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Biotic interactions may be more important than climate for shaping animal niches

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Biotic interactions may be more important than climate for shaping animal niches

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Abstract

The response of ecosystems to ongoing rapid climate change is dependent on individualistic species response and biotic interactions [1,2]. It is therefore critical to know how realised niches shift with changing climate and changing biotic interactions among species [3,4]. At present, empirical niche investigations rarely include biotic niche dimensions and are limited to short time spans [5]. Sedimentary ancient DNA (*sed*aDNA) is revolutionising our ability to study the development and dynamics of ecosystems by enabling the simultaneous identification of plants and animals from their past living environments [6,7]. Here, we develop this method by combining *sed*aDNA from ten lakes in northern Fennoscandia with a novel compilation of regional rock-art and bone records, as well as palaeo-topography, to reconstruct animal arrival times, changes in plant–herbivore-carnivore networks, and estimate shifts in the biotic and climatic niches for key animal species over the last 16 ka. Marine fauna and tundra plants appeared soon after deglaciation, and birds and freshwater species arrived at approximately 13 ka. However, reindeer did not appear until 5 millennia later at 11 ka, and most terrestrial mammals arrived only in the last 8 ka after vegetation had stabilised. Realised climatic and biotic niches shifted with increased herbivore niche-filling, and niche-overlap increased with ecosystem complexity build-up, implying increasing herbivore interactions. Our study provides the first long-term empirical evidence that shifts in biotic

interactions may be more important than climate for shaping ecosystems, and must be considered when attempting to mitigating effect of climate change.

Introduction

The ranges of plants and animals are shifting in most biomes in response to ongoing climate changes, with new areas also being colonised due to glacier and ice-sheet melting [8–10]. Rapid changes in species distributions and abiotic conditions can result in novel ecosystem assemblages with modified plant–herbivore-carnivore interactions, trophic network complexity, and realised ecological niches [11]. Plants form the basis of terrestrial food webs, however, we do not know how quickly herbivores track the plants that provide them with food and habitat, or whether the realised niches of herbivores are stable over time. Every species has a fundamental niche defined by the set of abiotic and biotic conditions necessary for their survival, growth and reproduction. However, their realised niche is narrower than their fundamental niche because of factors limiting their ability to reach the habitats and because of biotic interactions, such as forage availability, competition and predation preventing them from occupying habitats [12]. What we currently lack, is an empirical understanding on how these shifts in interactions have played out over long time scales ranging from hundreds to thousands of years. Current approaches to species distribution modelling often rely on the assumption that the realised niche aligns closely with the potential climatic niche, such that species distributions can be predicted and hindcasted based on climate variables alone. However, biotic factors can significantly alter the distribution of species as predation or lack of food resources exclude them from otherwise climatically suitable areas [13,14]. This is why an understanding of how realised niches change over time with changing ecosystem complexity is essential to understanding and modeling the effects of climate change on ecosystems.

Palaeodata can provide unique insights into patterns of species distribution over long time-spans [15,16]. For example, pollen data have enabled global vegetation changes to be quantified and their underlying drivers to be inferred [17]. For animals, records usually come from cave deposits, archaeological excavations and rock-art, which are non-continuous and do not necessarily reflect the natural habitats of the fauna [18]. They are also rarely from the same location as continuous pollen records, preventing the direct correlation between past animal occurrences and vegetation dynamics. Sedimentary ancient DNA (*sed*aDNA) allows the identification of plant and animal taxa often to the species level from the same sample, allowing to establish direct links between plant and animal occurrence and therefore revealing biotic interactions over time [6,19]. However, although *sed*aDNA data of high taxonomic and time resolution is now becoming available [20–22], this is not yet been used to reconstruct plant-herbivore-carnivore networks or niche dynamics.

The most urgent region to apply this approach to is the Arctic, due to the unprecedented rate of climatic change [23]. As northern Fennoscandia was almost entirely covered by the Fennoscandian Ice Sheet [24] (Fig. 1a), this region provides the ideal system for continuously

tracking ecosystem build-up and biotic interactions from the earliest arrivals to the present-day boreal and shrub–tundra ecosystems. Except for one bone of stoat (*Mustela erminea*) from the small ice-free refugium on Andøya [25], no records of mammals exist from the Late Glacial–Early Holocene period (20–9.2 thousand calibrated years before present (ka cal BP)) in northern Fennoscandia. Consequently, the 800 km minimum distance from the ice margin to the study sites is the minimum distance covered by colonising species (Fig. 1a, Supplementary Information 1). We have previously reconstructed plant arrival and vegetation changes of the region by analysing *sed*aDNA from ten sites covering the period 16.1 ka cal BP to present [26,27]. The past environment (temperature, moisture, pH, pollinators, etc.) and plant functional diversity was reconstructed by combining plant *sed*aDNA data with plant traits [27]. Plant arrival peaked at approximately 12 ka cal BP at the onset of the Holocene warming and coincided with a major breakpoint from rapidly increasing towards more stable plant functional diversity [27]. As also independent climate records are available for this region (CHELSA), it provides a unique opportunity to study and explore niche changes with changing abiotic and biotic conditions.

Here, we analyse sediment from the same sites in northern Fennoscandia for animal *sed*aDNA using metabarcoding. We target mammal DNA, and supplement our record by compiling all records of mammals from bones and rock-art to maximise our chance to detect the first arrival. We further reconstructed change in sea level and ice-dammed lakes to show possible dispersal barriers and corridors. Ultimately, we 1) provide the first regional-scale analyses of postglacial animal arrival in relation to landscape and vegetation development, 2) show how the plant–herbivore-carnivore network built-up over time, 3) estimate realised niche changes through time for key animals. The melting ice sheet created a fragmented landscape with ice-dammed lakes and higher sea levels that hindered terrestrial mammal dispersal, suggesting that current and future fragmentation may similarly impede species' ability to track environmental changes. However, once species arrived, biotic interactions such as the increasing complexity and shifting nature of plant–herbivore networks played a more critical role than climate in determining realised niches, challenging the assumption of their temporal stability in many species distribution models. Using high-resolution *sed*aDNA, our study provides long-term empirical evidence of these dynamics, offering a powerful tool to forecast ecosystem responses and species distributions in the face of ongoing climate change.

Results and Discussion

Arrival of first animals

Our reconstruction of past shoreline and ice-dammed lakes, combined with reconstruction of extent of glaciation [24], show how the terrestrial land in northern Fennoscandia gradually emerged from 16 ka, first as an island surrounded by ice and water, and then with emerging land-bridges along the southwest coast of Norway and to land masses in the southeast (Fig. 1a, Methods, Supplementary Information 1). The ten lake catchments we studied gradually emerged from the ice, providing a chronological record of biota (Supplementary Information 2), and our metabarcoding analyses of 342 samples resulted in 85 animal taxa detected in 244 of the samples: 13 terrestrial and 8 marine mammals, 14 birds, 1 amphibian, 3 freshwater/anadromous and 5 marine fishes, 6 freshwater and 9 marine invertebrates (including 4 worms), and 26 non-marine worms (including 4 earthworms) (Fig. 1b-f, Methods, Supplementary Tables 1-3, Supplementary Information 3-6). No native mammals were detected in any of our 89 controls x 8 PCR replicates (n=712). Furthermore, our compilation of bones included 239 records of 8693 terrestrial mammal bones from 67 archaeological sites for which indirect dating from archaeological context was available (Fig. 1, Supplementary Table 4, Supplementary Information 5). In addition, there were 12 dated bones from the regions; 10 of these bones were identified as reindeer, and 2 as reindeer/European elk [28]. Rock-art records were available of six terrestrial mammals from four sites (Fig. 1b, Methods, Supplementary Table 5). The presence of terrestrial mammals depicted in rock-art, or bone fragments from archaeological sites in the region, mostly occurred millennia later than any equivalent in *sed*aDNA (Fig. 1b), likely because human presence was scattered until 6 ka cal BP (Fig. 1c) [28]. Thus, *sed*aDNA provides a major extension back in time. Furthermore, 95% of the bone fragments were reindeer (Supplementary Information 5), which is also the most common species depicted in rock-art [29], whereas *sed*aDNA provides a more diverse representation of past mammal occurrences. While detecting the very first arrival of a species is challenging with any proxy [30–32], combining these records provides a clearer picture of when a species has reached significant population sizes and distributions and so may be most representative for abundant species. Together, the data are the first to show the arrival of different types of organisms (Fig. 1b-f) in relation to change in landscape (Fig. 1a), and indicate that new species arrived to the study region from deglaciation 16.1 ka cal BP to the last centennials.

The two lake sediment records going furthest back in time (16.1 and 12.3 ka cal BP), contained marine organisms, suggesting that the basal sediments were marine deposits. The sediments must have been deposited prior to isostatic rebound-induced lake isolation. Vegetation at that time was dominated by forbs and willows typical of arctic tundra vegetation (Fig. 1d). The *sed*aDNA revealed that marine species, such as the polar bear (*Ursus maritimus*), polar cod (*Boreogadus saida*), bowhead whale (*Balaena mysticetus*), and ringed seal (*Pusa hispida*), were already present during the Late Glacial period at 16.1–11.7 ka cal BP (Fig. 1e, Supplementary Information 4). The species assemblage was similar to that of the arctic regions of the North Atlantic and Barents Seas today [33] and the Norwegian west coast 38–28 ka cal BP [34,35], and the early presence of this arctic marine community shows that they tracked the melting ice-margin.

The first terrestrial birds, geese (*Anser* spp.) and rock ptarmigan (*Lagopus muta*) appeared in the *sed*aDNA at 12.8 ka cal BP, coinciding with the apperance of numerous freshwater worms, aquatic plants and brown trout (*Salmo trutta*) at 12.5-12.3 ka cal BP, three-spined stickleback (*Gasterosteus aculeatus*) at 11.5 ka cal BP and the somewhat later apperance of the common frog (*Rana temporaria*) at 8.8 ka cal BP (Fig. 1e, Supplementary Information 4). A similar rapid spread of aquatic plants has been reported in macrofossil studies [36], and our data suggest that animals, particularly geese, may have facilitated the colonisation of these plants. While the first fish species detected spend part of their life cycle in marine waters and likely arrived from the ocean [37], most freshwater species likely colonised from the east because large water bodies formed to the east during deglaciation (Fig. 1a, Supplementary Information 1). This may have been further facilitated by slower-running rivers with large catchments compared with the steep–small catchments of central Norway and Sweden [37], as shown by present-day genetic signatures in some fish species [38] and a high diversity of macrophytes [39].Thus, our study suggests that, like marine organism, birds and aquatic organisms, likely aided by bird-dispersal, may be able to track environmental changes rapidly

Lags in terrestrial mammal arrivals

In contrast to the marine and aquatic animals (Figs. 1e), the terrestrial fauna appeared at a slower pace. No terrestrial mammals appeared during the first five millennia (Fig. 1b). Reindeer (*Rangifer tarandus*) appeared in the Early Holocene at 11.1 ka cal BP (Fig. 1b), followed by grey-sided vole (*Myodes rufocanus*) and Norwegian lemming (*Lemmus lemmus*). The Eurasian beaver (*Castor fiber*) was detected in *sed*aDNA simultaneously with expansion of trees at approximately 9.2 ka cal BP, while the European elk (*Alces alces*), a species that currently also extends beyond the tree line, appeared 500 years after the arrival of trees and beaver (Fig. 1b, d). Other small mammals such as European water vole (*Arvicola amphibius*), mountain hare (*Lepus timidus*), and short-tailed field vole (*Microtus agrestis*) appeared in the Middle Holocene, and tundra vole (*Microtus oeconomus*) and wood lemming (*Myopus schisticolor*) only appeared in the Late Holocene. Omnivores, such as brown bears (*Ursus arctos*) and European pine marten (*Martes martes*), and the carnivore red fox (*Vulpes vulpes*), were sporadically detected (Fig. 1b). Thus, terrestrial mammals appeared after the major peak arrival of plants (Fig. 1e) and after the major break points of plant species traits (Fig. 1b-f). For most of them, the first appearence was also after the major stabilisation of plant species traits in the region (Fig. 1b-f). This raises the question of the role of vegetation development was limiting for mammal establishment, or whether other factors were more important.

For species moving over land, both dispersal barriers and the distance to potential refugia likely influenced the timing of their arrival. Ice-sheet and local glaciers, elevated sea-level and ice-dammed lakes (Fig. 1a), may have delayed arrival. For the most cold tolerant species that arrived in the early Holocene, reindeer, grey-sided vole and Norwegian lemming, the highly fragmented landscape may have limited dispersal. The narrow land strip along the western coast only gradually emerged and remained fragmented by wide and deep fjords and surging glaciers (Fig. 1a). The closest mammal records along this coast from Storsteinhola cave, approximately 160 km southwest of our study sites (Fig. 1a), that

date from 9.5 ka cal BP onwards [18], may indicate limited dispersal along the western coast prior to 9.5 ka cal BP. Norwegian lemming, a mammal never recorded outside Fennoscandia, is assumed to have survived glaciation in southwestern Fennoscandia during the last glaciation [40,41], and the almost simultaneous records from the Storsteinhola cave (9.5 ka cal BP) and the study region (9.4 ka cal BP), suggests that colonisation along the western coastal route was not possible earlier. Reindeer may have arrived from the east, where it is recorded throughout the Late Pleistocene [42,43]. Reindeer are highly mobile, as evident by their occurrences on arctic islands. Still, the late arrival of reindeer is likely because a fragmented landscape due to glaciers, ice-dammed lakes and higher sea-level blocked dispersal routes. Overall, our data suggest that the millennia time lags observed in the Late Glacial-Early Holocene due to dispersal limitations in a landscape fragmented by water and ice.

The first appearance of beaver and European elk occurred around the time of stabilisation of plant functional traits and the spread of trees in the region. For beaver, the appearance coincides with the arrival of three of the six tree species in the region (*Pinus sylvestris, Sorbus aucuparia* and *Populus tremula*), and beaver marks on tree fossils from northern Sweden dated to 9.5–9.2 ka cal BP [44] suggest an immigration route from the south. The arrival of elk may also have been related to development of vegetation, as they appeared during the period of increased abundance of trees (Fig. 1d). Thus, these highly mobile species may have tracked the vegetation changes. Many species did not appear until the Late Holocene. While a few species may have been overlooked, for example the mountain hare that is recorded in bone and rockart earlier than *sed*aDNA, others may have arrived late due to very specialised habitat like the wood lemming, that is rare in the region today. Altogether, this is the first dataset that represents an almost full assemblage of the mammals in a region through time in their specific ecosystem context. This allows us to further evaluate plant herbivore associations.

Increasing plant–herbivore network complexity

To explore how the ecosystem complexity build-up over time, we undertook a co-occurrence network analysis of plants, herbivores and carnivores (Fig. 2, Methods, Supplementary Information 7, Supplementary Table 6). Among the mammals and birds identified, there were 14 terrestrial herbivores, 12 of them with sufficient detection to test for significant co-occurrence. As records of carnivores were scattered, they were placed in the network according to all co-occurrences observed. The co-occurrence networks revealed increasing complexity in numbers of plants, herbivores and carnivores as well as their links over time. There were two herbivores in the Late Glacial period (12.8–11.7 ka cal BP), seven herbivores in the Early Holocene (11.7–8.3 ka cal BP), nine herbivores in the Middle Holocene (8.3–4.25 ka cal BP), and 11 herbivores in the Late Holocene (≤4.25 ka cal BP) (Fig. 2). The number of plants that co-occurred with each herbivore increased over time. For example, grey-sided vole co-occurred with 14 plant taxa in the Early Holocene, 35 plant taxa in the Middle Holocene, and 49 plant taxa in the Late Holocene (Fig. 2, Supplementary Information 7, Supplementary Table 6). Similarly, Norwegian lemming co-occurred with 14 plant taxa in the Early Holocene, 19 plant taxa in the Middle Holocene, and 27 plant taxa in the Late-Holocene. Thus, while herbivores generally arrived later than plants, they probably exploited new plants for food and/or habitat as they appeared.

These first reconstructions of region-wide past plant-herbivore associations showed that plant species that have been identified as frequent food items for the majority of the herbivores in contemporary studies, such as graminoids and nutrient-rich forbs [45–47], indeed co-occurred with the herbivores. However, other well-known food plants, such as blueberry (*Vaccinium myrtillus*), bog bilberry (*V. uliginosum*), lingonberry (*V. vitis-idaea*), birches (*Betula* spp.), and crowberry *(Empetrum nigrum*) did not show significant co-occurrence with any herbivores except the latter with reindeer (Fig. 2, Supplementary Table 6). Furthermore, willows (*Salix* spp.), which are important both as food and shelter for all herbivores in the region, did not show significant co-occurrence with any of the herbivores. This is likely because all these plants are both widespread and common in the region [27], and therefore the co-occurrence of herbivores with these plants is not statistically significant. We therefore also plotted plant taxa that occurred together with >75% of the occurrences of the respective herbivores (Supplementary Information 7), which shows that the most frequent food plants co-occur with the majority of herbivores. Additionally, we found that the small rodents were associated with plant communities with higher vascular plant and forb richness, whereas reindeer were marginally linked to communities with overall higher richness and graminoid abundance (Supplementary Information 7.5.) as expected based on the current food preferences of these species. The co-occurrence networks also revealed some differentiation in the use of habitats among herbivores. Beaver, European elk, and mountain hare were related to woody plants that generally have a high temperature optimum and thrive on nutrient-rich soils, in contrast to rock ptarmigan and Norwegian lemming, which occurred with cold-tolerant forbs adapted to open, nutrient-poor sites (Fig. 2). We also observed that reindeer, grey-sided vole, Norwegian lemming, and willow ptarmigan co-occurred with many plants and this suggests that their wide distribution is likely related to their wide-ranging habitat and diet [45]. In contrast, beaver was related to a vegetation type that had a restricted spatio-temporal distribution in the region. These co-occurrence networks summarize pair-wise associations between plant and herbivore at the species level, and provide a partial picture of the realised habitat niches of the herbivores and their changes through time to a detail that never has been possible before.

Biotic and abiotic niche dimensions over time

To explore further the niches of species, we explored more aspects of the realised habitat niche. A habitat suitable to sustain a population of a herbivore species is characterized by a set of attributes ranging from climate and possibly other abiotic factors, to plant species composition. Our *sed*aDNA records of animal occurrence over time provided a unique opportunity to investigate the relative importance of these attributes in predicting species presence and tracing potential changes in realised niches through time. Based on our data, we quantified four attributes of the environment: 1) climate niche dimensions were established using four key variables (January and July mean temperatures, annual precipitation, and snow cover duration) downscaled to each lake in the study area at a 100-year resolution, 2) local climate and other abiotic factors, such as nutrients, light, soil moisture and pH were inferred from the traits of the plants detected in *sed*aDNA, 3) plant taxonomic composition, and 4) relative abundance of plant functional groups. To reduce the numbers of dimensions within each attribute group (2-4), we used ordination, resulting in three dimensions for abiotic attributes and four for each of plant taxonomic richness and relative abundance of plant functional groups (Fig. 3, Methods, Supplementary Information

8). Four terrestrial herbivores and the frog were sufficiently abundant to analyse predictors of their occurrence. To identify the most important predictors of occurrence of these species, we used a boosted regression tree (BRT) analysis. The results showed that the relative importance of different factors varied among the species, indicating that the critical aspects of the niche are not the same for all species (Fig. 3a). So, climate was the most important predictor for reindeer and frog, plant taxonomic composition was the most important predictor for grey-sided vole and Norwegian lemming, and relative abundance of plant functional groups was the most important predictor for willow ptarmigan. Thus, for small herbivores, the realised niche may be characterised more by vegetation than by climate, possibly because vegetation expands the climate niche by creating microhabitats [48]. This findings has implications for environmental niche modeling commonly used to predict the impact of ongoing climate change, as most of these models use only climate niche dimensions [14], but may be improved by considering biotic niche dimensions.

To evaluate shifts in realised niches over time, we computed niche dimensions for each of the sub-periods of the Holocene as defined above and probability of overlap between these periods (Fig. 3b, Methods, Supplementary Information 8). In addition, we defined a recent "Historical" period starting 650 years ago that corresponds approximately to the period when northern Fennoscandian ecosystems were potentially impacted by reindeer herding [49]. For all five species, we observed a shift in both biotic and abiotic niche dimensions from the oldest to the most recent records. The magnitude of shifts varied among the species and periods, but we note that, overall, the probability of niche overlap between the Middle and Late Holocene was low for both abiotic and biotic niche dimensions of the terrestrial herbivores, suggesting that the largest changes was in the early period coinciding with largest changes in plant-herbivore networks. In comparison, the probability of overlap of the niche of the Late Holocene and the Historical period is >60% for most animals and niche dimensions (Fig. 3b, Supplementary Information 8), reflecting a period with less new species arriving and with stable vegetation. The niche changes were less for the frog, likely because as an ectotherm and insectivore more directly dependent on suitable climatic conditions than the terrestrial herbivores and less influenced by the vegetation. These documented important shifts in realised niches shows that habitats used by species are not static but adapted to increasing ecosystem complexity. Thus it is likely that realised niches and species associations will also display plasticity with the major ecosystem transformation happening with ongoing climate change, intensified human use and increase in introduced species, making it challenging to predict the future of ecosystems based on simple modelling.

We further explore changes in niche sizes and its relation to changes in available environmental space. The niche sizes of willow ptarmigan, grey-sided vole, and Norwegian lemming increased from the Middle to Late Holocene but decreased during the Historical period (Fig. 3, Supplementary Information 8). For reindeer, the niche increased in size over time and peaked in the last 650 years, which corresponds to the time of gradual reindeer domestication starting in 1300 AD [49]. At this time, reindeer appear in new locations such as islands and spruce forests (Supplementary Information 6), likely due to domestication and human introduction to new areas.

We further estimated the available environmental space through time as the space occupied by all analysed animals both for each of the four sets of attributes (climate, abiotic traits,

plant taxonomical diversity and plant functional groups) seperately and for all 15 niche dimensions combined (Fig. 3c-d, Methods, Supporting Information 9). In conjunction with the niche shifts of the species, we observed a change in the environmental space (Fig. 3c-d). The climate dimensions changed more than the other abiotic dimensions, with the largest environmental space in the Early Holocene. A decrease in environmental space was also observed for both taxonomic richness and plant functional types (Supplementary Information 9). When the 15 niche dimensions were summarised into four dimensions representing 70% of the total variation among samples, Historical environmental space represented only approximately one-third of the environmental space in the Early Holocene (Fig. 3c). This result may seem counterintuitive given the increasing complexity of the ecosystem observed over this time span (Fig. 2), however, the climate in the Early Holocene was less stable (Supplementary Information 9). This finding, combined with a homogenisation of the flora within the region over time [50], may explain why the overall environmental space decreases as ecosystem complexity increases. Thus, unstable conditions may provide larger environmental space than stable conditions. While there were considerable empty environmental spaces in the Early Holocene, the overall niche-space filled by herbivores increased over time to fill nearly 100% of the environmental space in the Historical period (Fig. 3c), suggesting potential increase in interaction among species.

Increases in herbivore niche overlap

To explore whether the increased niche filling caused an increase in niche overlap, we computed pair-wise niche overlap between herbivores for within each time period (Methods, Supplementary Information 10). The overall herbivore niche overlap increased over time (Fig. 4), suggesting increased habitat overlap with possibilities for interactions and spatio-temporal dietary differentiation among species. The mean posterior probabilities of finding the two small rodents within the reindeer niche were 46% and 60% for Norwegian lemming and grey-sided vole, respectively, prior to the Historical period, but these values increase to 87% and 94% during the Historical period (Supplementary Information 10, Supplementary Table 7). Similarly, the posterior probability of finding willow ptarmigan within the reindeer niche increased from 58–82% in the Middle and Late Holocene to 87% in the Historical period, suggesting that reindeer herding caused increased niche overlap and possibly even a niche size reduction in the smaller herbivores. A negative impact of high reindeer densities on ptarmigan populations has been suggested by studies of contemporary ecosystems in the region, whereas habitat overlap between reindeer and Norwegian lemming suggested a positive interaction between these species [51]. Overall, the total number and relative frequency of these small herbivores increased during the Historical period (Supplementary Information 6), arguing against a negative impact of interspecific overlap in realised niches. There may be other reasons for the reduction in the niche size of the rodents not captured by the data, such as changes in carnivore pressure or competition among rodent species.

Concluding remarks

The melting of the ice-sheet created a fragmented landscape with ice-dammed lakes and higher sea-level, causing obstacles to dispersal especial for terrestrial mammals. Thus, we argue that the current human-fragmented landscape may hamper the ability of animals to track the ongoing environmental changes. However, once arrived, the biotic interactions

were more important in determining the realised niche of some species than climate. Plant–herbivore network complexity increases as new species arrive. Although herbivores consistently show differentiation in plant associations over time, we also observe niche shifts, implying that the realised niche may change with species richness and network complexity. Thus, while our results support climate as an important driver of change in northern ecosystems, they call into question the temporal stability of realised niches and the ability of animals to track climate shifts, as is assumed in most species distribution models. We show for the first time how realised biological niches and biotic interactions change over millennia, and these result have only been obtainable due to the high taxonomic resolution of both plants and animals from the same samples provided by *sed*aDNA. This approach could be extended to other organism in the ecosystem, for example pathogens or parasites, to further increase our understanding of species distribution and ecosystem change. Moreover, our approach can be used to study other questions such as causes of megafauna extinction, impact of introduced species or potential impact of re-wilding. The finding that realised habitat niches changed with ecosystem complexity is the key to understanding ongoing rapid present day ecosystem change.

Methods

Ice dammed lake reconstruction

The potential extent of ice dammed lakes in NW Europe was reconstructed using the Hydrology toolset in Esri ArcGIS Pro at one thousand-year time slices between 16 and 9 ka. Glacio-isostatic and relative sea level optimised palaeo-topography data [52] for each time slice were used to derive the sea level contour, which was assumed to be at 0 m. False horizontal ice sheet surfaces based on the lateral extent of the most-credible DATED-1 time slice [24] were combined with the palaeo-topographies for each time slice to prevent hydrological routing toward the interior of the ice sheet. The hydrology toolset filled cells in the resulting raster that had an undefined drainage direction; the filled cells that were above sea level and intersect the most-credible DATED-1 ice sheet extent likely represent ice dammed lakes and were converted into ice dammed lake polygons. For the Ancylus Lake, the filled cells in the Baltic Sea region that were not connected to the North Sea were converted into an additional Ancylus Lake polygon.

Study sites and geochemistry

The ten sites represent the current major vegetation types of the regions, from northernmost pine and spruce as well as the more widespread birch forest and alpine heathlands. The sediment sampling and age depth models of all sites are presented in [26] with minor updates in [27]. Geochemistry was assessed from the core sections which were scanned for X-ray fluorescence (XRF) and high-resolution colour imagery. The XRF scanning was performed every 5 mm at 10 kV using an Avaatech XRF core scanner and high-resolution imagery using a Jai L-107CC 3 CCD RGB Line Scan Camera (mounted to the XRF core scanner). The age-depth models with key XRF data and core images are shown in Supplementary Information 2 and XRF data are given in Supplementary Data 1. This data shows that all the lakes are Si dominated with variable amounts of authogenic organic matter. As leaching from younger to older sediments does not occur in lake sediments [53,54] and we have no hiatuses

and very few date reversals (see Supplementary Figure 2.2), taphomic studies indicate that we should have a high fidelity data for catchment biota (Supplementary Information 2, [53,54].

Sedimentary ancient DNA

To conduct detailed studies of plant-animal interactions, high taxonomic, spatial, and temporal resolution is required. Metabarcoding achieves high-throughput identification of approximately 50% of the plants to species level [27,55,56] and has higher detectability than any alternative method [57]. Initial attempts to amplify mammal DNA through metabarcoding were problematic as we ourselves are mammals, and there will always be some human contamination from both reagents and the laboratory workers that may be co-amplification during PCR [58,59]. This problem has recently been overcome by a more effective human dual-blocking oligonucleotide strategy [7]. This improvement has enhanced the detection of native mammal DNA and enabled co-amplification of other taxa such as birds, fish, amphibians and worms [20]. When combined with plant metabarcoding, this high-throughput analysis significantly improves both the temporal and taxonomic resolution of taxa detections. The authenticity of ancient DNA was evaluated through extensive replication and use of negative controls [60].

We used the plant data originally presented in [26] re-analysed using the PhyloNorway DNA reference library as in [27]. From the ten lakes, a total of 355 samples were amplified eight times using the chloroplast marker P6 loop of the trn*L* (UAA) intron, which also allows the use of a more conservative PCR replicate-based quantification than the proportion of reads (see pros and cons of each quantification methods discussed in [27]).

To generate the animal data, we used the same DNA extracts as in [26,27] with the exception of EG13_L097a from Gauptjern, which was re-extracted using the same method used in [26,27]. We ran mostly eight PCR reactions using the mammalian 16S P007 primers [61] on each of 342 samples and 89 controls (65 negative and 24 positive controls), and using both forward and reverse blocking primers for inhibiting the amplification of human DNA as described in [7]. Unique flanking identification tags were added to the 5' end of the primers to allow for pooling of multiple PCR reactions (Supplementary Table S8). For Nordvivatnet, four of the 16S PCR replicates for each sample were previously published in [20].

Bioinformatic analyses

The sequence data were analysed with the OBITools software package [62] following the methods described in [7]. The animal barcodes were identified with a reference library based on the EMBL nucleotide database collected on 2022-10-06, with additional 16S reference sequences added for *Lemmus lemmus* (from [20]), *L. sibiricus* and *Microtus oeconomus* (Supplementary Information 11). The identified barcodes were filtered to only retain those that had a match ≥95% identity in the reference library, a minimum of 3 reads per PCR replicate detection, and at least 10 reads and 1 replicate across the total dataset.

The OBITools output was cross-checked by using the Basic Local Alignment Search Tool (BLAST), with the megablast or blastn function in August 2023, and with or without the low complexity filter. In some cases, taxa with more than 100 sequences were excluded to enable display of other matches. For sequences that had equal matches to several taxa, the taxa found in the region today were assumed to be the correct identification. When several

sequences matched the same taxon, we checked if the less frequent variant mainly co-occurred with the more frequent variant, and if so, they were assumed to be a sequence variant and so sequence counts were merged for quantitative analyses.

Of the 280 sequences with a ≥95% match to the reference library (Supplementary Table 2), five sequences were identified as nuclear mitochondrial DNA segments (NUMTs) of *Orcinus orca* (killer whale) and *Felis catus* (cat). Further, the following sequences were assumed to represent contamination: 20 sequences of human, one of chicken, three of dog, two of cat, one of turkey, one of cattle, three of pig and one tropical fish. The remaining 243 sequences were identified to 96 taxa (Supplementary Table S3).

Domesticated animals are regularly found as contaminants in *sed*aDNA analyses. While some, such as dog, cattle and cat, may be expected in the most recent samples of our dataset, we excluded them due to their occurrence in negative controls. Only for cattle (*Bos taurus*), the data show consistent high detection in recent samples and otherwise scattered occurrences. As domesticated mammals are not the focus of this paper, and as *Bos taurus* and *Sus scrofa* are known contaminants from lab reagents such as Bovine Serum Albumin (BSA) [63], we disregarded these records. Similarly, we disregard tentative identification of Grey wolf due to difficulties in distinguishing it from dog (Supplementary Table S2). No native mammals were detected in any of our 89 controls x 8 PCR replicates (n=712), showing that there was no background contamination of these species.

Some species were only detected during the last few millennia, possibly due to 1) decreasing *sed*aDNA quality with increasing age or 2) denser sampling towards the present. While the mammal data are too scattered for a meaningful analysis of quality parameters, we assume that the DNA quality of mammals follows that of plants, which do not show an overall decrease in quality with age [26]. Furthermore, as the frequency of samples containing species such as reindeer, grey-sided voles, and Norwegian lemming also increased (Supplementary Information 6), suggesting that sampling density is not the case of late detection. Thus, we assume that the observed increase in mammal abundance towards the present is a biological signal rather than a preservation artefact.

Mammalian bone record

We compiled all bone records from the Norwegian university museums in Oslo, Bergen, Trondheim, and Tromsø. As an age estimate, we used the range for the oldest samples. If the oldest samples had an age uncertainty overlapping with the second-oldest record, we used the youngest age of the second-oldest samples as the lower range. For example, the oldest record of *Arvicola amphibius* is 7.0-2.9 ka cal BP, whereas the second oldest is 6.5-5.5 ka. We then used the range 7.0-5.5 ka cal BP. All animal bones in the database were extracted from the database at the University Museum in Bergen compiled by Anne Karin Hufthammer. In addition, dated bones of animals other than humans were compiled from [28]. We restrict the comparison between *sed*aDNA and bones to terrestrial mammals because 1) the method used for *sed*aDNA is dedicated to detect mammals whereas birds and fish are regarded as by-catch [7,59], and 2) the majority of bird and fish bones from the regions are marine, but we only have marine sediments for the Late Glacial period, where there are no macrofossil records.

There were 46 radiocarbon dated bones from the region, compiled by [28]. They had been identified as reindeer (10), reindeer/European elk (2), seal (7), whale (1), fish (1), bird/fish (1), and unidentified (24). We include only the terrestrial mammals in our compilations. The oldest mammals from the region are two records identified to reindeer/European elk, with radiocarbon ages (^{14}C) of 8295±35 and 7880±35 ^{14}C years old, whereas the oldest bone identified as reindeer was 7180±55 ^{14}C years old. We assumed that the oldest record most likely represents reindeer.

Mammals in rock-art

Although the dating of rock-art may be less certain than bones and lake sediments, and although it may reflect cultural selection rather than local faunal diversity, it may add to the total knowledge of first arrival of mammals in the region. We compiled a list of mammals from all known rock-art from the counties of Troms and Finnmark [29,64,65]. Dating for all sites is provided by shoreline displacement curves and typology [66]. In addition to the sites in Finnmark mentioned in the main text; Alta (Hjemmeluft, Kåfjord, and Storsteinen sites), Gamnes and Slettnes, there is rock-art known from Skavberg (69.56ºN, 18.75ºE) near Tromsø, county of Troms. This rock-art is inferred to represent reindeer and brown bear, but the dating is problematic due to a long standstill of the shoreline between about 8500 and 5400 BP [29]. Thus, In Fig. 1, we display only the more confidently dated sites.

Statistical analyses

The time of stabilisation of plant trait composition diversity was calculated by breakpoint analyses following [27] and using only data from 12 ka cal BP to the present.

Networks

Plant-animal co-occurrence networks were constructed for all herbivorous animals (including the omnivorous brown bear) and terrestrial vascular plants with a minimum of four detections using all samples starting from the first occurrence of terrestrial herbivores (12777 cal BP; n=175 taxa of plants and 12 taxa of animals). We first identified all co-occurrences between animals and plants. Important co-occurrence patterns were identified using four complementary methods: 1) We selected all plants that were detected in 75% or more of the samples where an animal species was found (frequent co-occurrence). 2) We used the function *cooccur* from the package cooccur [67] in R (v4.4.2)[68] to test for significant association between pairs of species according to the method of [69]. We retained herbivore-plant pairs with co-occurrence frequencies that had a probability of less than 0.05 to occur by chance after correcting for multiple testing using false discovery rates . 3) We carried out permutations to test for significant associations relative to a null model of random distribution of the observed number of samples of each herbivore species after their first appearance in the study area. For each herbivore, 5000 permutations were carried out and co-occurrences that were more common than the upper boundary of the 95% confidence interval were retained. 4) Finally, we constructed networks based on Gaussian copula graphical models using the functions *stakedsdm* and *cgr* in the package *ecocopula* in R [70]. This method can distinguish between direct and indirect associations among species and can take into account covariables. As species richness of both plants and animals increased over time, we used time as covariable and retained herbivore-plant co-occurrences with a positive partial

correlation in the best networks selected by *cgr* using default setting. Selection of important associations according to all four criteria was carried out for the total dataset after arrival of the first terrestrial herbivores, as there were too few animal detections to consider each time period separately. We plotted separate networks of significant herbivore plant co-occurrences, where we conservatively included only co-occurrences retained by methods 2-4, and networks of frequent co-occurrences. We used the function *plotweb* from the package bipartite [71] and plotted networks for four different periods corresponding to sub-periods identified either before, or within. the Holocene by [72]: >11.7 ka cal BP (Late Glacial), 11.7 - 8.3 ka cal BP (Early Holocene), 8.4 - 4.25 ka cal BP (Middle Holocene), and <4.25 ka cal BP (Late Holocene). For each period, we plotted the subset of selected animal-plant pairs that were detected during that period. On the plots, plants were characterised by growth form, as well as three plant traits as described by Tyler et al. [73]: temperature optimum, light requirement, and nitrogen requirement. As predator occurrences were sporadic, all predator co-occurrences with herbivores were plotted without assessment of frequency or significance. The omnivorous brown bear was included in analyses of herbivores, but showed no significant co-occurrence patterns and was therefore only plotted on the 75% co-occurrence. It was also plotted as a carnivore in Fig. 2.

Predictors of herbivore presence

Four species of herbivore (reindeer, grey-sided voles, lemmings and willow ptarmigan) and frog were abundant enough to analyse predictors of their detections in more detail. We determined four different attributes of the environment that could be important predictors: 1) Climate variables downscaled to each lake at 100-year resolution from CHELSA - Climatologies at High Resolution for the Earth's Land Surface Area [74]. 2) Abiotic conditions inferred from the plant traits [27]. The values for heat requirement, cold requirement, temperature optimum, continentality, light requirement, moisture, nitrogen requirement, phosphorus requirement and pH were extracted from [73] for all the plant species present in each sample and averaged by weighting trait values for each species by the number of PCR repeats in which that species was detected [27]. The dimensionality of the abiotic trait data was then reduced with a principal component analysis (PCA). The first three axes, representing 87% of variation among samples, were retained to characterize the abiotic environment. 3) Taxonomic plant community composition (quantified as proportion of repeats) was summarised through non-metric multidimensional scaling (NMDS) using the Bray-Curtis distance and the function *metaMDS* from the package vegan in R [75]. Four dimensions resulted in a stress of 0.095, a level that is considered a good ordination with no real risk of drawing false inference. 4) Functional plant community composition was characterised based on the vegetation composition according to plant functional groups important to herbivores, and modified from [76]. The following groups were used: trees, deciduous tall shrubs, deciduous ericoids (except *Vaccinium* spp. and including *Dryas octopetala*), deciduous *Vaccinium* spp., evergreen forbs and shrubs, ferns, grasses, sedges, hemiparasites, legumes, other small dicotyledons, other large dicotyledons, and mosses. Crowberry (*Empetrum nigrum*), horsetails (*Equisetum* spp.), Dicranaceae mosses and the matt grass *Nardus stricta* were kept separate because their use by herbivores is ambiguous (e.g., crowberry leaves are not palatable but berries are eaten, [76]). Birches (*Betula* spp.) and willows (*Salix* spp.) were kept as separate groups as the P6 loop cannot differentiate the different species that would be classified into different functional groups, and both are ecosystem forming genera of shrubs/trees that are important for many herbivores. As a proxy for biomass of the different groups, we used the proportion of reads summed across

species and summarised the variation among samples using NMDS with four dimensions as above. Although we do not assume a one-to-one relationship between the proportion of reads and biomass due to differences in barcode size etc among species, this bias is assumed to be less when species are grouped and avoids underestimating the abundance of the most abundant taxa [27]. Environmental attributes for terrestrial herbivores were characterised for the period from the first detection of reindeer (11094 cal BP), and for frogs from their first detection (8776 cal BP). Algae, aquatic macrophytes, and liverworts were excluded for terrestrial herbivores, but aquatic macrophytes were included when calculating environmental attributes for frogs.

To determine the importance of the four different categories of niche dimensions in predicting occurrences of each of the five animal species, we used boosted regression trees as implemented in the function *gbm.step* of the package dismo in R and following [77]. The 15 environmental attributes described above were used as predictors. As several of the predictors were correlated with time, and detection of animals increased with decreasing age of samples, we also ran the analyses including age as an additional predictor to make sure results were not just driven by correlations with sample age.

Niche stability

The environmental attributes derived above together form a description of the habitats with which the animals were associated through time, and can thus be considered a description of the multidimensional realized niche of these species. For the five most detected animals, we assessed the stability of this realised niche over time. For each species, occurrences were divided into several periods. As for networks, we used the sub-periods of the Holocene defined by Walker et al. [72]. In addition we defined a Historical period starting 650 years ago that corresponds approximately to the period since when the northern Fennoscandian ecosystems were potentially impacted by animal husbandry - notably reindeer herding [49]. The increase in human land use and animal husbandry was gradual, thus we chose the exact date of 650 years also to assure sufficient sample size in this last period for all five species. This resulted in the following periods: Early Holocene (11700 - 8300; only reindeer was detected), Middle Holocene (8300 - 4250), Late Holocene (4250-650), and Historical period (650 to present). Niche stability was assessed regarding the four environmental attributes described above. Because of limited numbers of occurrences per period, we could not evaluate niche stability in a hypervolume with 15 dimensions at once, therefore we analysed each environmental attribute separately (climate, abiotic conditions, taxonomic plant community composition, functional plant community composition). We used a probabilistic method to calculate multidimensional niche size and overlap taking into account uncertainty resulting from uneven sampling as implemented in the package nicheROVER in R [78]. This method provides directional estimates of niche overlap in a Bayesian framework. For each environmental attribute, we estimated niche size for each species in each period with at least five occurrences, niche overlap between the different time periods for each species, as well as niche overlap between species for the Middle Holocene, Late Holocene and Historical periods. To quantify available habitat, we used the same method to estimate the size of the environmental space in each period and the overlap in environmental space between the periods for each environmental attribute.

To assess overall changes in niche size and available environmental space, we reduced the 15 niche dimensions by carrying out a PCA and keeping the first four dimensions explaining

70% of the variation among all samples more recent than 11095 cal BP (the first detection of reindeer). These new dimensions were used to calculate the size of the environmental space in each period, the size of the environmental space occupied by any herbivore (the four herbivore species analysed in more detail, as well as moose, beaver, rock ptarmigan, hare, field vole, brown bear, tundra vole, goose, wood lemming and water vole) as well as the size of the niche of each of the four terrestrial species analysed in more detail. Finally, we also used the axes of this summary PCA to calculate niche overlap between species in each period. A similar analysis of overall niche changes was carried out for the frog using all samples more recent than 8776 cal BP.

Effect of animal presence on plants

A possible top-down effect of herbivore presence on plants was assessed for reindeer and small rodents (Norwegian lemming, grey-sided voles, tundra vole, field vole and water vole). Small rodents were addressed as one group as they can all be expected to fertilise and create disturbance, potentially facilitating recruitment of, for instance, forbs and thus potentially having a positive effect on biodiversity [79]. A potential effect of herbivore presence was assessed for species richness of vascular plants, forbs and graminoids. Moreover, to assess a potential effect on biomass, the summed proportion of reads for forbs and graminoids was considered as an abundance proxy for these plant groups. For species richness, we used a generalized linear mixed effects model (GLMM) with a Poisson error distribution. In addition to presence or absence of the focal herbivores, we included variables known to affect plant species richness as fixed effects: mean July temperature [74], sample age and ecological sample quality [26]. Lake name was included as a random effect and a first order temporal autocorrelation term was included to account for autocorrelation between subsequent samples in the same lake. Models were fitted in the package glmmTMB in R [80] and model fit (normal distribution of the residuals, indications for overdispersion) was assessed using the package DHARMa [81]. The proportion of reads of forbs and graminoids was transformed as fourth root [7] and analysed in a linear mixed model with a normal error distribution. Fixed effects were sample age and ecological sample quality in addition to presence of the focal herbivore, and random effects and temporal autocorrelation were as described above.

Author contribution

Project design and acquisition of funding: IGA, NGY, DE, KAB; field work: IGA, AGB, DPR, PDH, KFH, JB, KAB; lake sediment analyses, dating, and subsampling: JB, IGA, DPR, PDH, KFH, JSS; DNA analyses: MKFM, DPR, PDH; bioinformatic analyses: YL, LDE, revision of worm data CE; compilation of bone data: AKH; compilation of rock-art: JMG; statistical analyses: DE, DPR, NGY, IGA, compiling maps of palaeo-topography and marine shorelines, and ice sheet and ice dammed lake extents: BMB, CDC, HED, SB; writing first draft: IGA, DE. All authors commented and approved the manuscript.

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Competing interests

The authors declare no competing interests.

Data and materials availability

All data needed to evaluate the conclusions in the paper are presented in the paper and/or the supplementary materials. The raw sequencing data is deposited in the European Nucleotide Archive (ENA) under the accession code PRJEB100581.

References

1. García Criado, M. *et al.* Plant diversity dynamics over space and time in a warming Arctic. *Nature* 1–9 (2025).
2. Chevalier, M., Broennimann, O. & Guisan, A. Climate change may reveal currently unavailable parts of species' ecological niches. *Nat Ecol Evol* **8**, 1298–1310 (2024).
3. Chen, I.-C., Shen, S.-F. & Chan, S.-F. Niche theory and species range limits along elevational gradients: Perspectives and future directions. *Annu. Rev. Ecol. Evol. Syst.* (2024) doi:10.1146/annurev-ecolsys-102722-123834.
4. Barrio, I. C. *et al.* Biotic interactions mediate patterns of herbivore diversity in the Arctic. *Glob. Ecol. Biogeogr.* (2016) doi:10.1111/geb.12470.
5. Post, E., Cahoon, S. M. P., Kerby, J. T., Pedersen, C. & Sullivan, P. F. Herbivory and warming interact in opposing patterns of covariation between arctic shrub species at large and local scales. *Proceedings of the National Academy of Sciences* **118**, e2015158118 (2021).
6. Wang, Y. *et al.* Late Quaternary dynamics of Arctic biota from ancient environmental genomics. *Nature* (2021) doi:10.1038/s41586-021-04016-x.

7. Garcés-Pastor, S. *et al.* High resolution ancient sedimentary DNA shows that alpine plant diversity is associated with human land use and climate change. *Nat. Commun.* **13**, 1–16 (2022).
8. Ficetola, G. F. *et al.* The development of terrestrial ecosystems emerging after glacier retreat. *Nature* **632**, 336–342 (2024).
9. Vitasse, Y. *et al.* Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. *Biol. Rev. Camb. Philos. Soc.* **n/a**,.
10. Elsen, P. R. *et al.* Accelerated shifts in terrestrial life zones under rapid climate change. *Glob. Chang. Biol.* (2021) doi:10.1111/gcb.15962.
11. Hobbs, R. J., Higgs, E. & Harris, J. A. Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* **24**, 599–605 (2009).
12. Jackson, S. T. & Overpeck, J. T. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* **26**, 194–220 (2000).
13. Schultz, E. L. *et al.* Climate-driven, but dynamic and complex? A reconciliation of competing hypotheses for species' distributions. *Ecol. Lett.* **25**, 38–51 (2022).
14. Oeser, J. *et al.* The best of two worlds: Using stacked generalisation for integrating expert range maps in species distribution models. *Glob. Ecol. Biogeogr.* (2024) doi:10.1111/geb.13911.
15. Fordham, D. A. *et al.* Using paleo-archives to safeguard biodiversity under climate change. *Science* **369**, (2020).
16. Di Marco, M., Pacifici, M., Maiorano, L. & Rondinini, C. Drivers of change in the realised climatic niche of terrestrial mammals. *Ecography (Cop.)* **44**, 1180–1190 (2021).
17. Birks, H. J. B. Contributions of Quaternary botany to modern ecology and biogeography. *Plant Ecol. Divers.* **12**, 189–385 (2019).
18. Boilard, A. *et al.* Ancient DNA and osteological analyses of a unique paleo-archive reveal Early Holocene faunal expansion into the Scandinavian Arctic. *Science Advances* **10**, eadk3032 (2024).
19. Kjær, K. H. *et al.* A 2-million-year-old ecosystem in Greenland uncovered by

environmental DNA. *Nature* **612**, 283–291 (2022).

20. Brown, T. *et al.* Paleoeconomy more than demography determined prehistoric human impact in Arctic Norway. *PNAS Nexus* **1**, gac209 (2022).

21. Liu, S. *et al.* Tibetan terrestrial and aquatic ecosystems collapsed with cryosphere loss inferred from sedimentary ancient metagenomics. *Sci. Adv.* **10**, eadn8490 (2024).

22. Garcés-Pastor, S. *et al.* Wild and domesticated animal abundance is associated with greater late-Holocene alpine plant diversity. *Nat. Commun.* **16**, 3924 (2025).

23. Rantanen, M. *et al.* The Arctic has warmed nearly four times faster than the globe since 1979. *Commun. Earth Environ.* **3**, 1–10 (2022).

24. Hughes, A. L. C., Gyllencreutz, R., Lohne, Ø. S., Mangerud, J. & Svendsen, J. I. The last Eurasian ice sheets – a chronological database and time-slice reconstruction, DATED-1. *Boreas* **45**, 1–45 (2016).

25. Alsos, I. G. *et al.* Last Glacial Maximum environmental conditions at Andøya, northern Norway; evidence for a northern ice-edge ecological ‘hotspot’. *Quat. Sci. Rev.* **239**, 106364 (2020).

26. Rijal, D. P. *et al.* Sedimentary ancient DNA shows terrestrial plant richness continuously increased over the Holocene in northern Fennoscandia. *Sci Adv* **7**, (2021).

27. Alsos, I. G. *et al.* Postglacial species arrival and diversity buildup of northern ecosystems took millennia. *Science Advances* **8**, eabo7434 (2022).

28. Jørgensen, E. K. The palaeodemographic and environmental dynamics of prehistoric Arctic Norway: An overview of human-climate covariation. *Quat. Int.* **549**, 36–51 (2020).

29. Gjerde, J. M. Rock art and landscapes : studies of Stone Age rock art from northern Fennoscandia. (University of Tromsø, 2010).

30. Murchie, T. J., Giguet-Covex, C., Heintzman, P. D., Slon, V. & Wang, Y. Terrestrial fauna and hominin DNA from sedimentary archives. in *Developments in Paleoenvironmental Research* 299–378 (Springer International Publishing, Cham, 2023).

31. Bennett, J. R. *et al.* How ignoring detection probability hurts biodiversity conservation. *Front. Ecol. Environ.* **22**, (2024).

32. Guthrie, A. M. *et al.* A quantitative analysis of vertebrate environmental DNA degradation in soil in response to time, UV light, and temperature. *Environ. DNA* **6**, (2024).
33. Descamps, S. *et al.* Climate change impacts on wildlife in a High Arctic archipelago – Svalbard, Norway. *Glob. Chang. Biol.* **23**, 490–502 (2017).
34. Larsen, E. *et al.* Cave stratigraphy in western Norway; multiple Weichselian glaciations and interstadial vertebrate fauna. *Boreas* **16**, 267–292 (1987).
35. Valen, V., Mangerud, J., Larsen, E. & Hufthammer, A. K. Sedimentology and stratigraphy in the cave Hamnsundhelleren, western Norway. *J. Quat. Sci.* **11**, 185–201 (1996).
36. Valiranta, M. *et al.* Plant macrofossil evidence for an early onset of the Holocene summer thermal maximum in northernmost Europe. *Nat. Commun.* **6**, (2015).
37. Økland, J. Ø. K. *Vann Og Vassdrag 4 Dyr Og Planter : Innvandring Og Geografisk Fordeling*. (Stabekk, 1999).
38. Borovikova, E. & Nikulina, Y. The Contact Zone of Phylogenetic Lineages of Freshwater Fish in Arctic Eurasia: Genetic Polymorphism of Coregonid Populations. *Diversity* **15**, 163 (2023).
39. Mjelde, M., Thrane, J.-E. & Demars, B. O. L. High aquatic macrophyte diversity in Norwegian lakes north of the Arctic Circle. *Freshw. Biol.* **68**, 509–522 (2023).
40. Lagerholm, V. K. *et al.* On the origin of the Norwegian lemming. *Mol. Ecol.* **23**, 2060–2071 (2014).
41. Fedorov, V. B. & Stenseth, N. C. Glacial survival of the Norwegian lemming (Lemmus lemmus) in Scandinavia: inference from mitochondrial DNA variation. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 809–814 (2001).
42. Bachura, O. P. & Kosintsev, P. A. The ranges of mammals in the Urals at the end of the late Pleistocene. *Biol. Bull. Russ. Acad. Sci.* **48**, S150–S165 (2021).
43. Hufthammer, A. K., Svendsen, J. I. & Pavlov, P. Animals and humans in the European Russian Arctic towards the end of the last Ice Age and during the mid-Holocene time.

Boreas **48**, 387–406 (2019).

44. Kullman, L. Early Holocene presence of beaver (Castor fiber L.) in the Scandes sustains warmer-than-present conditions and a patchily treed and rich mountainscape. *Int. J. Res. Geogr.* **7**, (2021).

45. Soininen, E. M. *et al.* Analysing diet of small herbivores: the efficiency of DNA barcoding coupled with high-throughput pyrosequencing for deciphering the composition of complex plant mixtures. *Front. Zool.* **6**, 16 (2009).

46. Soininen, E. M. *et al.* Not only mosses: lemming winter diets as described by DNA metabarcoding. *Polar Biol.* **40**, 2097–2103 (2017).

47. Steinthordsdottir, L. Investigating trophic interactions among herbivorous species in a rapidly changing Arctic tundra using DNA metbarcoding. (University of Oslo, 2019).

48. Kemppinen, J. *et al.* Microclimate, an important part of ecology and biogeography. *Glob. Ecol. Biogeogr.* **33**, (2024).

49. Salmi, A.-K., van den Berg, M., Niinimäki, S. & Pelletier, M. Earliest archaeological evidence for domesticated reindeer economy among the Sámi of Northeastern Fennoscandia AD 1300 onwards. *J. Anthropol. Archaeol.* **62**, 101303 (2021).

50. Rijal, D. P. *et al.* Millennia of metacommunity heterogenization, homogenization and stabilisation captured by sedimentary ancient DNA. *Ecol. Lett.*

51. Ims, R. A. *et al.* Can reindeer overabundance cause a trophic cascade? *Ecosystems* **10**, 607–622 (2007).

52. Bradley, S. L., Ely, J. C., Clark, C. D., Edwards, R. J. & Shennan, I. Reconstruction of the palaeo-sea level of Britain and Ireland arising from empirical constraints of ice extent: implications for regional sea level forecasts and North American ice sheet volume. *J. Quat. Sci.* **38**, 791–805 (2023).

53. Sjögren, P. *et al.* Lake sedimentary DNA accurately records 20th Century introductions of exotic conifers in Scotland. *New Phytol.* **213**, 929–941 (2017).

54. Giguet-Covex, C., Jelavić, S. & Foucher, A. The Sources and Fates of Lake Sedimentary DNA. *Change Using Lake …* (2023).

55. Revéret, A. *et al.* Environmental DNA of aquatic macrophytes: The potential for reconstructing past and present vegetation and environments. *Freshw. Biol.* (2023) doi:10.1111/fwb.14158.
56. Garcés-Pastor, S. *et al.* Terrestrial Plant DNA from Lake Sediments: Volume 6: Sedimentary DNA. in *Tracking Environmental Change Using Lake Sediments* (eds. Capo, E., Barouillet, C. & Smol, J. P.) vol. 21 275–298 (Springer International Publishing, Cham, 2023).
57. Strandberg, N. *et al.* Capture probe, metabarcoding, or shotgun sequencing: which best reflects local vegetation? *bioRxiv* 2025.10.06.680654 (2025) doi:10.1101/2025.10.06.680654.
58. Seeber, P. A. & Epp, L. S. Environmental DNA and metagenomics of terrestrial mammals as keystone taxa of recent and past ecosystems. *Mamm. Rev.* **52**, 538–553 (2022).
59. Lammers, Y. *et al.* Clitellate worms (Annelida) in lateglacial and Holocene sedimentary DNA records from the Polar Urals and northern Norway. *Boreas* **48**, 317–329 (2019).
60. Orlando, L. *et al.* Ancient DNA analysis. *Nat. Rev. Methods Primers* **1**, (2021).
61. Giguet-Covex, C. *et al.* Long livestock farming history and human landscape shaping revealed by lake sediment DNA. *Nat. Commun.* **5**, (2014).
62. Boyer, F. *et al.* OBITOOLS: a unix-inspired software package for DNA metabarcoding. *Mol. Ecol. Resour.* **16**, 176–182 (2016).
63. Renaud, G., Schubert, M., Sawyer, S. & Orlando, L. Authentication and assessment of contamination in ancient DNA. *Methods Mol. Biol.* **1963**, 163–194 (2019).
64. Gjerde, J. M. Frequency, phases and chronology of rock art: Spatiotemporal studies of the Alta rock carvings, northernmost Europe. *Oxf. J. Archaeol.* **43**, 108–134 (2024).
65. Tansem, K. Retracing Storsteinen: A deviant rock art site in Alta, northern Norway. *Fennoscandia archaeologica* **37**, 83–107 (2020).
66. Møller, J. & Holmeslet, B. *Sealevel Change. Computer Program, University of Tromsø*. (1998).

67. Griffith, D. M., Veech, J. A. & Marsh, C. J. cooccur: Probabilistic Species Co-Occurrence Analysis inR. *J. Stat. Softw.* **69**, 1–17 (2016).

68. R Core Team. R: A language and environment for statistical computing (R Version 4.4.2, R Foundation for Statistical Computing, Vienna, Austria, 2020). Preprint at (2024).

69. Veech, J. A. The pairwise approach to analysing species co-occurrence. *J. Biogeogr.* **41**, 1029–1035 (2014).

70. Popovic, G. C., Warton, D. I., Thomson, F. J., Hui, F. K. C. & Moles, A. T. Untangling direct species associations from indirect mediator species effects with graphical models. *Methods Ecol. Evol.* **10**, 1571–1583 (2019).

71. Dormann, C. F., Gruber, B. & Fründ, J. Introducing the bipartite Package: Analysing Ecological Networks. *R News* **8**, 8–11 (2008).

72. Walker, M. *et al.* Formal subdivision of the Holocene series/epoch: A summary. *J. Geol. Soc. India* **93**, 135–141 (2019).

73. Tyler, T., Herbertsson, L., Olofsson, J. & Olsson, P. A. Ecological indicator and traits values for Swedish vascular plants. *Ecol. Indic.* **120**, 106923 (2021).

74. Karger, D. N., Nobis, M. P., Normand, S., Graham, C. H. & Zimmermann, N. E. CHELSA-TraCE21k: Downscaled transient temperature and precipitation data since the last glacial maximum. *EnviDat* (2020) doi:10.16904/envidat.211.

75. Oksanen, J. *et al.* vegan: Community Ecology Package. R package version 2.6-8. https://cran.r-project.org/web/packages/vegan/vegan.pdf (2024).

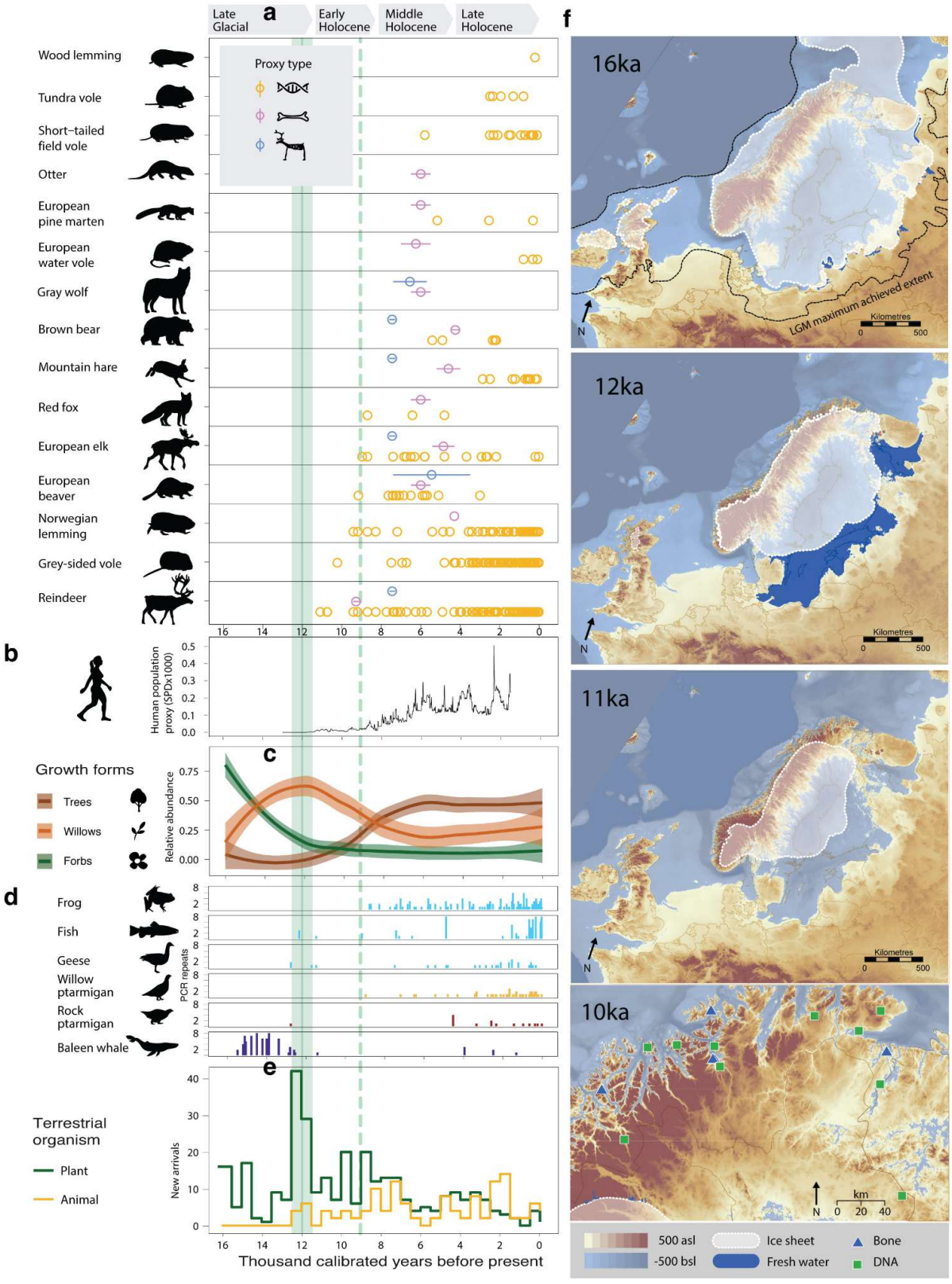
76. Bråthen, K. A. *et al.* Endozoochory varies with ecological scale and context. *Ecography* **30**, 308–320 (2007).

77. Elith, J., Leathwick, J. R. & Hastie, T. A working guide to boosted regression trees. *J. Anim. Ecol.* **77**, 802–813 (2008).

78. Swanson, H. K. *et al.* A new probabilistic method for quantifying n-dimensional ecological niches and niche overlap. *Ecology* **96**, 318–324 (2015).

79. Tuomi, M. *et al.* Herbivore effects on ecosystem process rates in a low-productive system. *Ecosystems* **22**, 827–843 (2019).

80. Brooks, M. *et al.* GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**, 378 (2017).
81. Hartig, F. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)Regression Models. (2024).



914

915 ***Fig. 1. Arrival of animals and plant to N Fennoscandia in relation to regional***
916 ***landscape change since the Last Glacial Maximum (LGM)***. ***a, f,*** *sedaDNA coring sites*
917 *and rock-art sites in relation to palaeo-topography [52], the most credible ice-sheet extent [24],*

and palaeo-shorelines (marine and ice-dammed lakes) at three time points (see Supplementary Fig. 1 for additional time points). ***b,*** *Arrival of terrestrial mammals recorded in sedaDNA, bones, and rock-art. The green vertical line shows a plant trait breakpoint at 12.0 cal ka BP, and the green dashed line shows the time of stabilisation of plant traits (9.0 cal BP calculated from [27]).* ***c,*** *Human population size based on models using the density of radiocarbon dates [28].* ***d,*** *Changes in the abundances of forbs, willows (*Salix*) and trees, including birch (which could represent shrubs or trees) calculated as proportion of sedaDNA sequence reads.* ***e****, Detections of selected animals. Note that the fish represent three taxa and the geese represent two taxa.* ***f,*** *New arrivals of terrestrial animals and plants in the study region within 500-yr time bins.*

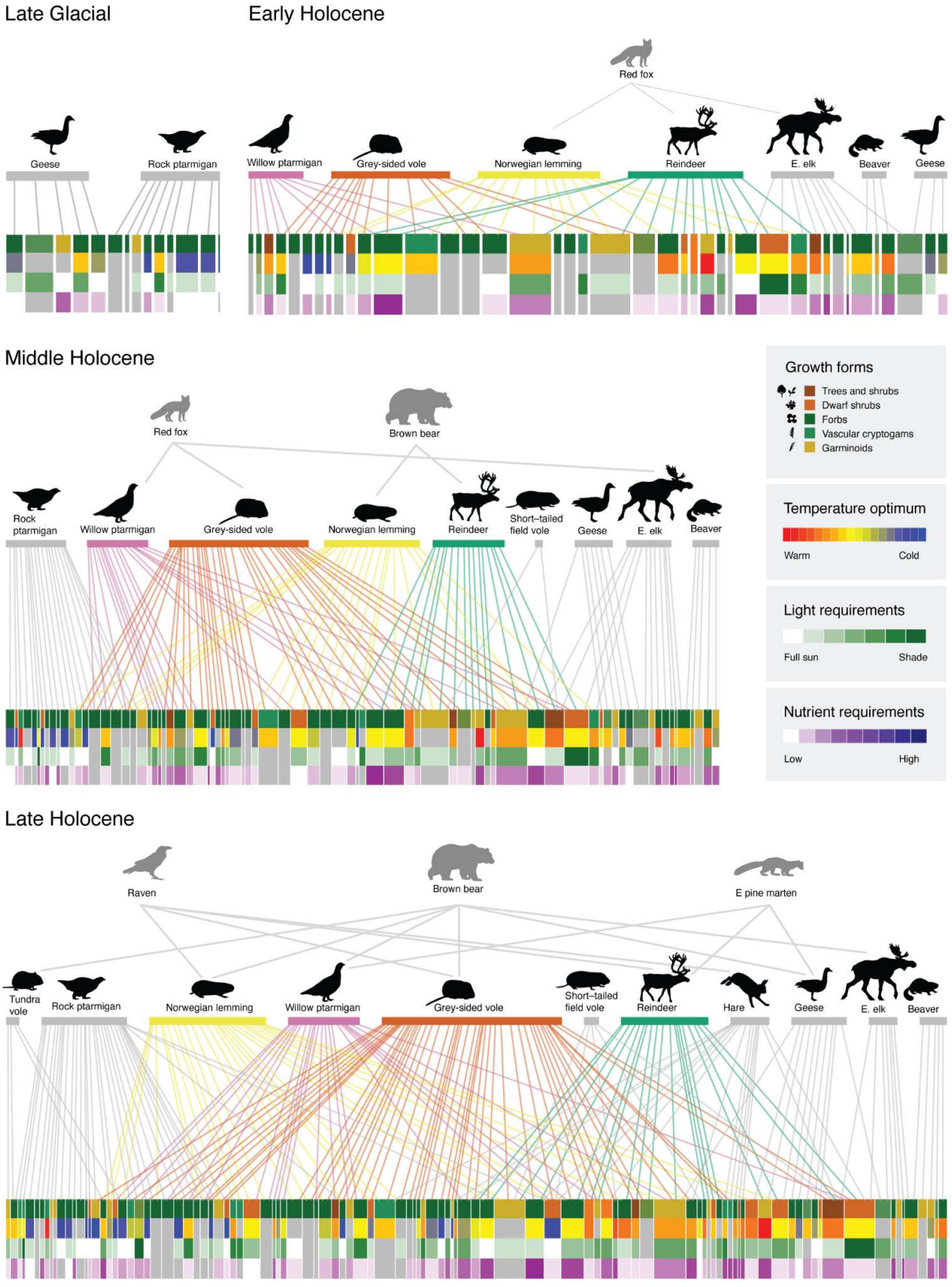
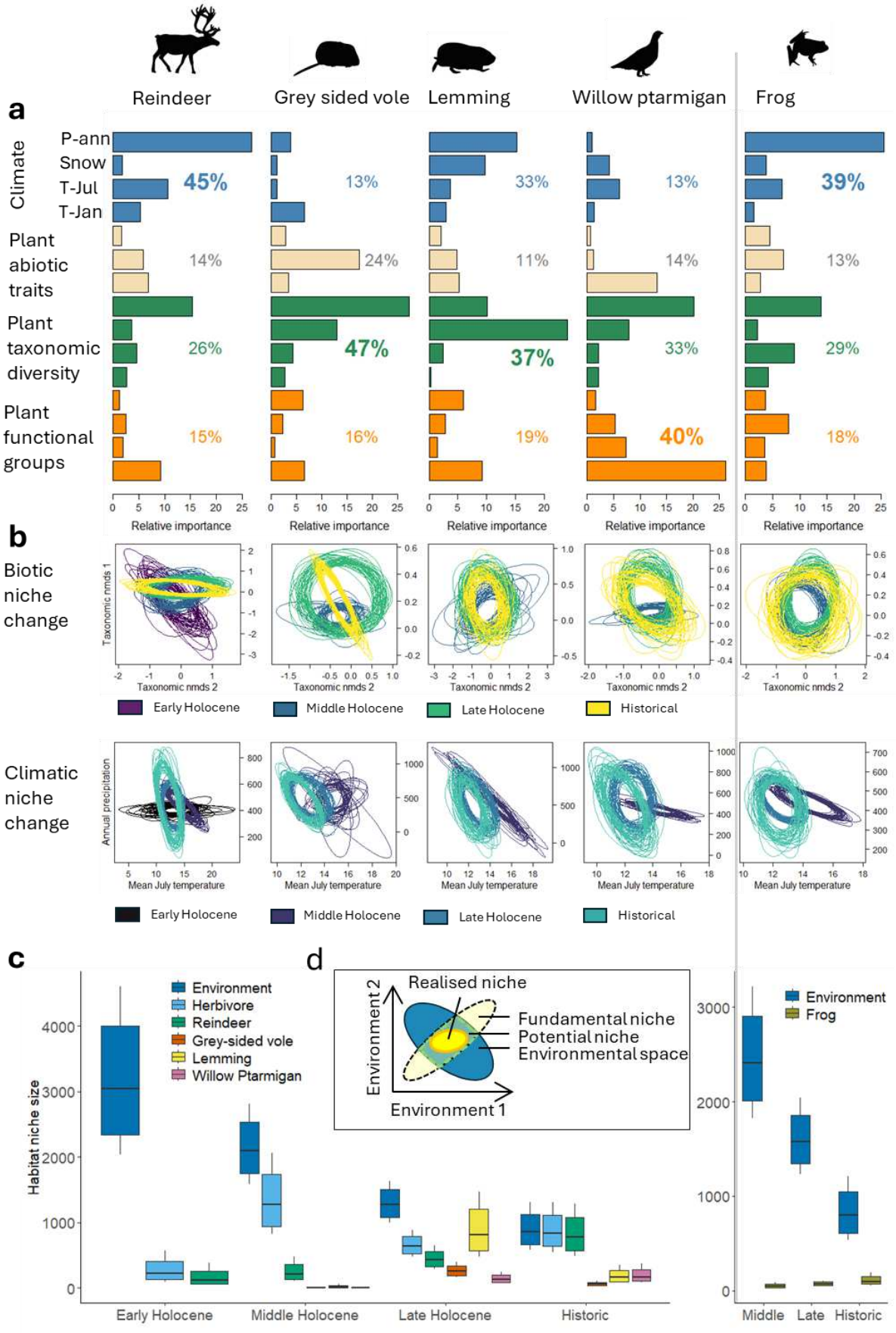


Fig. 2. Changes in plant-herbivore-carnivore networks through time. *Plant–herbivore network were based on significant co-occurrences ($p<0.05$) and the plants taxa are shown according to their traits.Networks are given for the periods Late Glacial (12.8–11.7 ka cal BP), Early Holocene (11.7–8.3 ka cal BP), Middle Holocene (8.3–4.25 ka cal BP), and Late*

Holocene (≤4.25 ka cal BP). Each line connects to a single plant taxon that is colour coded according to growth form and requirements for temperature, light and nutrients. For plant taxon names, see Supplementary Table S6; for all networks with 75% co-occurrence, see Supplementary Fig. 6.1.


Reindeer
Grey sided vole
Lemming
Willow ptarmigan
Frog
a
Climate
P-ann
Snow
T-Jul
T-Jan
Plant abiotic traits
Plant taxonomic diversity
Plant functional groups
45%
13%
33%
13%
39%
14%
24%
11%
14%
13%
26%
47%
37%
33%
29%
15%
16%
19%
40%
18%
Relative importance
b
Biotic niche change
Taxonomic nmds 1
Taxonomic nmds 2
Early Holocene
Middle Holocene
Late Holocene
Historical
Climatic niche change
Annual precipitation
Mean July temperature
c
Environment
Herbivore
Reindeer
Grey-sided vole
Lemming
Willow Ptarmigan
Habitat niche size
Early Holocene
Middle Holocene
Late Holocene
Historic
d
Realised niche
Fundamental niche
Potential niche
Environmental space
Environment 1
Environment 2
Environment
Frog
Middle
Late
Historic

939

Fig. 3. Relative importance of niche dimensions and changes in niches and environmental space over time. *Niche size and dimensions over time for the four key herbivores, reindeer (*Rangifer tarandus*), grey-sided vole (*Myodes rufocanus*), Norwegian lemming (*Lemmus lemmus*), willow ptarmigan (*Lagopus lagopus*) and the only widespread amphibian in the region common frog (*Rana temporaria*); for the latter, the estimates include aquatic plants.* ***a****, Importance of realised niches measured at different dimensions as climate variables only (P-ann is annual precipitation, T-July and T-Jan is mean July and January temperature), plant abiotic traits, plant taxonomic composition, and plant functional traits. The set of niche dimensions that best predict species occurrence is highlighted in bold.* ***b****, Niche change over time exemplified by the two most important biotic niche dimensions (plant taxonomic diversity NMDS with dimensions of 1 and 2) and climatic dimensions (annual precipitation and July temperature).* ***c****, Environmental space (see definition in insert* ***d****) and niche size changes over time on the basis of the first four dimensions of a PCA, which represents 70% of the variation in the 15 niche dimensions. The horizontal lines represent median values, with boxes representing 80% and bars representing 95% of the posterior probabilities. For full plots of the niche dimensions for each animal and the environmental space, see Supplementary Information 6-7.*

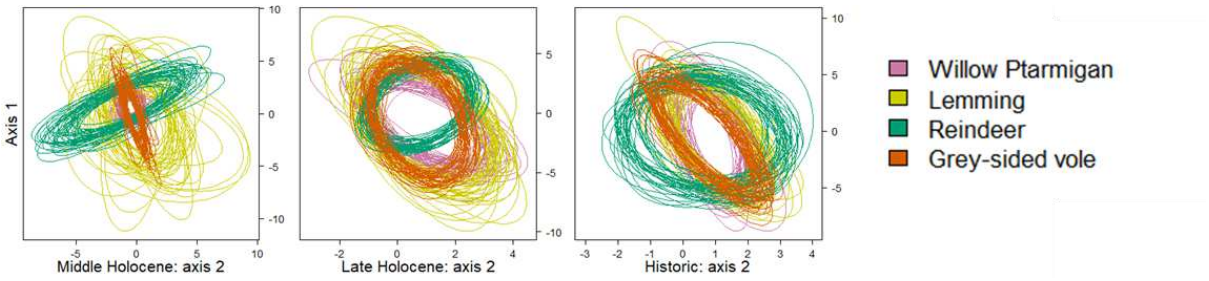


Fig. 4. Changes in niche overlap among four herbivores over time. *The plots show each of Early Holocene (11.7–8.3 ka BP), Late Holocene (≤4.25 ka cal BP), and Historical period (<0.65 ka BP) and are based on four dimensions of a PCA representing 70% of the variation in the initial 15 niche dimensions. See Supplementary Information 8 for overlap in each of the sets of traits and periods.*

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplTableS1S9.xlsx
- Suppl.Bioticinteractions.pdf
- NCOMMS26057786rs.pdf
- Suppl.BioticInteractionslinenumbered.pdf