mediterranean region. *Suppl Ric Biol Selvaggina* 25:7–29
- Masseti M (1999) The fallow deer, *Dama dama* L., 1758, in the Aegean region. *Contrib Zoogeogr Ecol East Mediterr Reg* 1(Suppl):17–30
- Masseti M, Mazza PPA (2013) Western European Quaternary lions: new working hypotheses. *Biol J Linn Soc* 109:66–77
- McDevitt AD, Zub K, Kawalko A, Oliver MK, Herman JS, Wójcik JM (2012) Climate and refugial origin influence the mitochondrial lineage distribution of weasels (*Mustela nivalis*) in a phylogeographic suture zone. *Biol J Linn Soc* 106:57–69
- Mucci N, Arrendal J, Ansoerge H, Bailey M, Bodner M, Delibes M, Ferrando A, Fournier P, Fournier C, Godoy J, Hajkova P, Hauer S, Heggberget TM, Heidecke D, Kirjavainen H, Krueger H-H, Kvaloy K, Lafontaine L, Lanszki J, Lemarchand C, Liukko U-M, Loeschke V, Ludwig G, Madsen AB, Mercier L, Ozolins J, Paunovic M, Pertoldi C, Piriz A, Prigioni C, Santos-Reis M, Luis TS, Stjernberg T, Schmid H, Suchentrunk F, Teubner J, Tornberg R, Zinke O, Randi E (2010) Genetic diversity and landscape genetic structure of otter (*Lutra lutra*) populations in Europe. *Conserv Genet* 11:583–599
- Münzel SC, Stiller M, Hofreiter M, Mittnik A, Conard NJ, Bocherens H (2011) Pleistocene bears in the Swabian Jura (Germany): genetic replacement, ecological displacement, extinctions and survival. *Quat Int* 245:225–237
- Musil R (2003) The middle and upper Palaeolithic game suite in Central and Southeastern Europe. In: van Andel TH, Davies W (eds) Neanderthals and modern humans in the European landscape during the Last Glaciation: archaeological results of the Stage 3 Project. McDonald Institute Monographs, Cambridge
- Nadachowski A, Lipecki G, Ratajczak U, Stefaniak K, Wojtal P (2016) Dispersal events of the saiga antelope (*Saiga tatarica*) in Central Europe in response to the climatic fluctuations in MIS 2 and the early part of MIS 1. *Quat Int* 420:357–362
- Ninov LK (1999) Vergleichende Untersuchungen zur Jagd und zum Jagdwild während des Neolithikums und Äneolithikums in Bulgarien. *Archäologie in Eurasien* 6:323–338
- Pacher M, Stuart AJ (2009) Extinction chronology and palaeobiology of the cave bear (*Ursus spelaeus*). *Boreas* 38:189–206
- Palkopoulou E, Dalen L, Lister AM, Vartanyan S, Sablin M, Sher A, Nyström Edmark V, Brandström MD, Germonpre M, Barnes I, Thomas JA (2013) Holarctic genetic structure and range dynamics in the woolly mammoth. *Proc R Soc B* 280:20131910
- Pilot M, Branicki W, Jędrzejewski W, Goszczyński J, Jędrzejewska B, Dykyy I, Shkvyrya M, Tsingarska E (2010) Phylogeographic history of grey wolves in Europe. *BMC Evol Biol* 10:104
- Prost S, Smirnov N, Federov VB, Sommer RS, Stiller M, Nagel D, Knapp M, Hofreiter M (2010a) Influence of climate warming on Arctic mammals? New insights from ancient DNA studies of the collared lemming *Dicrostonyx torquatus*. *PLoS One* 5:1–11
- Prost S, Knapp M, Flemming J, Hufthammer AK, Kosintsev P, Stiller M, Hofreiter M (2010b) A phantom extinction? New insights into extinction dynamics of the Don-hare *Lepus tanaiticus*. *J Evol Biol* 23:2022–2029
- Prost S, Klietmann J, van Kolfschoten T, Vrieling K, Stiller M, Nagel D, Rabeder G, Guralnick R, Waltari E, Hofreiter M, Sommer RS (2013) Effects of Late Quaternary climate change on Palearctic shrews. *Glob Chang Biol* 19:1865–1874
- Renssen H, Seppä H, Heiri O, Roche DM, Goosse H, Fichtfet T (2009) The spatial and temporal complexity of the Holocene thermal maximum. *Nat Geosci* 2:411–414
- Rodríguez-Varela R, Tagliacozzo A, Ureña I, García N, Crégut-Bonnouere E, Mannino MA, Arsuaga JL, Valdiosera C (2015) Ancient DNA evidence of Iberian lynx palaeoendemism. *Quat Sci Rev* 112:172–180
- Rohland N, Pollack JL, Nagel D, Beauval C, Airvaux J, Pääbo S, Hofreiter M (2005) The population history of extant and extinct hyenas. *Mol Biol Evol* 22:2435–2443
- Sandoval-Castellanos E, Wutke S, Gonzalez-Salazar C, Ludwig A (2017) Coat colour adaptation of post-glacial horses to increasing forest vegetation. *Nat Ecol Evol* 1:1816–1819
- Schmölcke U, Zachos FE (2005) Holocene distribution and extinction of the moose (*Alces alces*, Cervidae) in Central Europe. *Mamm Biol* 70:329–344
- Sommer RS (2007) When east met west: the sub-fossil footprints of the west European hedgehog and the northern white-breasted hedgehog during the Late Quaternary in Europe. *J Zool* 271:82–89
- Sommer RS, Benecke N (2004) Late- and post-glacial history of the Mustelidae in Europe (Mustelidae). *Mammal Rev* 34:249–284

- Sommer RS, Benecke N (2005a) The recolonisation of Europe by brown bears *Ursus arctos* Linnaeus, 1758 after the Last Glacial Maximum. *Mammal Rev* 35:156–164
- Sommer RS, Benecke N (2005b) Late-Pleistocene and early Holocene history of the canid fauna of Europe (Canidae). *Mamm Biol* 70:227–241
- Sommer RS, Benecke N (2006) Late-glacial and early Holocene colonisation history of felids in Europe (Felidae): a review. *J Zool* 269:7–20
- Sommer RS, Nadachowski A (2006) Glacial refugia of mammals in Europe: evidence from fossil records. *Mammal Rev* 36:251–266
- Sommer RS, Zachos FE (2009) Fossil evidence and phylogeography of temperate species: “glacial refugia” and postglacial recolonization. *J Biogeogr* 36:2013–2020
- Sommer RS, Zachos FE, Street M, Jöris O, Skog A, Benecke N (2008) Late Quaternary distribution dynamics and phylogeography of the red deer (*Cervus elaphus*) in Europe. *Quat Sci Rev* 27:714–733
- Sommer RS, Fahlke J, Schmölcke U, Benecke N, Zachos FE (2009) Quaternary history of the European roe deer (*Capreolus capreolus*). *Mammal Rev* 38:1–16
- Sommer RS, Benecke N, Lougas L, Nelle O, Schmölcke U (2011) Holocene colonization pattern of the wild horse (*Equus ferus*) in Europe: a matter of landscape openness? *J Quat Sci* 26:805–812
- Sommer RS, Kalbe J, Ekström J, Benecke N, Liljegren R (2014) Range dynamics of the reindeer in Europe during the last 25,000 years. *J Biogeogr* 41:298–306
- Sommer RS, Hegge C, Schmölcke U (2018) Lack of support for adaptation of post-glacial horses to woodlands in the Central European Lowlands. *Nat Ecol Evol* 2:582–583
- Soubrier J, Gower G, Chen K, Richards SM, Llamas B, Mitchell KJ, Ho SYW, Kosintsev P, Lee MSY, Baryshnikov G, Bollongino R, Bover P, Burger J, Chivall D, Crégut-Bonnoure E, Decker JE, Doronichev VB, Douka K, Fordham DA, Fontana F, Fritz C, Glimmerveen J, Golovanova LV, Groves C, Guerreschi A, Haak W, Higham T, Hofman-Kamińska E, Immel A, Julien MA, Krause J, Krotova O, Langbein F, Larson G, Rohrlach A, Scheu A, Schnabel RD, Taylor JF, Tokarska M, Tosello G, van der Plicht J, van Loenen A, Vigne J-D, Wooley O, Orlando L, Kowalczyk R, Shapiro B, Cooper A (2016) Early cave art and ancient DNA record the origin of European bison. *Nat Commun* 7:1–7
- Stewart JR, Cooper A (2008) Ice Age refugia and Quaternary extinctions: an issue of Quaternary evolutionary palaeoecology. *Quat Sci Rev* 27:2443–2448
- Street M, Baales M (1999) Pleistocene/Holocene changes in the Rhineland fauna in a northwest European context. *Archäologie in Eurasien* 6:9–38
- Stuart AJ (2015) Late Quaternary megafaunal extinctions on the continents: a short review. *Geol J* 50:338–363
- Stuart AJ, Lister AM (2011) Extinction chronology of the cave lion *Panthera spelaea*. *Quat Sci Rev* 30:2329–2340
- Stuart AJ, Lister AM (2012) Extinction chronology of the woolly rhinoceros *Coelodonta antiquitatis* in the context of Late Quaternary megafaunal extinctions in Northern Eurasia. *Quat Sci Rev* 51:1–17
- Stuart AJ, Lister AM (2014) New radiocarbon evidence on the extirpation of the spotted hyaena (*Crocuta crocuta* (Erxl.)) in northern Eurasia. *Quat Sci Rev* 96:108–116
- Stuart AJ, Kosintsev PA, Higham TFG, Lister AM (2004) Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth. *Nature* 431:684–689
- Theuerkauf M, Joosten H (2012) Younger Dryas cold stage vegetation patterns of Central Europe – climate, soil and relief controls. *Boreas* 41:391–407
- von Koenigswald W (1974) Die pleistozäne Fauna der Weinberghöhlen bei Mauern. In: von Koenigswald W, Müller-Beck H, Pressmar E (eds) *Archäologie und Paläontologie in den Weinberghöhlen von Mauern (Bayern) Grabungen. Selbstverlag für Urgeschichte, Tübingen*, pp 1937–1967
- von Koenigswald W (1977) Die Säugetierfauna aus der Burghöhle Dietfurt. *Kölner Jahrbuch für Vor- und Frühgeschichte* 15:123–142
- von Koenigswald W (1984a) Die jungpleistozäne Säugetierfauna der Spitzbubenhöhle. In: Hahn J (ed) *Die steinzeitliche Besiedlung des Eselsburger Tales bei Heidenheim. Landesdenkmalamt Baden-Württemberg. Konrad Theiss Verlag, Stuttgart*
- von Koenigswald W (1984b) Die Säugetiere der steinzeitlichen Station Malerfels I. In: Hahn J (ed) *Die steinzeitliche Besiedlung des Eselsburger Tales bei Heidenheim. Landesdenkmalamt Baden-Württemberg. Konrad Theiss Verlag, Stuttgart*
- von Koenigswald W (2002) *Lebendige Eiszeit. Klima und Tierwelt im Wandel*. Theiss Verlag, Darmstadt
- Weninger B, Jöris O, Danzglocke U (2008) CalPal 2007. Cologne radiocarbon calibration and palaeoclimate research package. <http://www.calpal.de>
- Wohlfarth B, Veres D, Ampel L, Lacourse T, Blauw M, Preusser F, Andrieu-Ponel V, Keravis D, Lallier-Verges E, Björck S, Davies S, de Beaulieu JL, Risberg J, Hormes A, Kasper HU, Possnert G, Reille M, Thouveny N, Zander A (2008) Rapid ecosystem response to abrupt climate changes during the last glacial period in Western Europe, 40–16 kyr BP. *Geology* 36:407–410
- Yalden DW (1999) *The history of British mammals*. T. and A. D. Poyser, London
- Yannouli E, Trantalidou K (1999) The fallow deer (*Dama dama* Linnaeus, 1758): archaeological presence and representation in Greece. *Archäologie in Eurasien* 6:247–281