RESEARCH ARTICLE

Megafauna diversity and functional declines in Europe from the Last Interglacial to the present

Marco Davoli[1,2] 🅾 | Sophie Monsarrat[1] 🅾 | Rasmus Østergaard Pedersen[1] 🅾 |
Paolo Scussolini[3] 🅾 | Dirk Nikolaus Karger[4] 🅾 | Signe Normand[1] 🅾 |
Jens-Christian Svenning[1] 🅾

[1]Center for Ecological Dynamics in a Novel Biosphere (ECONOVO) & Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Biology, Aarhus University, Aarhus C, Denmark

[2]Department of Biology and Biotechnologies "Charles Darwin", Sapienza University of Rome, Rome, Italy

[3]Institute for Environmental Studies, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

[4]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

Correspondence
Marco Davoli, Center for Ecological Dynamics in a Novel Biosphere (ECONOVO) & Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Biology, Aarhus University, Aarhus C 8000, Denmark.
Email: marco.davoli@hotmail.com

Abstract

Aim: Reconstructing megafauna diversity in the past before anthropogenic impacts is crucial for developing targeted restoration strategies. We estimated the diversity and functional decline of European megafauna in the present compared with the nearest in-time climate period analogue to the present but prior to the worldwide diffusion of Homo sapiens.

Location: Europe.

Time Period: Last Interglacial (LIG; ca. 127,000 years ago) to present.

Major Taxa Studied: Wild, large (≥10 kg) terrestrial mammals.

Methods: We assessed the distribution of 48 European megafauna species during the LIG using hindcasting modelling and fossil records. Then, we estimated the decline in megafauna community diversity and potential trait-based functional effects from the LIG to the present, accounting for climate differences between the two periods.

Results: Species richness and community biomass dropped by 70.8% (±11.7%) and by 94.5% (±9.9%). Functional diversity dropped by 80.3% (±15.3%) for herbivores and by 64.9% (±29.1%) for carnivores, while trait-informed potential vegetation and meat consumptions dropped by 82.3% (±13.4%) and 60.5% (±26.0%). The loss in megafauna diversity and associated ecological processes were high everywhere, but particularly in western Europe for carnivores and in the East European Plain for herbivores. Potential megafauna richness in the two periods was similar if only climate-driven differences were considered.

Main Conclusions: Severe, size-biased defaunation has degraded megafauna assemblages and megafauna-mediated ecological processes across Europe from the LIG to the present. These patterns cannot be explained by climate differences between the two periods, thus were likely driven by prehistoric Homo sapiens. The results suggest that the structure of wild ecosystems of the present strongly deviates from the evolutionary norm, with decreased functional heterogeneity and decreased fluxes of biogeochemical compounds across the trophic networks, highlighting the importance of ambitious policies of megafauna community restoration to support ecosystem functioning.

1 | INTRODUCTION

Megafauna are disproportionally important for the functioning of biological communities due to a broad range of effects linked to their large body size (Malhi et al., 2016; Enquist et al., 2020). They influence vegetation structure and dynamics (Bakker et al., 2016; Pringle et al., 2016), plant migration (Fricke, Ordonez, et al., 2022), species diversity (Ratajczak et al., 2022), fire regime (Karp et al., 2021), nutrient fluxes (Doughty et al., 2016) and long-term carbon storage (Kristensen et al., 2021). Functionally diverse megafauna communities were once prevalent globally, yet they have been severely downgraded due to worldwide extinctions in the late Quaternary (Smith et al., 2019). Although different causes of these extinctions have been long debated (Koch & Barnosky, 2006), a broad range of evidences increasingly attest a prominent role of the impact of *Homo sapiens* spreading out of Africa (Andermann et al., 2020; Sandom, Faurby, et al., 2014; Smith et al., 2019). As a result of these extinctions, megafauna worldwide are strongly diminished in numbers, with smaller species remaining, and overall simplified communities relative to the norm of the last millions of years (Smith et al., 2018).

While the macroscale patterns of the late Quaternary megafauna losses are increasingly clear, the pre-extinction megafauna distributions and the drop in the presence of associated ecological effects are still incompletely understood. A range of studies provide insights about megafauna role on past ecosystem structure and functioning at local scales, for example, large-herbivore heterogeneity and vegetation structure in Britain (Sandom, Ejrnaes, et al., 2014), or large-herbivore abundance, fire regime and vegetation composition in northern Australia (Rule et al., 2012). A global-scale study suggests a general rise in fire activity subsequent to megafauna declines (Karp et al., 2021). However, the literature remains limited, in large part because the palaeoecological record itself inherently is scattered. A more detailed, but comprehensive understanding would provide important baseline information for conservation, restoration and rewilding efforts worldwide (cf., e.g., Svenning et al., 2016; Fløjgaard et al., 2021). Here, a macroecological modelling approach has much to offer. It can help to reconstruct the distribution of different aspects of megafauna assemblage structure (Faurby & Svenning, 2015) and, by comparing such estimates with the present faunas, allows estimating changes in features relevant to ecosystem functioning, for example, plant migration rates (Fricke, Ordonez, et al., 2022) and trophic network structure (Fricke, Hsieh, et al., 2022). In addition, reconstructions of past distribution of megafauna help forecasting future scenarios of species range shifts in the face of predicted environmental changes and restoration interventions, notably by overcoming anthropogenic truncation of climate niches (Jarvie & Svenning, 2018; Sales et al., 2022). While spatial-explicit maps of distributions of both extant and late Quaternary extinct mammal species with such applications in mind exist (Faurby et al., 2020), these maps are limited to relatively coarse resolutions and specific, limited time frames, in large part due to limitations of the fossil record.

To overcome these limitations, we here provide detailed estimates of megafauna species ranges for the Last Interglacial (LIG;

129,000–120,000 years ago) in Europe, supported by the region's extensive literature on megafauna fossils. The LIG is a period of the Pleistocene with climate relatively similar to the present yet preceding the arrival of *Homo sapiens* in Europe. Hence, it is of interest as a natural baseline for better understanding and managing European nature (Svenning, 2002). The LIG European megafauna community shows continuity with that of previous Pleistocene interglacials, with successful recovery of the same or analogue regional communities following the preceding glacial climate cycles (Nenzén et al., 2014; Schreve, 2019). While *Homo neanderthalensis* was widespread in Europe during the LIG, and possibly had local, short-term effects on megafauna abundance (Dembitzer et al., 2022; Rosell et al., 2017), no selective megafauna extinction occurred globally or in Europe prior to the arrival of *Homo sapiens* (Smith et al., 2019). Since temperatures were just slightly warmer than at present in the Northern Hemisphere (Otto-Bliesner et al., 2021), the period has been indicated as the closest in time ecological analogue for the present and near-future Europe, but with an intact megafauna diversity and no widespread human-caused habitat transformations (Svenning, 2002).

Here, we developed detailed estimates of LIG megafauna species (wild terrestrial mammals ≥10 kg) distribution in Europe using a hindcasting species distribution modelling approach postinformed by fossil records (Svenning et al., 2011), to provide a first spatially explicit quantification of the megafauna losses in species richness, community biomass (assemblage body mass sum) and functional diversity relative to the present. Furthermore, based on trait-informed species-specific estimations, we tested the hypothesis that megafauna losses from the LIG to the present have dramatically reduced the magnitude of potential vegetation and meat consumptions by herbivores (cf. Pedersen et al., 2023) and carnivores in the European context, likely with strong effects on ecosystem structure and functioning in the absence of other human impacts. As the LIG and the present are not climatically identical, we furthermore used a modelling approach to test whether these climatic differences have had a substantial impact on the average levels and patterns of megafauna species richness.

2 | MATERIALS AND METHODS

The study area comprises the European mainland west to the Urals (mountains and river), including the Caucasus and Asia Minor (Figure S1). The European mainland geography, particularly coastlines, was considered comparable between the LIG and the present at the resolution of the work due to a relatively similar sea level (just 5–10 metres above today's; Dyer et al., 2021).

2.1 | Megafauna distribution data

We retrieved the "present-natural" range of every megafauna (wild terrestrial mammals ≥10 kg) occurring in Europe during the LIG from PHYLACINE v1.2.1 (Faurby et al., 2020; Supporting information Appendix 1 for species selection criteria; Table S1 for the list of

species considered at any point in the study). Present-natural ranges are estimates of current-day mammal species distributions, as they would be if *Homo sapiens* disturbance had never occurred. These estimations have been produced globally for all late Quaternary mammal species at a resolution of 96.5-km grid cell by applying a combination of range adjustments on IUCN historical range maps of still-existing mammals, considering evidence of human-caused extinctions in the late Pleistocene and early to mid-Holocene from literature and co-occurrence modelling for extinct species (Faurby et al., 2020; Faurby & Svenning, 2015).

We collated a record listing latitude, longitude and name of the excavation site of LIG fossils in Europe (Figure S1; Tables S3 and S5) for 38 megafauna species, performing a literature review of studies describing stratigraphic layers associated with the "Eemian optimum" (see Section 2.3 for more details). However, we also included few records collated by two studies from eastern Europe, which considered a wider temporal span for the LIG due to the scarcity of fossils for this region reported in the English-language literature. The review was conducted with Google Scholar using the keywords "Eemian", "Last Interglacial", "LIG", "MIS 5e", "Ipswichian" and "Mikulino", in combination with the words "fossil(s)", "record(s)", "stratigraphic layer(s)", "(mega)fauna" and "mammals". Each fossil record's description was carefully evaluated in reliability, cross-checking between references if possible. Moreover, we only included records with geographic coordinates or site's name available in the referred literature.

We collected the present range for all extant European wild megafauna species (Supporting information Appendix 1 for species selection criteria; Table S1 for the list of 57 species considered at any point in the study) from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (www.iucn.org; accessed June 2021). We added the species Barbary sheep (*Ammotragus lervia*), sika deer (*Cervus nippon*), Chinese water deer (*Hydropotes inermis*) and white-tailed deer (*Odocoileus virginianus*) gathered from Linnell et al. (2020), since the European ranges of these introduced species were not reported by the IUCN.

2.2 | Megafauna functional traits and estimated population densities

First, we classified species as herbivores (Table S6) or carnivores (Table S7) based on the HerbiTraits (Lundgren et al., 2021) and the CarniDIET (Middleton et al., 2021) databases. From these databases, we also collected functional traits for each species, adding further information on carnivores by Dalerum (2013). Functional traits of cave lion (*Panthera spelaea*) were not available, but estimated from Sandom et al. (2018). We also collected average body mass and percentage of plants and meat in the diet for each species from PHYLACINE v1.2.1 (Faurby et al., 2020). We gathered data on average species population density as estimated in conditions of low human impact and "field metabolic rate" for each species from Pedersen et al. (2023). As explained in detail in the reference, species population density and field metabolic rate were estimated

for each species as a result of phylogenetically adjusted allometric models. Specifically, both traits were modelled as a function of body mass, with phylogeny serving as a random effect. All extant mammalian species for which empirical data were available were considered for training the models. These included, for example, African species whose body size is comparable to that of extinct European species, and which belong to the same or closely related phylogenetic groups. We assumed that estimated population densities are not influenced by neglecting trophic interactions, such as herbivore populations that may have been suppressed by now-extinct predators, since empirical data were gathered mainly from studies in protected areas where rich megafauna communities still exist, for example, in sub-Saharan Africa. Furthermore, the species for which there is no empirical data to collect because they are globally extinct are particularly the larger species, such as megaherbivores, which are not top-down controlled by carnivores (Owen-Smith, 1988).

2.3 | Palaeoclimate of the LIG and climate of the present

For the LIG palaeoclimate, we calculated 12 bioclimatic variables based on climate variables obtained from a set of palaeoclimate simulations. These simulations targeted the maximum anomaly in Northern Hemisphere summer insolation, which reached 127,000 years ago, thought to be the driver of the warmest phases of the LIG in Europe (Otto-Bliesner et al., 2017). Simulations were performed with six climate models (Table S2), each forced according to the protocol for experiment *lig127k* of the Paleoclimate Modelling Intercomparison Project phase 4 (PMIP4; Otto-Bliesner et al., 2017; data provided in supporting information). We used the climatological mean of monthly values of the following climate variables: total precipitation, near-surface air temperature and minimum daily near-surface air temperature. We downscaled the climate variables to a resolution of 30-km grid cell. We corrected biases in the climate variables from the models. For this, we compared these variables between the historical simulation with the same climate models and the dataset CHELSA V2.1 (Karger et al., 2021), also aggregated at the resolution of 30-km grid cell, as both datasets represent the period 1981–2010. Based on this comparison, we applied a delta correction to the temperature results of the climate model, and a ratio correction to the precipitation results, similar to the procedure applied in, for example, Scussolini et al. (2020). With the bias-corrected variables, we calculated 12 bioclimatic variables (Table S2). LIG palaeoclimate is warmer than 20th-century average but similar to the early 21st-century average climate, thus providing a reasonable analogue for global warming thus far (Sánchez Goñi et al., 2012), although spatial and seasonal differences in temperature and precipitation were likely quite accentuated (Otto-Bliesner et al., 2021; Scussolini et al., 2019). For the present climate, we retrieved the same bioclimatic variables (Table S2) from CHELSA V2.1 (Karger et al., 2021) for the period 2010–2020.

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2.4 | Modelling European megafauna species distribution during the LIG

We estimated the distribution of the LIG European megafauna by joint inference of hindcasting species distribution modelling (SDM), fossil records and geographical constraints on species dispersal.

For the SDM, we generated pseudo-occurrences and pseudo-absences using the species' present-natural range. We chose this approach since, despite our extensive literature review, the collated fossil record was too scarce to provide reliable estimates of species' realized niche (Wisz et al., 2008). Present-natural ranges can serve as spatially explicit representations of the multispace environmental niche of a species in modern-like environmental conditions (Jarvie & Svenning, 2018). One pseudo-occurrence was generated per grid cell within the present-natural range at its original resolution (i.e., raster cell of 96.5-km grid cell at 30° latitude) as well without the present-natural range at the same resolution, limited to a surrounding range buffer with extension equal to one further grid cell. We deleted pseudo-occurrences above 2000 m following Berti and Svenning (2020), since this elevation represents a spatial constraint for most species that is not accounted for in present-natural ranges. For some species with a very small present-natural range, the number of pseudo-presences generated was too small to use in an SDM. For these, we merged their range with that of a closely related species with similar environmental preferences and treated them as one "species group" (e.g., grouping the Alpine and chamois *Rupicapra. rupicapra* and *Rupicapra. pyrenaica* in a *Rupicapra* spp. group). This concerns 17 species merged into eight groups (see Supporting information Appendix 2 for further details). To estimate the environmental niche for every species, we used the present climate predictors retrieved for the decade 2010–2020 (Table S2). We used four SDM algorithms to run the models: "Bioclim", "Boosted Regression Trees" (BRTs), "General Additive Models" (GAMs) and Maximum Entropy Modelling (MaxEnt). We run the models using the *package sdm v1.1–8* (Naimi & Araújo, 2016) in the software R v4.1.0 within an ensemble framework. For each algorithm, the modelling procedure was repeated three times assessing its performance through fivefold cross-validation via computing the area under the curve of receiver operating characteristics (AUC-ROC; see Supporting information Appendix 3 for further details). We used the AUC-ROC modelling performance of each single model to weigh its contribution to the ensemble prediction, and we computed the mean AUC-ROC as overall evaluation of modelling performance for each species.

The ensemble results for the species were projected both for the present climate and for LIG with a spatial resolution of 30-km grid cell (see Supporting information Appendix 3 for rationale). Amongst the available LIG palaeoclimate simulations (Table S2; Otto-Bliesner et al., 2021) we utilized the "GISS-E2-1-G" model since it accurately captures the extension of oceanic climate towards the east during the LIG period, as indicated by direct palaeobotanical proxies (Pearce et al., 2023). The projected predictions for both the present climate and LIG were then converted into binary (presence/absence) outputs (Supporting information Appendix 3 for details) to obtain the present-projected ranges and the LIG ranges, respectively. The quality of LIG range predictions was also externally evaluated through the fossil record of LIG megafauna (Table S5). In this case, we accounted for omission errors only since the probability of finding fossils reflects environmental conditions favouring fossilization rather than the species most likely distribution (Varela et al., 2011). Specifically, we (1) counted the proportion of fossils located inside the species-corresponding range before range clipping (see below), and we (2) systematically checked whether the model failed in predicting the correspondence of fossils and estimated species range across 10 European macro-regions that we defined to encompass the study area (Figure S1; Table S3). The modelling evaluation was performed for 37 species, those for which we both estimated the LIG distribution and retrieved fossil records.

The resulting SDM predictions are estimates of species' potential—rather than realized—distributions. To improve our estimate of the realized distribution of each species, we clipped the predicted ranges using information on the long-term geographical distribution of each species. Particularly, we compared the estimated LIG megafauna ranges to the late Quaternary megafauna geographic history reconstructed by various sources in literature, PHYLACINE v1.2.1 present-natural ranges, considerations over geographic barriers such as mountain ranges and sea, known competitive exclusion (in the case of Eurasian lynx *Lynx lynx* and Iberian lynx *Lynx pardinus*), and the gathered LIG fossil records. If geographic constraints were evident for a species, for example, its Pleistocene fossils were never found in a particular area separated from the species main range by geographic barriers, we trimmed the estimated range accordingly (Table S4 for details). Although palaeontologists may have missed evidence of species presence in areas outside the defined boundaries, we considered this procedure as fundamental to integrate our estimations of potential ranges at "high" resolution with available evidence of large-scale species endemicity, thus, to estimate species' true geographic distribution in the LIG. In addition, we accounted for topography as habitat constraint for some species adapted to steep terrain (Supporting information Appendix 3 for details).

2.5 | Quantifying the decline in species richness, community biomass and functional diversity from the LIG to the present

For both the LIG and the present, we counted the number of megafauna species occurring in each grid cell across the study area, quantifying species richness patterns. For the LIG, we used estimated ranges, while for the present we used ranges collected from the IUCN and Linnell et al. (2020; Section 2.4).

For both the LIG and the present, we estimated the biomass occurring per grid cell for each species independently by multiplying average species body size for species population density in "natural" conditions (Tables S6 and S7 for functional data). Importantly, population densities were assumed constant for the species across their estimated range following Pedersen et al. (2023). In our case, this was further necessary since quantitative estimates for the whole continent of Europe are missing for most species for the present and are not possible to estimate with any reliability for any species for the LIG given data scarcity. We then calculated community biomass patterns summing the biomass of all species in every grid cell across the study area, based on species richness distribution.

For both the LIG and the present, we calculated functional diversity (FD) using the functional traits within species assemblages in each grid cell across the study area based on the species richness distribution (Tables S6 and S7 for functional data). Considered FD traits and their relative importance (rel. imp.) in FD computation for herbivores, following Schowanek et al. (2021), were: (i) % of graminoids in diet (0.5 rel. imp.); (ii) % of fruits or other plant fractions in diet (0.5 rel. imp.); (iii) gut fermentation efficiency (1 rel. imp.); and (iv) body mass (2 rel. imp.). Considered functional traits and their rel. imp. for carnivores were: (i) hunting group size (2 rel. imp.); (ii) mean prey size (1 rel. imp.); (iii) maximum prey size (1 rel. imp.); (iv) body mass (2 rel. imp.); and (v) selectivity in diet (i.e., assessed spectrum of animal prey considering census by Middleton et al. (2021); 1 rel. imp.). FD was calculated as "functional richness" for herbivores and carnivores in a scale from 0.00 (relatively null traits diversity) to 1.00 (relatively full traits diversity). Calculated outputs were then spatially projected across the study area using the *package FD 1.0–12* (Laliberté et al., 2014) in R v4.1.0.

The patterns of megafauna richness, biomass and functional diversity were then compared between the LIG and the present by subtracting values of the present from values of the LIG for each grid cell across the study area.

2.6 | Quantifying the decline in contribution to biogeochemical fluxes (vegetation and meat consumptions) from the LIG to the present

To calculate potential vegetation consumption in $kgC \times km^{-2} yr^{-1}$ (PVC) for each herbivore species independently, we applied the formula in Pedersen et al. (2023) for each grid cell in the study area:

$$PVC = SEN \times \frac{CC}{ME}$$

where the species energy needs in $kJ \times km^{-2} yr^{-1}$ (SEN) is calculated for a period of 1 year by multiplying estimated species field metabolic rate with estimated population density and percentage of plants in the diet (data in Table S6; details on the equation in Pedersen et al., 2023). CC (carbon composition) in $kgC \times kgDM^{-1}$ is the percentage of carbon

contained in dry vegetation matter (DM; 45% on average; $SD = 5.23$; Ma et al., 2018), and ME in $kJ \times kgDM^{-1}$ is the metabolic energy available in the selected dry mass of the diet (see Pedersen et al., 2023 for further details).

To calculate potential annual meat consumption in $kg \times km^{-2} yr^{-1}$ (PMC) for each carnivore species independently, we used the equation:

$$PMC = WMC \times K \times P \times 365.25 \text{ days / year}$$

where wet meat consumption in $kg \times day^{-1}$ (WMC) is estimated in kilojoules as daily energy intake scaling with body mass, using the pairwise equation in Carbone et al. (2007), multiplied by percentage of meat in the diet (K) and estimated population density per square kilometre (P; data in Table S7), multiplied by the numbers of days per year. Daily energy intake was then transformed in kilograms (kg) of daily consumed wet meat by applying the caloric conversion for food types presented in SI of Carbone et al. (2007; 6682 kJ/kg for small vertebrate prey and 10,050 kJ for large vertebrate prey).

PVC and PMC values were summed, respectively, across all species per grid cell based on species richness distribution, in this case splitting herbivores and carnivores, and compared between the LIG and the present.

2.7 | Testing megafauna habitat shift due to difference in climate between the LIG and the present

We estimated to what extent the climate difference between the LIG and the present would shift European megafauna ranges, and thus, the distribution in species richness would differ in the two periods. We did this to test for the potential impact of climate patterns in two different interglacials on the average megafauna diversity in Europe. Low or absent climate difference would imply a primary role of *Homo sapiens* during the late Quaternary in creating the actual differences observed. With the SDM projections for the present climate converted to binary form (present-projected ranges, see Section 2.4), we recalculated the species richness pattern as described in Section 2.5. In this way, the two metrics of megafauna diversity were estimated for both the LIG and a potential present without human impact and were directly comparable, as they were derived from sets of species ranges obtained by the same modelling parameters, with differences only due to differences in climate between the two periods as extrapolated in the modelling projection. We tested for statistically significant difference in the patterns of species richness comparing (1) "LIG ranges" vs "present-day projected ranges" and (2) "LIG ranges" vs "present ranges". For these comparisons, we used the paired Student's *t*-test. Importantly, since the test does not distinguish the distribution of the *t*-test and the normal distribution with more than 30 samples (Kim, 2015), we randomly gathered from the recomputed maps of species richness values from the same 30 grid cells in the compared patterns, repeating the process at each *t*-test iteration.

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3 | RESULTS

3.1 | The distribution of European megafauna during the LIG

We gathered 364 fossil records for 38 species of European megafauna of the LIG for which we also estimated LIG distribution: the most represented species are red deer (*Cervus elaphus*; $n = 35$), Eurasian beaver (*Castor fiber*, $n = 27$), fallow deer (*Dama dama*; $n = 21$), straight-tusked elephant (*Palaeoloxodon. antiquus*; $n = 20$) and roe deer (*Capreolus capreolus*; $n = 19$; Figure S2; Tables S3 and S5). The evaluation of modelling performance to predict LIG megafauna distributions (Figure S2) showed an average AUC of 0.87 (±0.06 Standard Deviation; Table S5). Omission error evaluation on LIG predicted megafauna ranges using the fossil records (Table S5) showed that 18.7% ($n = 68$ on the total) of the fossils were predicted outside of the correspondent species range. The mean distance of these fossils from the closest point on the modelling estimated range perimeter was only 61.7 km (±78.4 km SD), however.

3.2 | Megafauna species richness, community biomass and FD from the LIG to the present

During the LIG, estimated mean megafauna species richness across Europe was 20.1 species per 30-km grid cell (95% interquartile Range: 14.1–26.1; Figure 1). In contrast, at present the mean species richness is only 5.6 species per grid cell (IQR: 2.6–9.6; Figure 1). Mean loss in species richness from the LIG to the present is estimated as 70.8% (±11.7% SD; Figure 1), with relevant differences amongst present-day countries (Figure S3).

During the LIG, estimated mean megafauna community biomass across Europe was 18.9 ton/km² (IQR: 6.3–31.4; Figure 1), with the
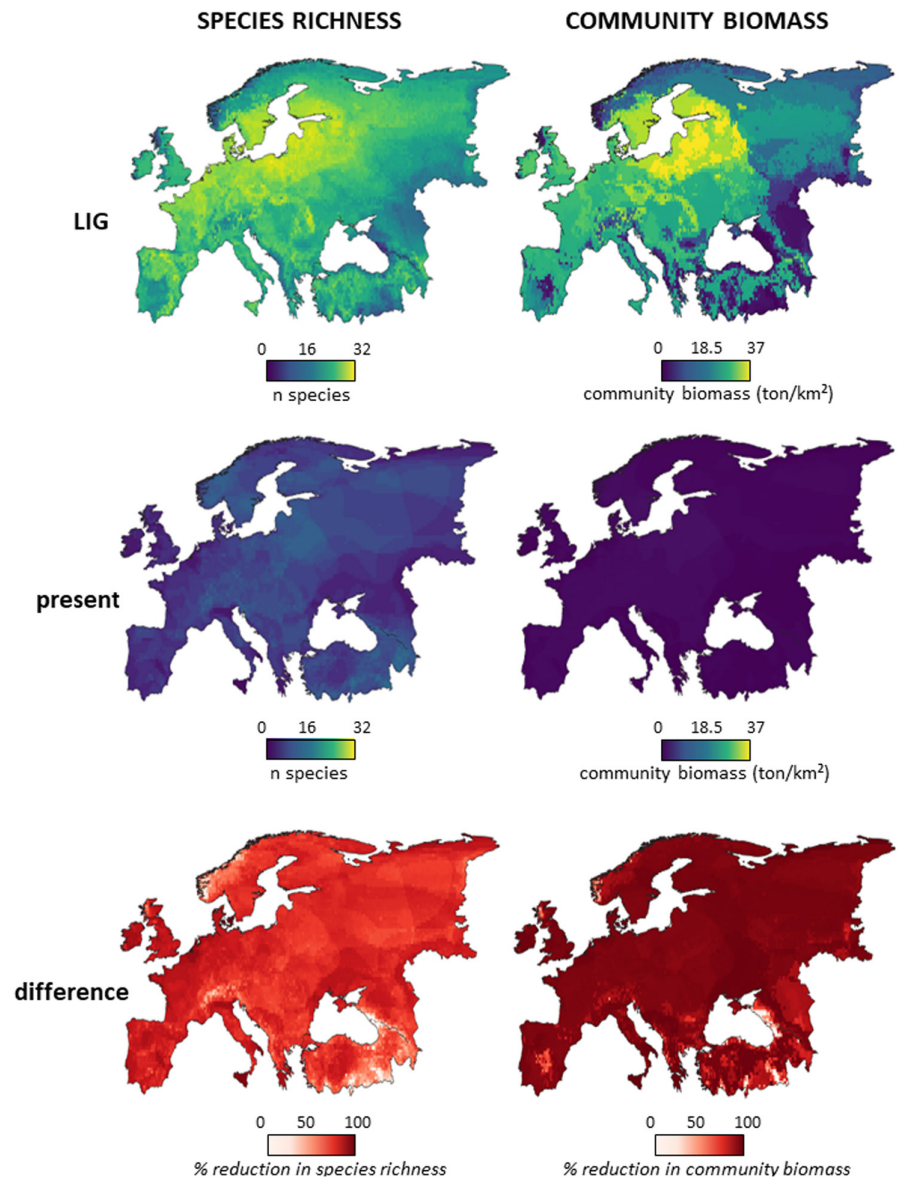

FIGURE 1 Comparison of megafauna species richness and community biomass between the LIG (cc. 127,000 years ago) and the present (decade 2010–2020).

TABLE 1 Summary of the megafauna biodiversity metrics calculated, with estimated results for the LIG and the present, and quantified loss between the two periods.

Megafauna biodiversity metric	LIG[a]	Present[a]	Loss
Species richness[b]	20.1 (14.1–26.1)	5.6 (2.6–9.6)	70.8%
Megafauna community biomass[c]	18.9 (6.3–31.4)	0.6 (0.1–1.0)	94.5%
Functional diversity (FD) herbivores[d]	0.71 (0.59–0.83)	0.15 (0.02–0.29)	80.3%
Functional diversity (FD) carnivores[d]	0.61 (0.22–0.99)	0.28 (0.22–0.34)	64.9%
Vegetation consumption[e]	26.7 (18.4–35.1)	4.0 (0.6–7.4)	82.3%
Meat consumption[e]	0.6 (0.3–1.0)	0.1 (0.0–0.4)	60.5%

[a]Results reported as mean with 95% interquartile in brackets.

[b]Computed as number of species.

[c]Computed as ton/km^2.

[d]Computed as index from 0 (null traits diversity) to 1 (full traits diversity).

[e]Computed as ton/km^2/year of dry vegetation matter and wet meat.

highest biomass (≥25 ton/km^2) across the eastern part of central Europe and south Fennoscandia and the lowest biomass (<10 ton/km^2) in south-eastern Europe and the Mediterranean coasts. In stark contrast, mean biomass in the present is 0.6 ton/km^2 (IQR: 0.1–1.0; Figure 1), with the highest biomass (>1.0 ton/km^2) in northern parts of east Europe and the lowest biomass (<0.25 ton/km^2) in the Mediterranean area. Estimated mean loss in megafauna community biomass from the LIG to the present is 94.5% (±9.9% SD; Figure 1), with dramatic losses everywhere, but least so in mountain ranges (Table 1).

Mean estimated LIG functional diversity, on a scale from 0.00 to 1.00, was 0.71 (IQR: 0.59–0.83; Figure S4) for herbivores and of 0.61 (IQR: 0.22–0.99; Figure S4) for carnivores. In the present, mean FD is 0.15 (IQR: 0.02–0.29; Figure S4) for herbivores and 0.28 (IQR: 0.22–0.34; Figure S4) for carnivores. Overall, Europe has lost a grid cell mean of 80.3% (±15.3% SD) of the large-herbivore FD and 64.9% (±29.1% SD) of the large carnivore FD from the LIG to the present (Figure 2).

3.3 | Vegetation and meat consumptions by megafauna from the LIG to the present

During the LIG, potential mean vegetation consumption—as estimated from the species assemblage and their traits—was 26.7 ton/km^2/year (IQR: 18.4–35.1; Figure S5). In the present, potential average vegetation consumption is 4.0 ton/km^2/year (IQR: 0.6–7.4; Figure S5). We estimated that potential average vegetation consumption in Europe is diminished by 82.3% (±13.4% SD) from the LIG to the present, with biggest differences (≥90%) in the East European Plain and the smallest differences (≤50%) are found in mountainous regions of the Mediterranean area (Figure 3a).

During the LIG, estimated potential mean meat consumption across Europe was 0.6 ton/km^2/year (IQR: 0.3–1.0), while in the present potential mean meat consumption is only 0.1 ton/km^2/year (IQR: 0.0–0.4; Figure S5). In terms of relative loss, estimated potential meat consumption is diminished by 60.5% (±26.0% SD) across Europe, with the biggest differences in western Europe and the smallest differences in the Balkans and Asia Minor (Figure 3b).

3.4 | Estimated megafauna habitat shift due to different climate between the LIG and the present

To estimate the effects of overall faunal differences and removing any effects of climate differences between the LIG and the present, we also compared species richness patterns constructed by (1) "LIG ranges", (2) "present-projected ranges" and (3) "present ranges" (Figure S6). On average, megafauna species richness computed with present-projected ranges is 0.7 species/grid cell higher than megafauna species richness computed with LIG ranges, without estimated statistical difference ($t(29)=-1.36$, p-value$=0.12$). Megafauna species richness computed with LIG ranges is 15.3 species/grid cell higher than megafauna species richness computed with present ranges, with estimated high statistical difference ($t(29)=40.15$, p-value$=<0.001$).

So, there is a weak and nonsignificant difference in the potential mean species richness and community biomass patterns driven solely as a result of LIG vs. present-day climate differences, while in reality there are very strong differences in the megafauna ranges and thus in the diversity of ecological effects patterns between the two periods, as assessed in this study.

4 | DISCUSSION

Wild megafauna diversity and associated potential ecological effects in the ecosystems of Europe are dramatically reduced in the present day compared with the LIG. Megafauna losses have occurred everywhere across Europe, with relatively small geographic variability, with the least losses in mountainous regions. Species richness is on average 71% lower and megafauna community biomass is 95% lower. Functional diversity loss for both herbivores and carnivores exceeds 50% across most of Europe. Importantly, the associated ecosystem impacts as indicated by our estimates of potential vegetation and meat consumptions are similarly reduced, by 82% and 61% on average across Europe. Importantly, our results also show that the small climate differences between the LIG and the present included in our modelling do not explain these reductions and would instead have led to a small increase in megafauna richness in the present. The
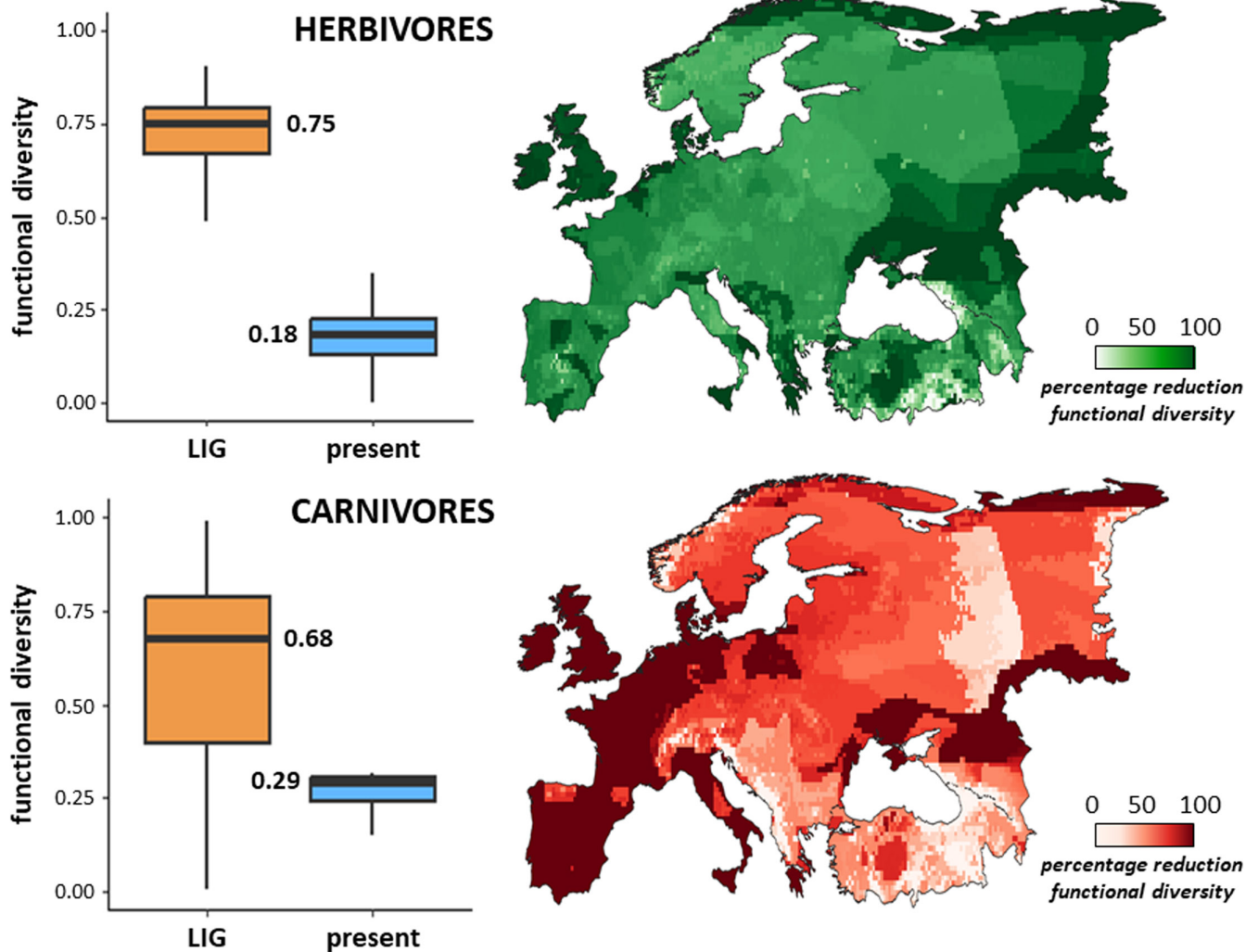
FIGURE 2 Comparison of functional diversity (FD) between the LIG and the present, considering 37 herbivore species (Table S6) and 14 carnivore species (Table S7) occurring in one or in both periods (NB. *Ursus arctos* was considered as both herbivore and carnivore). Boxplots represent the variability in functional diversity across the study area. The maps show the estimated percentage loss in FD between the LIG (cc. 127,000 years ago) and the present.

actual difference is largely due to species becoming globally extinct in the late Pleistocene or prehistoric Holocene due to human causation (Sandom, Faurby, et al., 2014; Smith et al., 2019). However, some studies suggest a combined human overhunting and early Holocene climate change synergy in the extinction of at least some species (e.g., woolly mammoth *Mammuthus primigenius*; Fordham et al., 2022), especially considering the possibility that climate change may favour fragmentation of a species' distribution (Mondanaro et al., 2021). Our results cannot rule out this interpretation, as some LIG ranges were indeed fragmented potentially as a result of abrupt warming, which also poses a risk to biodiversity in the foreseeable future (Asamoah et al., 2022). Regardless of the causes leading this massive decline in megafauna diversity and the potential functional impacts in Europe from LIG to the present, the most important indication from our results is that today's natural ecosystems in Europe deviate strongly from the evolutionary norm.

4.1 | Loss in ecological functions sustained by megafauna herbivores

The potential effects of megafauna herbivores on European ecosystems have reduced dramatically from the LIG to the present. Notably, we found that the functional diversity of herbivores in Europe is reduced by 80% on average, and overall potential vegetation consumption in wild ecosystems is 82% lower. By comparing the estimated diversity and biomass of the LIG European megafauna herbivores guild with data from today's sub-Saharan African reserves (Fløjgaard et al., 2021; Hempson et al., 2015), we found fairly similar or even higher values, likely leading to comparable processes of primary-consumers control on vegetation succession and fire prevalence. As in other parts of the world (Schowanek et al., 2021), late Quaternary extinctions therefore strongly reduced megafauna herbivore assemblages in Europe until the present, and
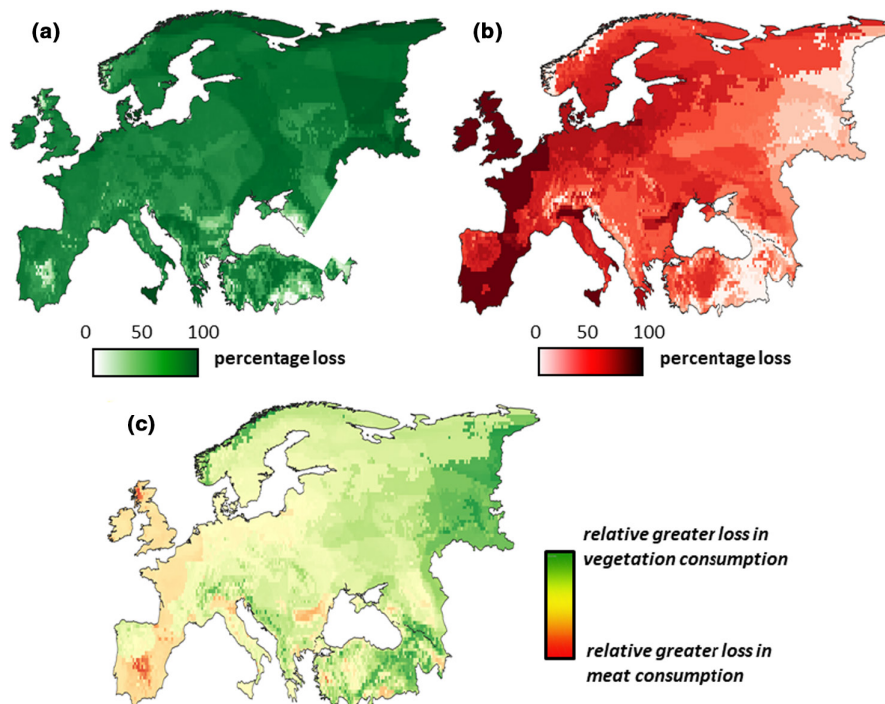
FIGURE 3 (a) Estimated loss in dry vegetation consumption and in (b) wet meat consumption from the LIG to the present. (c) Relative greater loss in either vegetation or meat consumption, that is, whether a disproportional demise in herbivore or carnivore consumption happened in a particular area based on the consumption demise ratio. This was calculated as (% loss in vegetation consumption - % loss in meat consumption per unit area); resulting positive values represent greater loss in vegetation consumption, and resulting negative values represent greater loss in meat consumption, on a scale from −100 to 100.

this trend is not recent (Smith et al., 2019). This is in line with the analyses on British dung beetle assemblages from the LIG, which indicated more frequent high abundance of large herbivores than during the early Holocene (Sandom, Ejrnaes, et al., 2014) and strong downsizing of dung beetle communities subsequently (Schweiger & Svenning, 2018). Such high abundance of large herbivores has the potential to generate heterogeneous vegetation including open and semiopen components (Bakker et al., 2016), as also seen on fertile soils in European rewilding areas today (Cornelissen et al., 2014). Temperate Europe indeed shows evidence of substantial presence of open vegetation during late Pleistocene interglacials, including the LIG, especially in floodplain areas, on marginal soils and dry climates (Sandom, Ejrnaes, et al., 2014; Svenning, 2002). High heterogeneity in vegetation is generally associated with high species richness (Vera et al., 2006). Many European species depend on open and semiopen vegetation, for example, three groups of light-demanding plants: many forb species, many thorny shrubs and tree species that cannot regenerate in present-like deep shade, such as oaks (*Quercus* spp.) and hazel (*Corylus avellana*; Bobiec et al., 2018; Pykälä et al., 2005).

4.2 | Loss in ecological functions sustained by megafauna carnivores

The functional diversity of carnivores in Europe is reduced by 61% on average, and potential overall meat consumption is 61% lower in the present compared with the LIG. While these declines are not as steep as for herbivores, the demise of carnivores in Europe compared with an evolutionary baseline likely has had nontrivial consequences for ecosystems. Meat consumption was particularly diversified in the LIG and abundant in some areas of carnivore

co-occurrence, with clear niche partitioning and thus competition avoidance (Konidaris, 2022) due to heterogeneity in body weights, diet and social structure. Cave lion (*P. spelaea*), whose ecological niche was similar to today's African lions but was physically much bigger (De Manuel et al., 2020), was widespread in central and northern Europe. The diet of this animal was oriented towards large ungulates such as equids (*Equus* spp.) and aurochs (*Bos primigenius*) but also included the cave bear (*Ursus spelaeus*; Bocherens et al., 2011). Other top carnivores in Europe during the LIG were the spotted hyena (*Crocuta crocuta*) and the grey wolf (*Canis lupus*), pack hunters feeding on mid-to-high size herbivores, including scavenging on bones. We estimated these species as widely distributed across Europe, also in accordance with the fossil record, most likely hunting in wide-open areas (Diedrich, 2014). The diversified LIG guild of large carnivores was also composed of ambush predators such as the Eurasian lynx (*L. lynx*) and the leopard (*Panthera pardus*). The presence of ambushing carnivores triggers fear-driven mesoherbivore aggregations in open areas and thus redistribution of soil fertilization by faeces (le Roux et al., 2018). Interesting, most of these carnivores co-occurred in western Europe where at present they are all virtually absent, determining a dramatic functional diversity drop in this region. Particularly in the British Isles, this has also been associated with the overabundance of herbivores such as deer, which overgrazing causes homogenization of the landscape but also leads to conflict with humans relative to the danger of car collisions, crop damage and potential for the spread of diseases (Côté et al., 2004).

At present, fundamental ecological functions provided by extant carnivores are largely relegated not only to remote areas and mountainous regions, such as in the central Apennines, the Carpathians, the north of Scandinavia, but also in lowlands between Belarus and Poland. In these areas, carnivores still exert density-mediated and

behaviourally mediated effects on their prey, with cascading consequences on the lower trophic levels (Kuijper et al., 2013). Only the Balkans, Turkey and Caucasus have conserved levels of meat consumption and carnivores' functional diversity that approach the LIG. However, local people frequently poach carnivores in the southeast of Europe given high intolerance towards coexistence in shared landscapes (Ghoddousi et al., 2020; Ripple et al., 2014). Yet, large carnivores have been a focus for conservation efforts during the last decades and are generally in a positive trend of comeback particularly in south and central Europe (Chapron et al., 2014).

4.3 | Reliability of estimated LIG European megafauna diversity

The record of LIG megafauna fossils is scarce for most species. Consequently, we were forced to implement our SDM using present-natural ranges as the source of species occurrence data, rather than using the LIG fossil record. These last were used only to estimate realized ranges from modelled potential ranges and to evaluate SDM model performance externally. The method of using present-natural ranges as the source of species occurrence data in SDM has been used previously to spatially explicitly estimate the total climatic niche of mammalian species (Jarvie & Svenning, 2018) and allowed us to estimate LIG potential distribution ranges for all species included in the study. However, the main limitation of this method is that other environmental factors that may have restricted the LIG realized distribution of species, such as trophic interactions or physical barriers, cannot be directly taken into account. A more exhaustive LIG record would allow the combination of habitat models trained directly with LIG environmental features, including topography, and of co-occurrence analyses to infer spatial competition. As the LIG fossil record is particularly scarce in Eastern Europe, investigating literature in non-English languages might alleviate this problem to some extent, but strong undersampling and geographic bias is likely to be a persistent feature. Notably, some of the species have a very sparse fossil record, a situation that is unlikely to change anytime soon.

While the number of omission errors, that is, fossils out of estimated species ranges, were relatively high, the average distance of these fossils from the estimated range perimeter was <100 km, that is, well within the range of the movement distances of individuals of most megafauna species. Hence, effectively our range estimates did not result in substantial omissions in most cases. There were, however, LIG fossil records with substantial omission errors, particularly for the woolly mammoth (*M. primigenius*; three records at distance higher than 100 km from the perimeter of the predicted range). These records are reported by Markova (2000), which defines the LIG broadly from 140,000 to 120,000 years ago. Hence, the fossil could reflect species occurrence from outside the optimal phase of the LIG, but other possibilities such as underestimation of the niche of woolly mammoth (*M. primigenius*) are possible. Importantly, while this species is often understood as a cold-climate-associated species, it has LIG records from southern parts of the East European Plain

as do woolly rhinoceros (*Coelodonta antiquitatis*; Markova, 2000) as well as other records from relatively mild climates (Álvarez-Lao & Garcia, 2012; West, 1969).

Due to lacking reliable data on LIG population densities for individual megafauna species or their species variation, we had to estimate these based on their traits (Pedersen et al., 2023) as constant population density values throughout the species ranges. Range-wide constant population densities are unlikely in most cases (Martínez-Meyer et al., 2013), but should here be seen simply as a general indication of the species' typical potential density. Similarly, the dependent estimated consumption rates should therefore also only be seen as generalized estimates of each species' potential effect.

4.4 | Key message for restoration ecology and conclusion

With the severe reduction in megafauna diversity and associated potential functional effects from the LIG to the present, a unique phenomenon in the last >10 million years (Smith et al., 2016), current European natural ecosystems deviate strongly from their long-term evolutionary conditions. While Europe has experienced a remarkable comeback of megafauna during the last decades (Deinet et al., 2013), our results show that present megafauna diversity is still just a small fraction of what has characterized European ecosystems prior to the *Homo sapiens*-linked fauna losses of the last 50,000 years (Figure 4). This faunal simplification has strong implications for European nature, not least in relation to the widespread occurrence of land abandonment and associated passive rewilding (Navarro & Pereira, 2015). Woody densification is a widespread phenomenon in European nature and a threat to a large proportion of Europe's biota and is in large part associated with reduced presence of large herbivores in the landscape (e.g., Buitenwerf et al., 2018). At the same time, natural areas in some regions experience biodiversity losses linked to extremely high, uniform presence of deer, likely in large part linked to reduced or absent large carnivore assemblages. These dynamics seem obviously linked to the downsizing and simplification of the European fauna quantified here. At least partially restoring faunal functionality through trophic rewilding interventions (Svenning et al., 2016) should therefore be amongst the priorities for the agenda of European countries to safeguard and restore the continent's biodiversity. A rising number of real-world implementations of trophic rewilding provide empirical support for positive effects on biodiversity, in Europe (e.g., Dvorský et al., 2022) as well as on other continents (Guyton et al., 2020; Ratajczak et al., 2022). Furthermore, megafauna-based trophic rewilding can also be seen as a contribution to nature-based solutions to climate change via assisting ecological adaptation to climate change and hence maintenance of climate change mitigation contributions, such as vegetation and soil carbon sinks (Malhi et al., 2022). Our study thus supports the restoration of megafauna diversity and ecological effects to European natural and seminatural landscapes as an important countermove against the current environmental crisis.
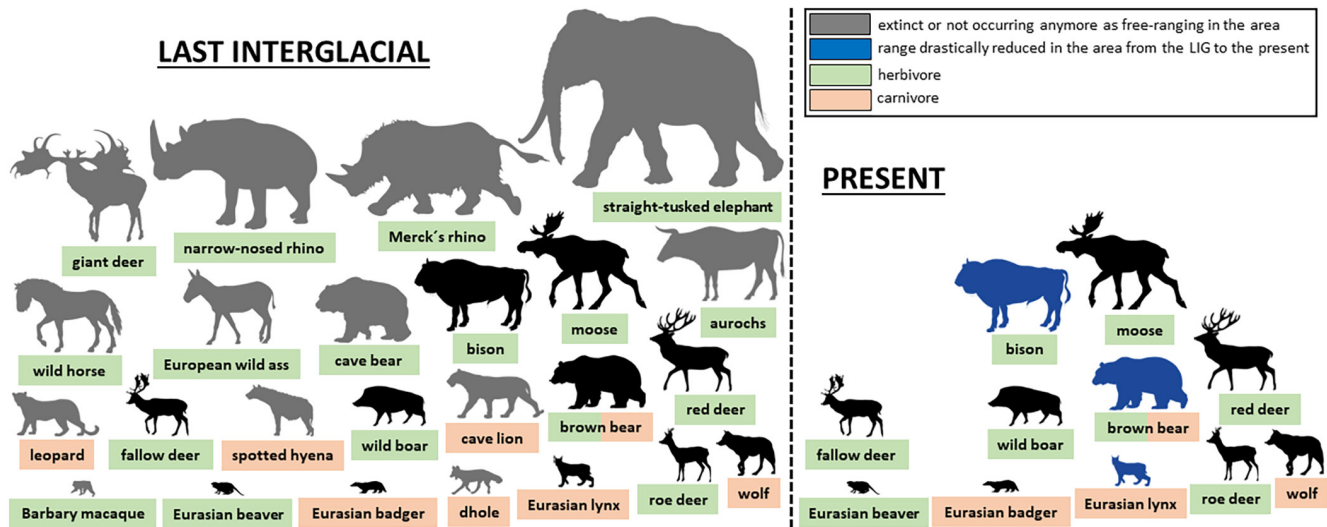
FIGURE 4 Example of species found in fossil sites of the LIG in Central Europe (see Figure S1) and which of these species currently occur in the same area. Additional species such as the woolly mammoth (*Mammuthus primigenius*) also have rare probable LIG records from the area, but are not shown. In addition, two introduced species, the sika deer (*Cervus nippon*) and the white-tailed deer (*Odocoileus virginianus*), currently occur in the area but are not shown. The correspondent scientific names of the species can be found in Table S1.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study, that is, Tables S5–S7, the estimated LIG ranges of European megafauna (raster format; EPSG: 54017) and the twelve LIG bioclimatic variables for six palaeoclimate models (raster format; EPSG: 54017), are openly available in Figshare at https://doi.org/10.6084/m9.figshare.22350907. R scripts for SDM are available from the corresponding author upon reasonable request.

ORCID

Marco Davoli https://orcid.org/0000-0001-5926-130X
Sophie Monsarrat https://orcid.org/0000-0002-6220-5306
Rasmus Østergaard Pedersen https://orcid.org/0000-0001-8538-8646
Paolo Scussolini https://orcid.org/0000-0001-6208-2169
Dirk Nikolaus Karger https://orcid.org/0000-0001-7770-6229
Signe Normand https://orcid.org/0000-0002-8782-4154
Jens-Christian Svenning https://orcid.org/0000-0002-3415-0862

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BIOSKETCH

Marco Davoli is a postdoctoral researcher at Roma La Sapienza University, Italy, who has recently obtained his PhD from Aarhus University, Denmark. His research primarily focusses on historical ecology, human–wildlife coexistence, ecological restoration and rewilding, with a specific emphasis on European biotic communities. Presently, his work involves establishing favourable reference values of conservation for nonmammalian species within the European Union.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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