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Arctic defaunation initiated a cascade of mammal–plant interaction shift through dispersal dynamics

Sisi Liu[1]*, Kathleen S. Leichsenring[1], Marc-Thorsten Hütt[2], Boris Biskaborn[1], Bernhard Diekmann[1], Darrell S. Kaufman[3], Hanno Meyer[1], Martin Melles[4], Luidmila A. Pestryakova[5], Ulrike Herzschuh[1,6,7]*

[1]Polar Terrestrial Environmental Systems, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Potsdam 14473, Germany

[2]Computational Systems Biology, Constructor University, Bremen 28759, Germany

[3]School of Earth and Sustainability, Northern Arizona University, Arizona 86011, USA

[4]Institute of Geology and Mineralogy, University of Cologne, Cologne 50674, Germany

[5]Institute of Natural Sciences, North-Eastern Federal University of Yakutsk, Yakutsk 677007, Russia

[6]Institute of Environmental Science and Geography, University of Potsdam, Potsdam 14469, Germany

[7]Institute of Biochemistry and Biology, University of Potsdam, Potsdam 14476, Germany

*Corresponding author:

Sisi Liu (sisi.liu@awi.de); Ulrike Herzschuh (Ulrike.Herzschuh@awi.de)

Abstract:

Most large terrestrial mammals are declining rapidly under climate change, but whether their loss triggers broader ecosystem collapse remains unresolved. Using sedimentary ancient metagenomics, we reconstructed ecological networks and community turnover of Arctic mammals and plants over the past 25,000 years. We identified rewiring of mammalian interactions between 25–15 ka initiating cascading effects, culminating in the steppe–tundra's transition to open woodland by 10 ka. Incorporating traits analysis, we revealed this prolonged process was buffered by long-distance seed dispersal—especially via megaherbivores—but loss of dispersal due to defaunation ultimately drove steppe–tundra collapse. Trophic interactions by megaomnivores and small mammals were insufficient to prevent turnover. Our findings identify resilient interactions and key megafaunal functions, offering insights for targeted rewilding to restore Arctic ecosystem functioning.

Main Text

Introduction

Climate change is accelerating global declines, extinctions, and local extirpations of terrestrial animals (*1*)—with large-bodied mammals—particularly megaherbivores and top predators—being most at risk (*2*). The extent to which these declines disrupt trophic (e.g., predation, herbivory) and mutualistic (e.g., seed dispersal) interactions—and how such disruptions unfold over time—remains insufficiently understood (*3*, *4*). Yet defaunation is not a uniquely contemporary phenomenon (*5*). A similar pronounced event happened around the end of the last glacial period (*6*), when many large-bodied mammals like mammoths disappeared. This was concurrent with the collapse of the vast mammoth-steppe ecosystem (*7*), once the largest biome on Earth.

While megafaunal extinction drivers have been debated for decades, the ecological consequences—particularly the collapse of biotic interactions—are only beginning to be understood (*8*). Crucially, Holarctic megafaunal declines unfolded gradually (*6*), likely altering terrestrial ecosystems well before final extinction (*9*). This raises the hypothesis—so far untested in paleoecology—that cascading losses of biotic interactions due to defaunation may have contributed to the ecological reorganization of the mammoth-steppe ecosystem.

Alternative to biotic interaction loss, the role of defaunation in enabling the emergence of novel interactions has received far less attention (*10*, *11*). Different types of reconstructed interaction networks offer complementary insights: for example, predator-prey webs suggest greater functional redundancy in the Pleistocene than Holocene, with release from top-predator loss leading to increases in megaherbivore density and distribution (*12*). Herbivory-plant interactions indicate that some surviving small-bodied herbivores shifted from browsing to mixed feeding between the Pleistocene and Holocene (*13*), potentially forming new trophic interactions. Plant–frugivore seed dispersal interactions exhibited profound rearrangement rather than complete structural collapse after late Pleistocene megafaunal loss (*10*). While this

suggests a degree of functional replacement, it raises open questions about whether such interaction rewiring may have influenced the composition of plant communities.

Additionally, the mechanisms behind the re-establishment of lost interactions—so-called "resilient links"—are still not well understood. Clarifying the role of functional traits in this process could provide important insights for coextinction risk assessments—particularly by accounting for interaction rewiring, the ability of taxon to switch partners in response to perturbations—as a potential buffer against cascading extinctions (*14*).

While much has been learned about past changes in taxonomic abundance across space and time, the dynamics of ecological interactions remain underexplored, as interactions are rarely preserved due to the sparse fossil record. Sedimentary ancient DNA (sedaDNA) holds promise to infer biotic interactions by providing spatially and temporally extensive evidence of past taxonomic co-occurrence. When combined with species traits, sedaDNA can help infer potential ecological interaction pathways with greater resolution than fossil records and more empirical grounding than trait-matching models alone.

To address these knowledge gaps, we conducted ancient metagenomic (shotgun sequencing) analyses of terrestrial mammals and plants from 119 lake sediment samples across Siberia and the North American Arctic spanning the past 25,000 years (Fig. 1A). These samples, collected from six lake cores located in regions that overlap with known megafaunal fossil distributions, provide the spatial and temporal resolution necessary to track changes in size-selective defaunation such as woolly mammoth and associated plant community dynamics and their interaction networks.

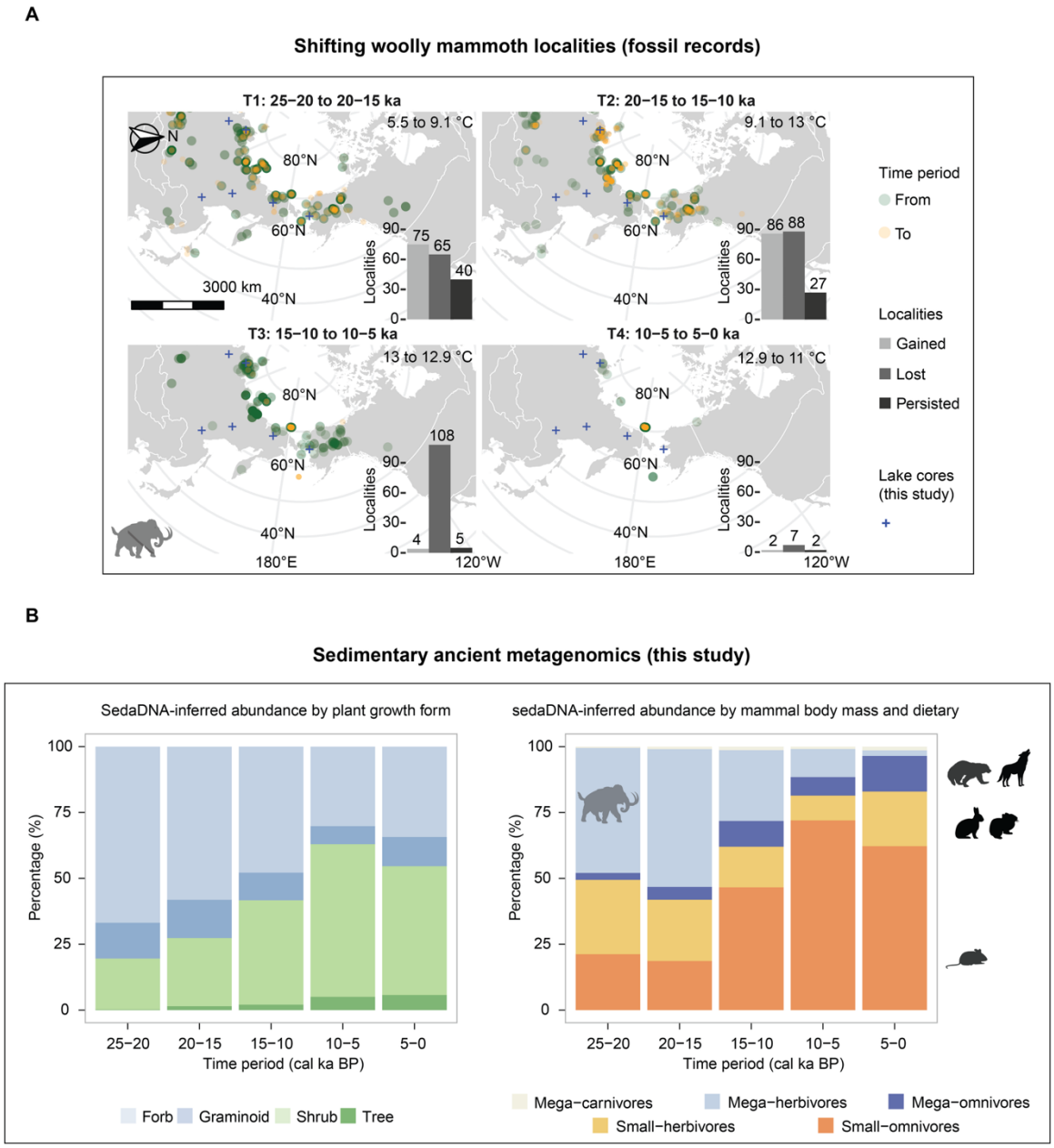

Fig. 1 Evidence of community changes in northern Eurasia and North America over the past 25 ka. (**A**) Illustration of woolly mammoth range changes across four time periods based on fossil and genetic records, showing progressive expansion and contraction of its geographical distribution, broadly reflecting population trends across cold and warm climatic phases (June-July-August temperature 5.5–11°C) (*15*), culminating in extinction during the late Holocene (5–0 ka) (*7*, *16*, *17*). Locations of study lake sediment cores are indicated. Fossil records are colored by time, with green for earlier periods ("from") and orange for later ones ("to"). (**B**) In this study, sedaDNA-inferred vegetation shifts from steppe-tundra to open woodland ecosystems. Concurrent sedaDNA-inferred shifts in mammal communities, from mega-herbivore-dominated to mega-omnivores with smaller-bodied mammals, indicate collapse of the mammoth steppe ecosystem. Silhouette images illustrate the growth forms and main mammalian taxa in each category, and are provided under the CC0 1.0 Universal license. Source data and codes are detailed in Materials and Methods.

Robust reconstruction of millennial-scale ecological interactions and compositional dynamics from sedimentary ancient metagenomics

In total, 23,484,571 reads were used for terrestrial ecosystem reconstruction, corresponding to 16 mammalian and 50 seed-bearing plant families (data S1). These reads, with a best identity of ⩾95% against the comprehensive taxonomic reference database, were retained as part of a multi-step strategy to minimize false positives and noise (table S1, Materials and Methods). The ancient origin of the reads was authenticated by read length distribution (fig. S1) and characteristic C-to-T substitutions at the 5' and 3' ends, with sufficient reads over time for samples (fig. S2) and the represented mammals (fig. S3) and plants (fig. S4).

Our sedaDNA-inferred composition changes (Fig. 1B) in four time transitions (T) that represent terrestrial ecosystem shifts in Arctic (*7*, *16*, *18–20*): (T1) a homogeneous steppe-tundra with abundant megaherbivores during the coldest and driest Last Glacial Maximum (LGM, 25–20 ka), transitioning to herbaceous plants with megafauna still abundant, while woody plants began to advance during the cold and dry Late Glacial (20–15 ka); (T2) rapid warming towards the early Holocene (15–10 ka), coinciding with a substantial increase in the abundance of woody plants while decline in megaherbivores; (T3) a transition from open landscapes to denser woody vegetation during the optimal Holocene warming phase (10–5 ka); (T4) re-expansion of herbaceous vegetation and the extinction of mammoths during the cooling Late Holocene (5–0 ka). Based on these ecological transitions and addressing the fundamental challenge of inferring past ecological interactions from sedaDNA (*21*), we developed a comprehensive validation pipeline (detail in Materials and Methods) that establishes the reliability of ancient ecological network reconstruction.

Cascading effects: mammalian interactions shaped ecological turnover

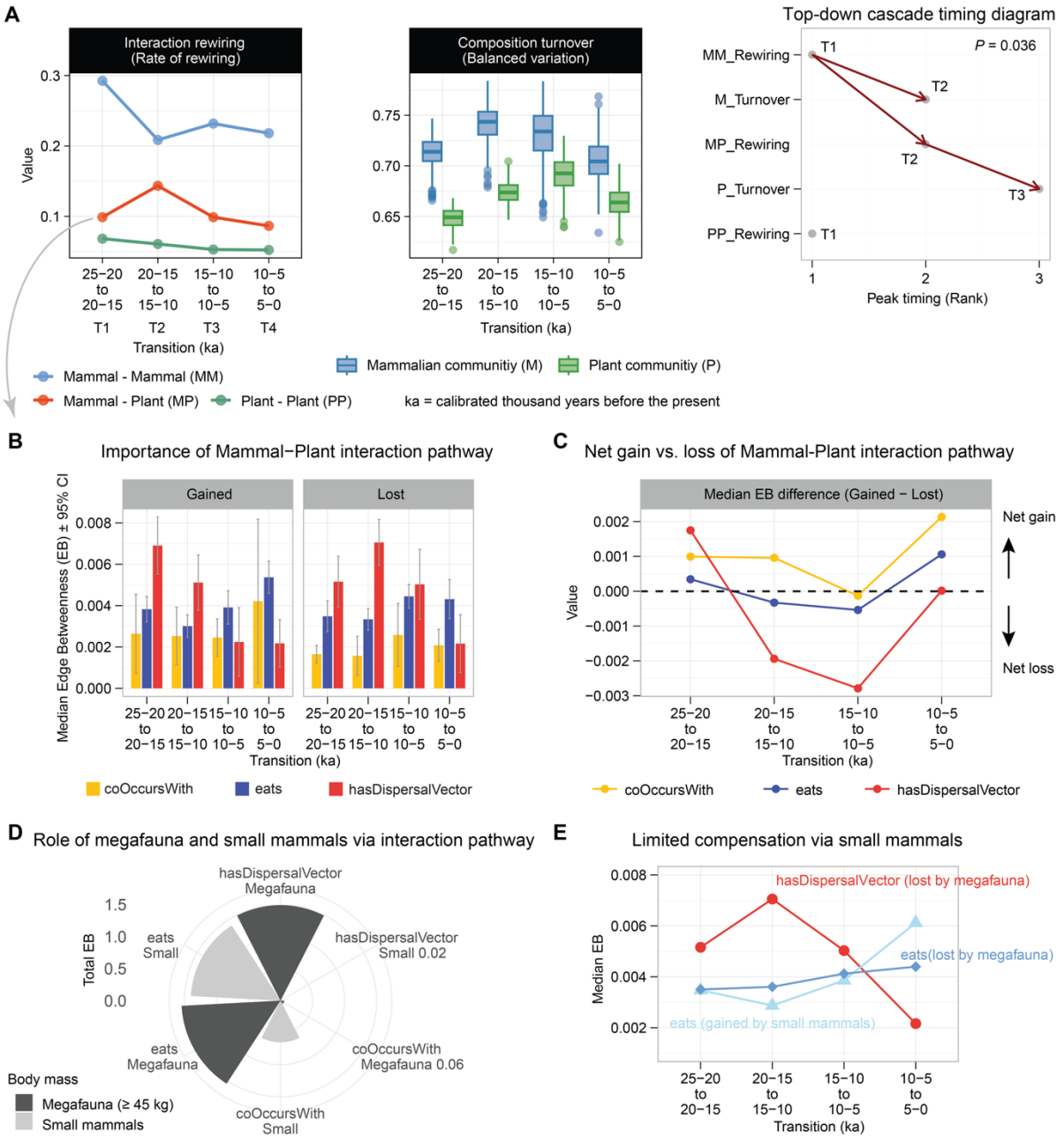

Fig 2. Cascading top-down regulation: mammal interaction dynamics drive ecological turnover over the past 25 ka. (**A**) Interaction rewiring (rate of rewiring) and composition turnover (balanced variation) reveal a top-down temporal cascade. (**B**) Mammal-plant interaction importance, measured by edge betweenness (EB), is shown across four-time transitions via three pathways—seed dispersal (hasDispersalVector), trophic (eats) interaction, and habitat co-occurrence (coOccursWith)—and categorized by fate (gained vs. lost). (**C**) Net gain (positive) versus net loss (negative) of mammal–plant interactions across time. (**D**) Interaction pathway importance grouped by body mass highlights that megafauna (N = 8) primarily contribute to seed dispersal and trophic, while small mammals (N = 8) are more involved in trophic and habitat co-occurrence. Total EB values < 1 are displayed directly. (**E**) Small mammals gained trophic links with lower EB than those lost through megafauna seed dispersal and trophic interactions by megafauna until a partial compensation in the late Holocene (5–0 ka). Source data and codes are detailed in Materials and Methods.

Our reconstructed ecological networks—comprising mammal–mammal, mammal–plant, and plant–plant interactions—varied in both the number of taxa (nodes) and ecological interactions (links) across the five time periods (table S2). A high rate of rewiring suggests rapid turnover in interaction structure, reflecting dynamic shifts in ecological roles or partner availability. We further quantified composition turnover (higher values indicate greater community heterogeneity) (*22*), alongside interaction rewiring, to characterize cascading ecological effects over time.

Our time-series sedaDNA data reveal a cascading effect of ecological change initiated by high mammal-mammal interaction rewiring (25–20 to 20–15 ka), followed by delayed peaks in mammalian composition and mammal-plant interaction rewiring (20–15 to 15–10 ka). Sequentially, mammal-plant interaction rewiring triggers maximum plant composition turnover (15–10 to 10–5 ka). We formally tested this cascade by comparing observed peak timing across interaction rewiring and compositional turnover events to a null model generated by permutation testing. This revealed that the temporal sequence is significantly driven by mammalian interaction rewiring, which acts as an initial trigger (P = 0.036, one-side, 999 permutations, Fig. 2A).

We propose that the peak in mammalian interaction rewiring from 25–20 to 20–15 ka may reflect the ecological consequences of top predator loss (*23*). For instance, the extinction of large carnivores such as scimitar-tooth cats (*Homotherium serum*) in Eurasia around 24.7 ka (*19*), as a generalist predator of large herbivores in open landscapes (*24*), may have reduced predation pressure and enabled the expansion of megaherbivore populations. This supported by our detection of a marked increase in relative abundance of megaherbivores (e.g., Elephantidae, Bovidae, Equidae, and Cervidae) from LGM (25–20 ka) to the late-glacial period (20–15 ka; Fig. 1B). Similar accelerated population growth of large herbivores following predator loss have been reported elsewhere (*25*, *26*). This likely reshaped mammal–mammal interactions by altering competition and predation dynamics. Surviving megaherbivores and carnivores, with flexible diets (*24*), may have supported this rewiring. Their large ranges and mobility (fig. S5) enabled rapid reorganization of interactions across regions. We suggest that such flexibility—amplified by reduced top-down control—helped stabilize community composition, delaying turnover despite major shifts in interaction structure.

We detected a sharp decline in the relative abundance of megaherbivores—alongside a marked drop in mammalian interaction rewiring—from 20–15 to 15–10 ka (Fig. 2A). A concurrent rise in network modularity (fig. S6) suggests that, rather than forming well-connected webs, surviving mammals increasingly clustered into more isolated groups with fewer cross-trophic interactions. Lower interaction redundancy made mammalian communities more vulnerable to perturbations, contributing to the pronounced turnover in composition during this transition. Thereafter, mammalian interaction rewiring remained low and compositional turnover declined into the late Holocene (5–0 ka), supporting the view that the decline in interaction redundancy and replacement capacity drove community simplification and reduced resilience (*13*).

Remarkably, our sedaDNA records show no concurrent peak in plant compositional turnover with abundant megaherbivores from 25–20 to 20–15 ka. According to isotopic evidence of

fossil remains (40 ka to 13 ka) suggests pronounced dietary partitioning among coexisted megaherbivores in the mammoth steppe (*24*)—potentially supporting marked heterogeneous plant communities. In contrast, our finding suggests that trophic effects alone did not drive vegetation shifts, conflicting with the commonly held view that grazing necessarily causes strong vegetation change such as herbivory reducing tree cover (*27*) or favoring grazing-tolerant grass and forbs (*28*, *29*). One plausible explanation for this discrepancy is that surveys conducted in already-defaunated ecosystems may be biased (*30*).

To explore this megafaunal grazing paradox, we measured edge betweenness centrality for mammal–plant interactions—capturing how critical each link is to maintaining network connectivity (*31*). We found that seed dispersal interactions (hasDispersalVector) (Fig. 2B), primarily associated with megafauna (Fig. 2C), exhibited higher median edge betweenness than trophic and habitat co-occurrence (coOccursWith) during 25–20 ka and 20–15 ka. This suggests that megafaunal-mediated seed dispersal served as a key integrative force, supporting ecological connectivity. Notably, this transition also showed the highest net gain in dispersal interactions (Fig. 2C) and the lowest plant compositional turnover (Fig. 2A). Given that seed dispersal distance and gut retention time scale positively with mammalian body mass (*32*), the expansion of megaherbivores during this transition (Fig. 2B) likely promoted long-distance seed dispersal and enabled plants to track shifting habitats. This process, which in turn, may have promoted gene flow and reduced the likelihood of local plant extinctions (*18*), thereby buffering vegetation compositional differentiation across the mammoth-steppe landscape.

However, this buffering prominence diminished over time, with dispersal interactions showing lower edge betweenness values than the other two pathways from 15–10 ka onwards (Fig. 2B). Moreover, we found that dispersal interactions underwent consecutive net losses in edge betweenness from 20–15 ka to 10–5 ka, with the most pronounced decline occurring between 15–10 ka and 10–5 ka (Fig. 2C). This indicates that, although seed dispersal was initially crucial for maintaining connectivity, the newly established interactions failed to fully compensate for lost functions, resulting in reduced dispersal redundancy and weakened cohesion within the plant community. We detected that this dramatic loss coincided with a peak in plant community turnover (Fig. 2A), characterized by a notable increase in the relative abundance of woody taxa and a decrease in forbs and graminoids (Fig. 1B), which likely further enhanced beta diversity and contributed to habitat fragmentation. As a whole, our results highlight that the collapse of seed dispersal, escalating challenges to ecosystem integration, likely contributed to the ultimate collapse of the steppe-tundra biome.

Another key finding is that trophic interactions increased from 25–20 ka to 20–15 ka and showed only minor net losses from 15–10 ka to 10–5 ka, in contrast to the sharp decline in dispersal links (Fig. 2C). This likely reflects stable dietary partitioning among Late Pleistocene megafauna, as supported by isotopic data (*24*), which helped maintain trophic functions despite faunal turnover. In contrast, from the early to late Holocene (10–0 ka), trophic links showed a marked net gain, likely driven by shifts toward generalist diets in carnivores (*24*), and partial functional replacement of megafauna by smaller mammals (Fig. 2E). However, this transition lacked compensatory dispersal capacity, leaving open, woody-prone ecosystems increasingly vulnerable to grazing pressure.

Moreover, we propose that this buffering mechanism may offer a new perspective on the long-standing no-analog vegetation debate: landscapes characterized by extensive megafaunal movement likely lack modern analogs (e.g., in eastern North America during 17–10 ka), whereas ecosystems with limited dispersal have been suggested to show greater compositional similarity to present-day vegetation (e.g., in eastern North America during 23–20 ka) (*33*). Furthermore, although plant richness increased markedly during 10–5 ka in the Arctic (*7*, *20*, *34*), our results show a net loss of trophic interactions in edge betweenness from 15–10 ka to 10–5 ka (Fig. 2C). This suggests that newly added plants do not necessarily translate into functional trophic connectivity. While modern empirical studies recognize high plant diversity as important for maintaining ecosystem services (*35*), our findings indicate that diversity alone may overestimate functional reassembly if the functional trait matching and interaction efficiency of mammal–plant pairs are not accounted for.

While small mammals are frequently overlooked, our results highlight their important functional role. Notably, compared to the other two interaction pathways, interactions involving small mammals showed net gains only after the collapse of seed dispersal buffering during the late Holocene (5–0 ka) (Fig. 2E). While some small mammals are important agents of ecosystem functioning in modern Arctic ecosystems—for instance, through effects on soil nutrients and vegetation dynamics (*36*, *37*)—our findings suggest that their contributions were insufficient to compensate for the loss of ecological functions with respect to dispersal following megafaunal decline.

Cumulatively, our findings reveal a previously overlooked mechanism: seed dispersal interactions played a pivotal role in buffering vegetation change—long-distance megafaunal movement helped delay plant community turnover by millennia, even after mammalian community turnover had peaked.

Key mammal-plant interactions and their ecosystem-level influence

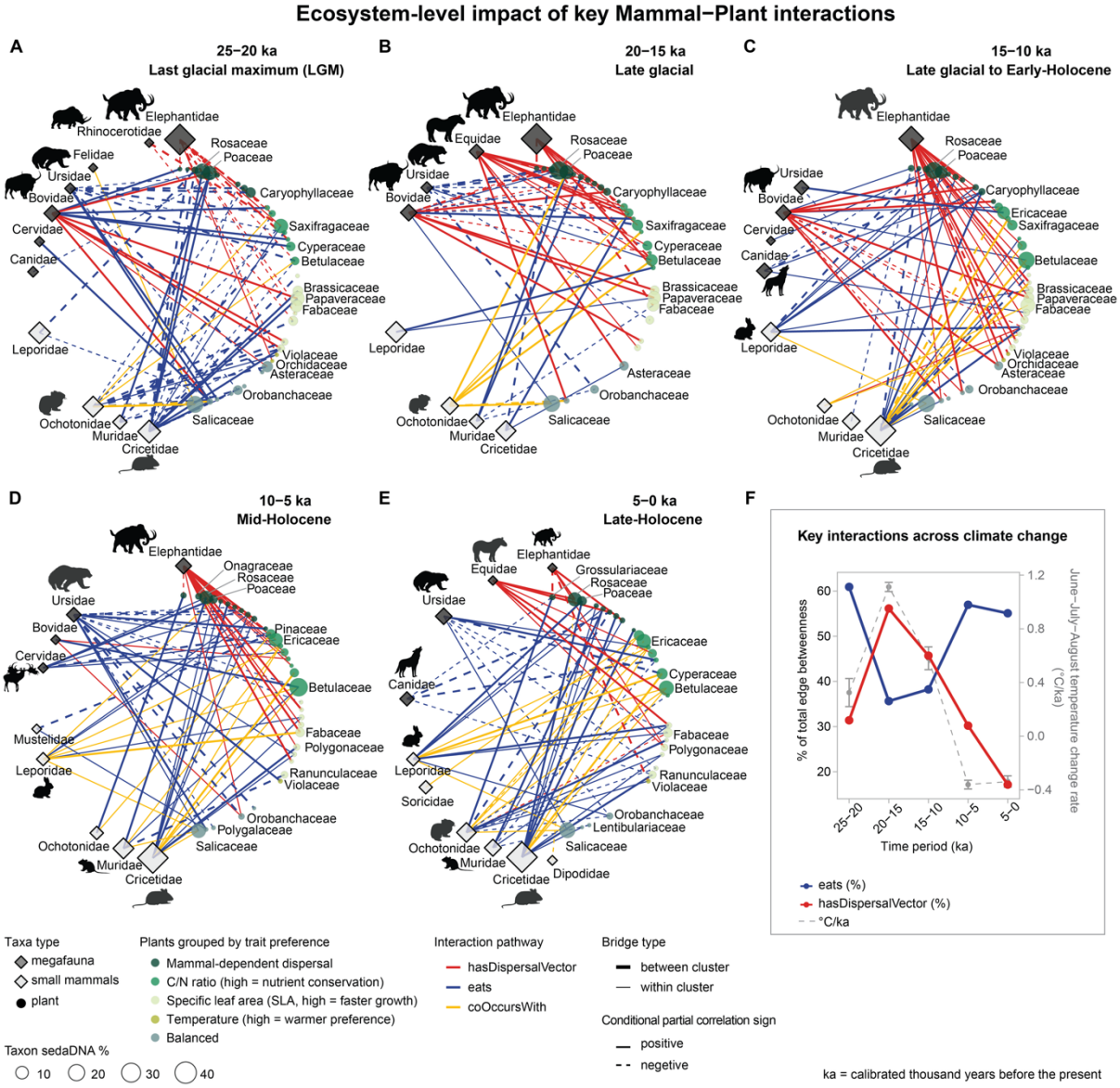

Fig. 3 Temporal dynamics of key mammal–plant interactions at ecosystem-level. (**A-E**) Key mammal–plant interactions over time. (**F**) The rate of summer (June–July–August) temperature change coincides with a shift in the dominant interaction pathway contributing to ecosystem connectivity, measured as the percentage of total edge betweenness (EB) of key interactions. Seed dispersal and trophic interactions are presented here. Node size reflects sedaDNA-based relative abundance; shapes distinguish megafauna, small mammals, and plants. Mammals are ordered by decreasing dispersal distance, plants by trait preferences. Link colors indicate interaction pathways; link borders indicate structural role within the network (within- vs. between-cluster bridges). Key interactions are defined as those with EB above the third quartile (Q3). Silhouette images are provided under the CC0 1.0 Universal license. Source data and codes are detailed in Materials and Methods.

Beyond overall patterns, we focused on key mammal-plant interactions—those with EB above the third quartile (Q3)—to determine which mammals regulate plant community structure and function, and through which interaction pathways, across time.

We found that key seed dispersal interactions were strongly associated with megaherbivores (e.g., Elephantidae, Bovidae, and Equidae) and were predominantly positive, except during the

LGM (Fig. 3A–E). This suggests their role as effective long-distance dispersers, maintaining ecological connectivity by linking otherwise distant or isolated taxa (*38*). In contrast, key trophic interactions involving mega-omnivores (e.g., Ursidae) were mainly negative (Fig. 3A–B and D–E), likely reflecting an extractive foraging strategy shaped by low site fidelity and dietary opportunism (*39*). Unlike some herbivores with high spatial fidelity (e.g., Bovidae and Elephantidae) (*40*, *41*), Ursidae's highly mobile behavior likely led to intensive consumption in localized areas before moving on, likely imposing diffuse consumptive pressure across plant taxa with varying traits (*42*). This pattern of foraging may have limited opportunities for mutualistic interactions. Moreover, cervids, though also classified as megaherbivores, primarily contributed to positive trophic interactions. This likely reflects their relatively short dispersal distances and generalist herbivory (fig. S5), including browsing on nutrient-poor, high C/N ratio plants such as Ericaceae (10–5 ka, Fig. 3D) and consumption of some fleshy fruits (e.g., Rosaceae during 15–5 ka, Fig. 3C and D). These patterns suggest cervids function more as localized consumers than landscape-scale seed vectors. These findings highlight that megafauna–even within herbivores–are functionally diverse.

As the relative abundance of megaherbivores as key dispersers peaked around 20–15 ka, coinciding with the highest relative contribution of seed dispersal interactions to total edge betweenness (Fig. 3F), indicating strong ecosystem-level dispersal efficacy. Despite rapid climate warming during this interval (Fig. 3F), plant compositional turnover remained low (Fig. 2A), suggesting that strong dispersal efficacy helped buffer vegetation change. However, these interactions gradually eroded afterwards: while still contributing more to connectivity than trophic interactions during 15–10 ka, their relative importance declined markedly and were eventually surpassed by trophic interactions during 10–5 ka and 5–0 ka, as the climate entered a more stable, warm phase. This progressive defaunation likely weakened overall ecosystem connectivity, limiting the ability of many plant species to colonize fragmented or newly available habitats. In turn, surviving mammals—including cervids, ursids, and mustelids—increasingly relied on locally available vegetation, intensifying grazing and browsing pressure on a broader range of plant taxa (Fig. 3D). Although key negative trophic interactions involving ursids were already present during the glacial periods (25–15 ka; Fig. 3B and C), their ecological impact was likely buffered by high mobility and the elevated importance of seed dispersal interactions (Fig. 3F) (*43*). However, ongoing defaunation reduced this buffering capacity, resulting in a sharp rise in both the relative importance and negativity of trophic interactions during the 10–5 ka (Fig. 3D and F). By the late Holocene (5–0 ka), neither trophic nor seed dispersal interactions regained dominance (Fig. 3F), indicating a breakdown of previously dominant function roles and a shift toward loss of functional integrity and redundancy. This convergence, following the earlier decline of megaherbivores, suggests that low dispersal efficacy may have undermined the structural conditions necessary to sustain key trophic dynamics. As functional redundancy eroded, ecosystems became increasingly vulnerable, setting the stage for an extinction debt that likely manifested as progressive taxonomic and functional simplification during the late Holocene, relative to the megafauna-rich glacial ecosystems.

Surprisingly, facilitation of seed dispersal via mammal movement appears to be context-dependent. During the LGM, many key dispersal links were negative (Fig. 3A). Our analysis shows that greater plant height tends to strengthen these negative associations (Effect size = –0.72 ± 0.32 SE, $P = 0.037$, table S3). This is likely because taller plants (e.g., Pinaceae) were mainly restricted to glacial refugia (*44*, *45*) and struggled to survive beyond them, making seed dispersal via mammal movement an ineffective colonization strategy. Instead, such interactions may have increased survival pressure on these taxa.

Interestingly, plants with higher leaf dry matter content (LDMC)—a trait associated with slow-growing, stress-tolerant strategies—exhibited weaker negative associations (effect size = 0.52 ± 0.26 SE, $P = 0.056$; table S3). High LDMC, indicative of tougher, more durable leaves with greater structural investment, likely enhanced resilience to harsh environmental conditions, making mammal-mediated dispersal less detrimental. This trait-based advantage may explain the continued abundance of dwarf shrubs such as Ericaceae and Betulaceae—families well known for stress tolerance—throughout the LGM and into the late glacial period.

Functional traits determine turnover and resilience in mammal-plant mutualisms

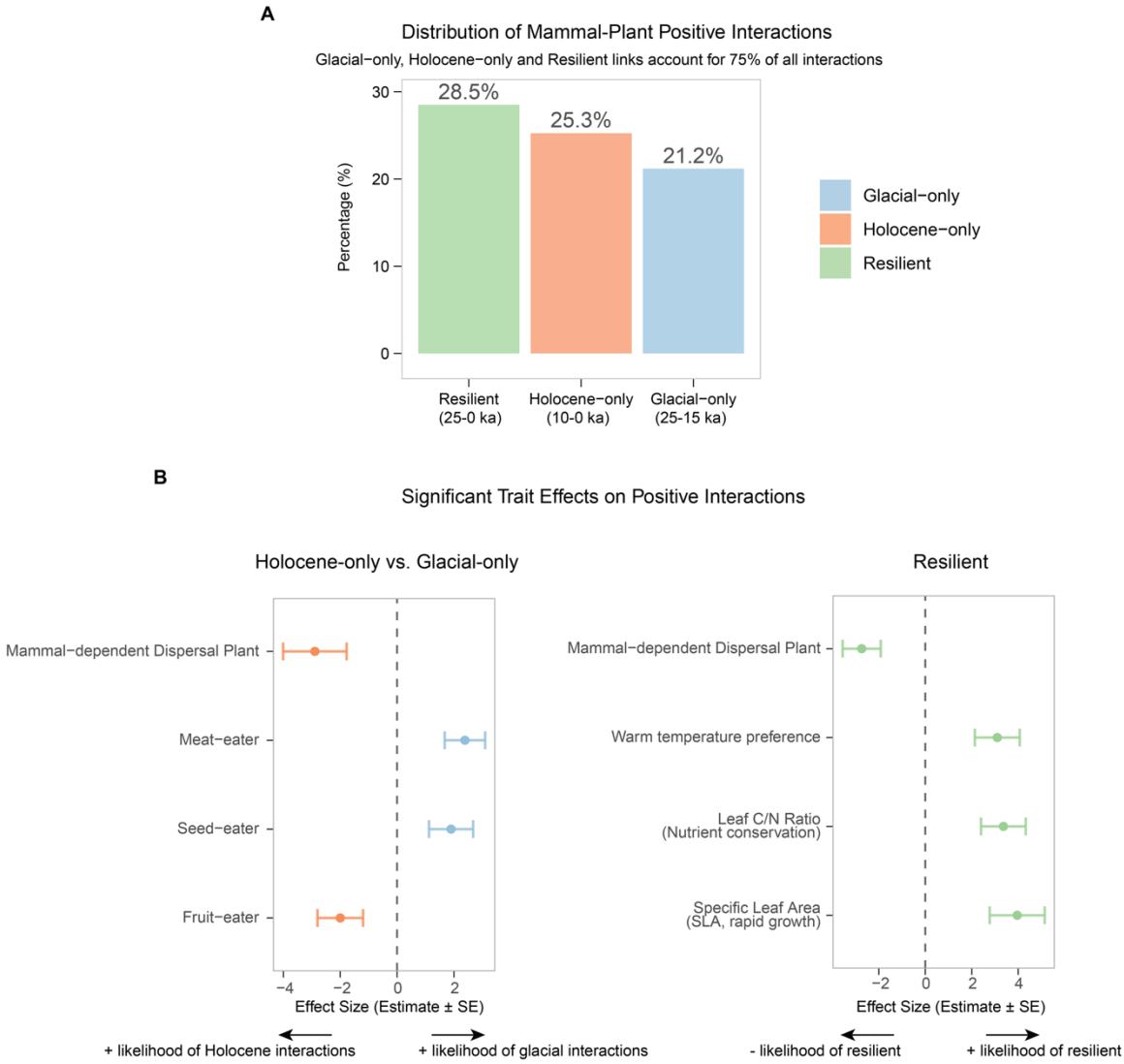

Fig. 4. Trait effects in mammal–plant positive interactions over the past 25 ka. (**A**) Classification of positive interactions into glacial-only, Holocene-only, and resilient categories. (**B**) Effects of traits on the likelihood of glacial-only, Holocene-only, and resilient positive interactions. Values represent generalized linear model (GLM) coefficients (effect size) ± standard errors (SE); only traits with significant effects ($p < 0.05$) are shown. Source data and codes are detailed in Materials and Methods.

Understanding which functional traits support persistent positive interactions can reveal the mechanisms that underpin long-term ecosystem resilience (*46*). We observed positive interactions, with 28.5% classified as resilient, 25.3% specific to the Holocene, and 21.2% specific to the glacial period (Fig. 4A). This pattern indicates that many glacial-period interactions were not reassembled under warmer Holocene conditions. The disappearance is associated with mammalian dietary specialization, with seed- and meat-eating mammals showing a higher likelihood of glacial-specific interactions (Fig. 4B). This highlights the prevalence of positive associations involving omnivorous and granivorous taxa under resource-

constrained conditions. In contrast, Holocene-specific positive interactions were more frequently associated with fruit-eating mammals and mammal-dependent dispersal plants (Fig. 4B). These findings reveal a fundamental ecological shift from mammal-benefiting commensalistic interactions during glacial periods to specialized mammal-plant mutualistic relationships in the Holocene.

During the glacial period—when megafaunal dispersers were abundant—plants likely faced minimal dispersal limitation and thus had little need to maintain stable, long-term associations permitting greater flexibility in partner switching. Meanwhile, omnivores (e.g., ursids) and granivores (e.g., sciurids) likely relied on plants as fallback or supplementary food sources, gaining benefits while offering little in return. Their foraging was opportunistic, and any seed dispersal that occurred was incidental rather than the result of tight mutualistic relationships. Instead, the warmer and more stable conditions in the Holocene made long-distance dispersal particularly beneficial for plants—by improving the likelihood of successful recruitment and range shifts for energy-intensive fruiting plants (*47*). Likewise, these conditions likely enabled plants to invest more in resource-demanding reproductive traits, such as fleshy fruits (*48*).

At the same time, reduced availability of dispersers intensified partner dependency in these mutualistic relationships. This was further exacerbated by weaker wind regimes compared to the glacial period (*49*), which limited the effectiveness of wind dispersal and increased reliance on mammal-mediated seed dispersal. As a result, remaining partnerships showed stronger reciprocal specialization, with plants increasing investment in fruit rewards to secure critical dispersal services. Thus, the loss of these commensalisms and mutualisms due to defaunation likely increased plant extinction occurred during the early Holocene (*18*) and may have driven compositional turnover toward smaller seed sizes (fig. S7).

Resilient interactions were primarily associated with plant traits such as adaptation to temperature increases, higher leaf C/N ratios, and greater specific leaf area (Fig. 4B)—traits that confer stress resistance, enable rapid growth in disturbed environments, and support adaptation to shifting climatic conditions.

Conclusions

Our time-series sedaDNA data offer novel evidence that rewiring of mammalian interactions triggered ecological cascades unfolding over millennia, ultimately contributing to the collapse of the Arctic mammoth-steppe. We identified that mammal-mediated seed dispersal functioned as a critical for maintaining ecosystem connectivity, but this role deteriorated as dispersers—particularly megaherbivores—were lost. These insights underscore the long-term, often delayed consequences of defaunation, implying that today's human-driven losses may likewise trigger ecological shifts that unfold far beyond the current century.

Our findings challenge the traditional perspective, which attributes the disappearance of the mammoth-steppe biome solely to climate warming—leading to vegetation change and, subsequently, to the loss of megafauna (*7*). Instead, our results highlight the active role of megafauna in shaping vegetation composition through long-distance seed dispersal, suggesting that restoring lost ecological functions via rewilding may support greater resilience under

ongoing environmental change. Furthermore, we show that different megafauna contributed to ecosystem functioning via distinct interaction pathways with plants, highlighting that effective rewilding depends on restoring these ecological functions—not merely reintroducing species.

Looking ahead, our findings suggest that interaction rewiring—detectable before major compositional shifts—may serve as an early-warning signal of ecosystem reorganization. With finer temporal resolution, ancient metagenomic records could help identify subtle but functionally significant changes, offering a quantitative framework to anticipate ecological tipping points.

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