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# Pests and partners: synanthropic insect roles in reindeer herding of North Asia and their implications for multispecies archaeologies

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Across Northern Eurasia, reindeer have long shaped the socio-cultural fabric of hunter-fisher societies. Today, descendant communities continue multispecies lifeways, forming symbiotic relationships within boreal ecosystems. Reindeer, regarded as animate persons, exist as both herded and wild partners. While the dynamics of these communities have been widely studied, the smallest actors in this system-namely insects-have remained largely overlooked, particularly in discussions of reindeer domestication and archaeology. Expanding ontological perspectives and engaging with new narrative approaches open avenues for recognizing other animate beings as co-constructors of social, economic, and cultural systems. Traditional hunter-herding practices in the West Siberian and Northwest Mongolian taigas offer insights into early human-reindeer cooperation, domestication, and their archaeological traces. This study employs a collaborative, multidisciplinary approach to examine how synanthropic insects-such as mosquitoes, midges, and horseflies-shape hunter-herder lifeways, despite their absence from the archaeological record. Fieldwork with Sel'kup, Khanty, and Tsaatan communities highlights the critical role of insects in herding and mobility patterns, influencing niche construction strategies. These case studies reveal new multispecies parameters that will enhance interpretations of the archaeological record.

#### KEYWORDS

insects, domestication, reindeer husbandry, traditional ecological knowledge, North Asia, archaeology

## Introduction

Insects, Earth's most diverse and abundant animal class with an estimated 1 to 80 million species, form the biological foundation of terrestrial ecosystems and act as significant geo- and zoogeomorphic agents (Bétard, 2021; Scudder, 2017; Stork, 2018). They are also integral to both terrestrial and marine food webs, influencing ecological stability and resource flows (Weisser and Siemann, 2013). However, despite their ecological prominence, insects have been historically underexamined in archaeological

research, largely due to methodological constraints and biases favoring other, larger, animal classes.

Interest in insect roles in the human past has grown, particularly due to archaeoentomology, a subfield originating in British archaeology in the late 1960s (e.g., Coope and Osborne, 1967). This discipline has demonstrated that insect remains offer valuable insights into past human environments and activities. For instance, insects aid in reconstructing macro- and micro-ecological conditions (Engels and Whitehouse, 2023; Magni et al., 2023) and serve as indicators of anthropogenic impacts on local environments (Forbes et al., 2015). They also provide proxies for human diet, trade, hygiene, and climate, significantly complementing other palaeoecological sources (Buckland et al., 2020; Costa-Neto and Dunkel, 2016; Meyer-Rochow and Changkija, 1997; Olivadese and Dindo, 2023; Stephenson et al., 2020; Van Itterbeeck and Van Huis, 2012).

While insects are increasingly recognized as proxies for human lifeways, especially in studies incorporating Indigenous Knowledge, this represents only one dimension of human-insect relationships. Today, these interactions span a paradoxical spectrum: insects are viewed as both harmful pathogens and nuisances, yet also as integral ecological actors and cultural symbols (Claessen, 2022; Raffles, 2011). These diverse relationships likely have significant time-depth, shaping human cultural and subsistence practices over millennia. However, archaeological research has yet to fully explore the social and cultural roles of insects, largely due to challenges in recovery and analysis techniques.

Using a collaborative archaeology approach with Indigenous communities in Siberia and Mongolia, we examine the role of insects in reindeer herding lifeways. This study explores how insect-human-reindeer interactions could influence broader multispecies archaeologies and reindeer domestication, contributing to more nuanced understandings of past humananimal-environmental dynamics.

# Posthumanism & multispecies studies: beyond binary relations

Academic traditions that separate humans from nonhuman animals are deeply embedded in Western philosophical views of humanity, relying on Cartesian dualism and the notion of human exceptionalism (e.g., Descola, 2006). Over the last 20 years, scholars in anthropology have increasingly moved toward fluid, interactive views of species relationships (Feinberg et al., 2013; Haraway, 2008; 2003; Kirksey and Helmreich, 2010). This shift challenges anthropocentric perspectives, encouraging human-animal interactions to be viewed within broader ecological and cultural frameworks. Posthumanist theory seeks to reconceptualize human-world relations; rather than placing humans as central actors, it embeds them within a vast interspecies, multi-entity network (Fuentes, 2010; Haraway, 1991; Haughton, 2023; Kirksey and Helmreich, 2010). These approaches attempt to identify and counter the limitations of the humanist paradigm. As a result, posthumanist and multispecies perspectives are gaining popularity in archaeology, broadening interpretations of the past (Crellin and Harris, 2021).

In archaeology, posthumanism can beter highlight the roles of nonhuman animals in human history, challenging archetypal human-animal relationships (Bogaard et al., 2021; Boyd, 2018; Weitzenfeld and Joy, 2014). Traditionally, archaeozoology examines human-animal relationships through a resourceoriented framework, categorizing them into primary products (e.g., meat, hide) and secondary products (e.g., transport, milk, wool) (Sherratt, 1981; Sherratt, 1983). This approach has been criticized for reinforcing an anthropocentric divide between nature and culture, overlooking the roles of nonhuman animals in social relationships and interspecies interactions (Boyd, 2017; Overton and Hamilakis, 2013). By focusing on archaeozoological records, researchers can gain access to material evidence of the intricate relationships among humans, animals, and the environment. However, to interpret these interactions across various historical moments and in the longue durée, archaeologists must navigate broader ecological webs, a task that remains highly complex (Boyd, 2017). Recent perspectives challenge the human/nonhuman binary, advocating for a more integrated view of human-animal relationships when studying the past. Consequently, until recently, archaeozoology often simplified the complex dynamics between human techno-economic activities and especially synanthropic relationships (Hussain, 2024). Despite these theoretical advancements, insect-human relationships remain largely underexplored, often filtered through Western biases that classify insects as either "good" or "pests" based on appearance and interaction with human environments (Beisel and Wergin, 2022; Claessen, 2022; Gunderman and White, 2021; Haraway, 2016). This normative lens reduces insects to empirical factors rather than recognizing them as integral agents in shaping communities and cultures, leaving their roles in multispecies systems even more overlooked.

Indigenous Knowledge systems, such as Traditional Ecological Knowledge (TEK), offer valuable insights into complex interspecies relationships. TEK, developed through and cultural adaptation transmission, emphasizes interconnectedness among all living beings and their environment (e.g., Berkes, 2009; 2008; Berkes et al., 2000; Huntington, 2000). Incorporating these perspectives, aligning archaeological approaches with Indigenous perspectives on nonhuman entities could deepen understandings of historical human-animal cooperations (TallBear, 2015; Weismantel, 2015). Integrating TEK and posthumanism provides conceptual and technical tools to enrich archaeological interpretations, bridging divides between Western/non-Western, past/present, and Indigenous/colonial viewpoints (Atalay, 2008; Crellin and Harris, 2021). Addressing these gaps could then offer potent avenues for more inclusive perspectives (Cassino et al., 2025; Fitzpatrick, 2022; Hamilakis, 2016; Motta and Porr, 2023). Integrating posthumanist theory and TEK into archaeological research offers a more inclusive framework for understanding past human-animal-insect relationships, challenging anthropocentric biases and expanding interpretations of multispecies histories.

# Niche construction theory and the concept of synanthropy

In archaeology, Niche Construction Theory (NCT) has been instrumental in exploring the origins of plant and animal domestication, offering insights into how species-including humans-modify their environments and influence evolutionary trajectories (Laland and O'Brien, 2010; Zeder et al., 2006). NCT posits that all organisms, deliberately or inadvertently, alter selective pressures in ways that shape not only their own development but also that of other species (Laland et al., 2017; Odling-Smee et al., 2003; 2013). While domestication has traditionally been examined through human-driven processes, growing research highlights how nonhuman species actively shape their ecologies, contributing to the formation of multispecies communities.

Zeder (2012) identifies three primary pathways to domestication: the commensal pathway, where animals voluntarily adapt to human environments; the prey pathway, where humans selectively manage wild species for subsistence; and the directed pathway, where humans intentionally domesticate animals for specific purposes. The commensal pathway is often invoked to explain early domestication, yet it does not fully account for the reciprocal ecological changes that emerge through prolonged human-animal interactions. Many organisms, from rodents to insects, modify their own ecologies by gravitating toward human settlements, fostering interspecies entanglements that reshape evolutionary pathways.

While NCT provides a valuable framework for recognizing nonhuman agency, it is often conflated with commensalism, a concept emphasizing neutral interactions between species, where neither party is significantly harmed nor benefited (Mathis and Bronstein, 2020). However, commensalism fails to acknowledge how animals and other organisms actively modify their own ecologies within human-altered environments, influencing both their own behaviors and those of other species. Synanthropy offers a more precise lens for understanding these entanglements, particularly in how certain species, such as rodents or insects, establish themselves in anthropogenic spaces, inadvertently fostering multispecies communities. This is because it describes how free-ranging animals adapt to human-modified environments, which can benefit from shared ecologies through behavioral and physiological adjustments (Klegarth, 2017).

Synanthropic relationships emerge through both bottom-up processes, where species exploit new resources, and top-down processes, where environmental modifications shape survival strategies (Hussain, 2024; 2023; O'Connor, 2013). Unlike commensalism, which implies incidental interactions, synanthropy explicitly acknowledges human and nonhuman mediated ecological changes that shape animal behaviors. This dynamic has been particularly explored in early Holocene studies, demonstrating how sedentary human societies provided novel adaptive landscapes for numerous species (Baumann, 2023; Hussain and Baumann, 2024). The expansion of the house mouse from the Near East into Europe (ca. 10,000-7,000 BCE) and the spread of wildcats alongside Neolithic farmers (Cucchi et al., 2012; Krajcarz et al., 2020; 2022) further exemplify how synanthropy influenced early domestication. While synanthropic relationships exist along a spectrum, from species that rely entirely on human environments to those with occasional interactions (Johnston, 2001; McKinney, 2006), shifting toward exploring synanthropic relationships could help illuminate the early development of interspecies relationships that later contribute to domestication.

To deepen this perspective, we examine niche-constructing practices among North Asian reindeer herders through synanthropy and Traditional Ecological Knowledge (TEK). Reindeer herding exemplifies a multispecies lifeway where insects play crucial roles, highlighting how diverse theoretical frameworks enrich archaeozoological and domestication research. Building on these interdisciplinary efforts, we propose a conceptual toolkit integrating niche construction, multispecies theory, and TEK. By combining posthumanist perspectives with Indigenous ecological knowledge, this framework offers new methods for examining interspecies relationships. Applying it to contemporary North Asian reindeer herding communities provides a case study for refining archaeological approaches to reindeer domestication.

## The history of reindeer husbandry

Reindeer, unlike other domesticates, have not been the focus of decades of targeted archaeological research into their domestication. This was because human-reindeer systems appeared to contradict contemporary normative humananimal relationships and domestication archetypes in archaeological research (Losey, 2021; Nyyssönen and Salmi, 2013). Reindeer are not necessarily industrially husbanded, and aspects of physical (Stammler et al., 2010), reproductive (Soppela et al., 2022), and dietary control (Salmi et al., 2015; Windle et al., 2025) are often lacking in reindeer herding systems. Morphological differences between ecotypes or from their wild counterparts proved difficult to differentiate (Nieminen and Helle, 1980; Puputti and Niskanen, 2008; 2008). Wild and

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herded reindeer regularly mix, and it is not uncommon for domestic reindeer to join wild herds or, perhaps more interestingly, *vice versa* (Brandišauskas, 2019). It is also widely documented that herded reindeer can guide and dictate human mobility (Golovnev et al., 2018; Stépanoff et al., 2017). Amongst herders, reindeer are also animate beings both as domestic herd animals and their wild counterparts that are hunted as game (Krupnik, 2000). Altogether, reindeer tended to be on the periphery of broader discussions on the trajectory of animal domestications until very recently.

## Northern Fennoscandia

Recent improvements in osteological and biomolecular techniques have provided new methodological parameters for identifying domestic reindeer archaeologically and for detecting anthropogenic influences especially in Fennoscandian reindeer morphology (Pelletier et al., 2020; Salmi et al., 2021). However, there is a need to better capture the complexity of humanreindeer socio-economic processes, as well as to understand the intersection between Fennoscandia and North and Inner Asia. In doing so, the possible implications for reindeer domestication research can be identified.

Many scholars assume that reindeer husbandry developed to provide a means of transport to facilitate wild game hunting (Bjørklund, 2013; Golovnev, 1993; Ingold, 1980). Historical accounts support that reindeer transport was maintained in tandem with local modes of hunter-fisher-gathering subsistence, but the archaeological evidence is broadly lacking. In Northern Fennoscandia, reindeer are thought to have been domesticated during the Late Iron Age (ca. 600/700 CE) (Halinen et al., 2013; Salmi, 2023; Salmi et al., 2021). For other regions, an extensive geographic variation in the timing of the adoption and growth of reindeer pastoralism is assumed (Bergman et al., 2013; Bjørklund, 2013; Sommerseth, 2011). The earliest historical evidence dates to the ca. 890 CE Norwegian Viking Ohthere's account to King Alfred the Great in the Anglo-Saxon kingdom of Wessex mentioning Ohthere's possession of 'tame' reindeer (Bately, 2007). Archaeological sites from Sweden contemporaneous with this account are interpreted as reindeer herder camps, due to their similarity with later Sami sites, and may represent the oldest evidence of reindeer in the region (Bergman et al., 2013; Sommerseth, 2011). Despite this, the oldest palaeopathological markers in the archaeological record date to ca. 1300 CE as documented by Salmi and colleagues (2021).

## North and Inner Asia

In North Asia, the earliest archaeological evidence of reindeer domestication comes from the Siberian Iron Age (260 BCE – 140 CE) in the Yamal Peninsula of arctic Russia. *Rangifer* bones (Nomokonova et al., 2024), several reindeershaped knife and spoon handles with design elements suggestive of headgear (Nomokonova et al., 2021), and possible headgear artifacts (Gusev, 2017; Losey et al., 2021) suggest the presence of herded reindeer. Further south, rock art images from northwest Mongolia ((Tumurbaatar and Damchaabadgar, 2023) and southern Yakutia, Russia (Alekseev, 2014; Kochmar, 1994; Okladnikov and Mazin, 1976) possibly dating to the Bronze Age (though no absolute dating can be applied) appear to show reindeer being tethered or involved in transport. Beyond this, our grasp of reindeer domestication in the deeper past of North Asia is tenuous.

The legacy of reindeer herding in North and Inner Asia today is uniquely enduring, though it varies significantly due to environmental conditions, cultural traditions, and shifting economic landscapes (Baskin, 2005; 2003; 1990; 1986; Davydov, 2015; Dudeck, 2015; Filchenko and Jordan, 2005; Forbes, 2013). Ethnographic and ethnohistorical research into reindeer herding groups has been ongoing for over a century, and recent ethnoarchaeological studies have provided insights into settlement patterns, mobility strategies, and seasonal activity zones within subsistence systems (Anderson, 2006; Groß et al., 2019; Piezonka et al., 2020). These studies demonstrate valuable methodological and theoretical pathways for investigating hunter-gatherer-pastoral interfaces in archaeological contexts.

Multispecies approaches, especially those that incorporate archaeologically underrepresented actors like insects, provide a vital perspective for understanding the ecological and social dynamics that shaped human-reindeer interactions. Investigating modern herding practices alongside insect behaviors is key, as it offers valuable insights into multi-agent processes. Insects may have influenced the proximity between humans and reindeer by altering movement patterns, creating seasonal stressors, or impacting herd management techniques-potentially playing a significant role in the domestication process.

## The study area

In this study, we explore the multispecies dynamics, particularly a trilateral human-reindeer-insect interface, of two modern reindeer herding groups, and how these dynamics may impact mobility, seasonality, and potential archaeological footprints. The two regions (Figure 1) we focus on are (i) the northern boundary of the West Siberian taiga bordering the tundra and (ii) the northwest forest-shrubland zone of the north Mongolian "taiga."

## West Siberian taiga

Located between the Ob and Yenisei Rivers in West Siberia, the northern taiga features flat landscapes with thin forests of pine, Siberian cedar, fir, and larch, as well as large quantities of lichen. The landscape is dominated by mature river floodplains forming oxbow lakes and wetlands. This wet habitat is ideal for



large numbers of water breeding insects like mosquitos and midges, while also supporting a number of fruit bearing plants like bog cranberries and blueberries. Temperatures once ranged from  $-26.5^{\circ}$ C in January to  $+15^{\circ}$ C in July but have risen significantly due to global warming (Piezonka et al., 2020). The fauna includes large ungulates (elk, wild reindeer), bears, small fur-bearing animals, forest fowl, aquatic birds, and abundant fish (Adaev, 2014). This ecotone offers rich seasonal resources ideal for hunting, fishing, and gathering.

### The Taz Sel'kup

The Sel'kup, meaning "forest, taiga people" in the Sel'kup language, are an Indigenous group of ca. 3650 people originally speaking a Samoyedic language of the Uralian language family, occupying two separate regions in Western Siberia. The southern Narym group is located in the Middle Ob region of Tomsk province, its members are mostly settled and the language is today only spoken by a very small portion of the community. The northern Taz-Turukhan group is dispersed across various parts of the Yamalo-Nenets autonomous district of Tyumen province and the Turukhan district of Krasnovarsk province; here, the local dialects of the Sel'kup language are better preserved and more frequently spoken (Aksyanova, 2005; Golovnev, 1995). Northern Sel'kup families west of the River Yenisei occupy the headwaters of River Taz which flows northwest into the Taz Gulf and joins the Ob Gulf (Kenig, 2010). The Northern Sel'kup migrated north from the Tomsk region to the Taz River in the 17th and 18th centuries due to Russian settler-colonial pressures and related inter-group conflicts. In the north, they evicted local Enets groups from the area (Golovnev, 1995; Golovnev and Tuchkova, 2005; Tuchkova, 2005) and adopted local subsistence and cultural traits (Golovnev and Tuchkova, 2005; Piezonka et al., 2024). As a result, various socio-cultural and economic characteristics became modified over the centuries of residing in this northern taiga region, resulting in substantial overlap in cultural features with neighboring groups, such as the Forest and Tundra Nenets, the Khanty, the Kets and the Evenks (Adaev, 2014; Piezonka et al., 2020). One of the most significant adaptations of the Taz Sel'kup to life in the north was the incorporation of small-scale reindeer herding. Small herds of ca. 10-100 head of deer are used almost exclusively for transport purposes, aiding by sled-pulling in seasonal migrations between winter and summer dwelling sites and during winter hunting expeditions, traveling along the frozen Taz River and into the tundra-taiga boundary area (Windle et al., 2021). The Sel'kup, like other neighboring groups, also continue to hunt wild reindeer along with the breeding of domestic reindeer.

### The Khanty

Communities of the Indigenous group of the Khanty inhabiting the Khanty-Mansiysk Autonomous Okrug and Yamalo-Nenets Autonomous Okrug are included in this study, adding new aspects to the abundant ethnographic and anthropological literature on their culture and lifeways (Badger

and Balikci, 1993; Dudeck, 2012; Istomin, 2012; 2020; Jordan, 2004; 2001; Moldanova, 2007; Sasaki, 2010; Yuzhakov, 2020). Linguistically, Khanty is a part of the Ugrian branch of the Uralic language family (Filchenko and Jordan, 2005). Khanty groups have historically engaged in small-scale reindeer herding and hunter-fisher migrations along the river valleys of the middle and lower Ob and Irtysh rivers. According to some scholars (Glavatskaya, 2005; 2004; 1995) the Khanty were influenced by proximity to Nenets reindeer herding communities and changed their migration patterns in the wake of the Russian colonization in the 16th-17th century due to increased pressure to engage in fur hunting. This pressure was largely driven by the need to pay taxes, using zobel, squirrel, and other furs. The Khanty became more mobile, their settlement patterns more dispersed, and led to the development of small-scale transportation reindeer herding and migration between fishing grounds near the Ob-River and winter-pastures in the hinterland. Previously, their small-scale reindeer husbandry involved sledpulling but reindeer are also an important source for clothing and economic technologies and are sacrificial animal alongside other domestic animals (Dudeck, 2012; Wiget, 2004; 1999; Wiget and Balalaeva, 2011; 2001). The symbolic role of reindeer was likely a consequence of rising importance of reindeer transportation on sledges.

## Northwest Mongolian taiga

In northern Mongolia's Sayan Mountains, west of the Darkhad depression and Khuvsgul Lake, lies a vast region of alpine tundra and larch forest, locally known as the "taiga." The lower-lying areas are characterized by larch forests, interspersed with mountain meadows and bogs, while the alpine tundra is dominated by dwarf birch scrub. At higher elevations, perennial ice patches play a crucial role in summer, providing thermal relief, insect reprieve, freshwater, and useful plant species (Ion and Kershaw, 1989; Reckin, 2013). Historically a habitat for wild reindeer, this lichen-rich region is now the southernmost area where reindeer herding is practiced (Taylor et al., 2019). Today, the use of natural resources in the taiga is highly regulated by the government through strict grazing limitations for reindeer herders and hunting bans.

### The Tsaatan

The reindeer herders in the Northwest Mongolian taiga originally were part of a larger community including Tuvans, Tofalar, and Oka Soyots who are all Sayan Turkic speakers. Following the political upheavals of the early 20th century, Tuvan communities—now known as Dukha or Tsaatan—left the Russian and later Soviet influence zone and began using the southern limits of the migration range more consistently (Peemot, 2024; Vainshtein, 1980). The Tsaatan communities have been largely isolated since 1944 due to the delineation of

the Soviet-Mongol border (Purev and Plumley, 2003; Wheeler, 2000). Reindeer herders in Mongolia can be referred to as Dukha, while the portion of families who continue Tuvan traditional lifeways (and can be intermarried with other local minority ethnic groups) as mobile hunter-herders are often referred to as Tsaatan, Mongolian for "reindeer people" (Rasiulis, 2016). In our experience, Dukha is used to describe the ethnic group itself, whereas Tsaatan describes all the people (including intermarried community members who are not Dukha) that herd reindeer. Their reindeer husbandry today is part of an integrated economic mosaic that features both taiga- and steppe-based pastoralism, as well as hunting, fishing, gathering, agriculture, inter- and intraregional trade and wage labour (Rasiulis, 2021; 2016; Wheeler, 2000). The Tsaatan reindeer herding community today constitutes around 30 households/families, encompassing less than 200 people (Inamura, 2005; Küçüküstel, 2021; Rasiulis, 2021; 2016). The community is further divided today between two areas, the East Taiga and West Taiga. This geographic division affects the day-to-day practices of the Tsaatan. In recent decades members of the eastern group engaged more with the state and outsiders than the western group, concentrating their urts (traditional conical tents) in a single location (Hatcherson, 2019). In contrast, the western Tsaatan remain more distributed across their range in smaller groups in groups of 3-5 families (Hatcherson, 2019). In the mountains, Tsaatan rely almost exclusively on their reindeer to facilitate their nomadic lifestyles both as pack and riding animals for their mobile seasonal migrations as well as everyday transport when herding deer, visiting neighbors, or searching for telephone connections at elevation. Mobility of the communities is currently limited due to the surrounding environment being a strictly protected nature reserve.

# Materials and methods

The three reindeer herding communities in this study differ in practices shaped by their environments and socio-political contexts (both historic, and current). The types of reindeer husbandry between the communities are a key distinction. The Khanty, historically, and the Taz Sel'kup currently practice small-scale sled-pulling husbandry. For the Khanty, reindeer symbolize Indigeneity, identity, and prestige, while for the Sel'kup, they are mainly used for transport, such as hunting, with symbolic value also being important. The Tsaatan, in contrast, engage in small-scale reindeer riding and milk husbandry. Our research re-evaluates these practices within a multispecies framework, exploring their historical and longterm implications and their relevance in archaeological research.

An interdisciplinary team of archaeologists, anthropologists, ethnologists, and local experts conducted fieldwork from 2016 to 2023 to document herd management practices among reindeer herders in the three multispecies communities, focusing on their lifeways and potential archaeological impact. Members of our team visited and investigated (a) multiple active summer and abandoned winter settlements of a Taz Sel'kup community; (b) various Kazym Khanty communities; (c) and a diverse array of abandoned and active seasonal stations of the Tsaatan communities in the West taiga. The local individuals involved with the project either currently or previously husbanded reindeer herds.

The fieldwork combined participant observation, interviews, photography, graphic documentation, archaeological surveys and excavations, all guided by collaboration with community partners and local epistemologies. Drawing on Wylie's (2015) dynamic pluralism, as well as Smith and colleague's (2023) approach to ethical norms, the goal was to achieve cultural discernments and reciprocity for the community. Smith et al. (2023) advocate blending local and academic knowledge to foster Indigenous collaborations. Fieldwork strategies, such as interviews and participative approaches, following Traditional Knowledge principles, Niche-Construction Theory, and Natureculture theory were all integrated embracing "two-eyed seeing" (Bartlett et al., 2012; Smith et al., 2023; Wright et al., 2019), where Indigenous knowledge is valued equally alongside Western scientific methods.

## Results

# Reindeer management in the West Siberian taiga

### Insect mitigation through smoke fires

Both the Khanty and Taz Sel'kup utilize seasonal settlements and stations, which tend to be located in areas with easy access to both open landscape for good summer grazing and the forested areas with rich lichen cover for the deer in winter. Insect pressure is a key factor in shaping settlement locations, as summer camps must be positioned to facilitate effective smoke mitigation. Traditional dwelling structures include winter earth houses with ground-level floors (Sel'kup poi mot = 'wooden house'), as well as tents (Sel'kup etillaka, mot, and others; Russian chum) for both summer and winter. In the Khanty communities, wooden log houses are used for both winter and summer dwellings replacing historically diverse forms of birch bark covered tents for summer and in winter conical tents with reindeer fur cover and sunken-floor earth houses. Additional buildings on the summer settlements include stilted storage houses, wooden storage containers (particularly for storing fish to feed the multispecies community in winter, including the reindeer), and also reindeer smoke infrastructure (Figure 2).

The reindeer management techniques employed by the Khanty and Taz Sel'kup tend to allow the deer autonomy, utilizing the constellation of human-animal coexistence to intervene in mobility, breeding, and herd demographics. However, bloodsucking insects, particularly the abundant mosquitoes and horse flies, play a central role in structuring these interventions. The main task is to find a balance between restricting the movements of the reindeer, so they can be easily managed by people, and enabling their roaming through pastures for feeding without overgrazing.

Female reindeer, uncastrated males, as well as calves are left free to graze in the forest within 10–15 km of the camp. Because of the extreme insect harassment in summer, fencing is used in a limited context, with the perimeter of the roaming range sometimes fenced—a practice originating from Soviet times. In the case of the Khanty, such fences existed as small sections, preventing the crossing of particular places of the landscape during particular seasons (for instance closing of small bridges of land between lakes to keep the reindeer on the calving grounds). Hobbles and shackles are used to control castrated males in most cases, as they are most often used as draft animals. However, herd mobility is controlled mainly through smoke facilities.

A range of architectural/infrastructural features on the summer settlements are specifically built and utilized in connection with the insects and reindeer, namely 'smoke houses' with either one entry (common in Khanty architecture), or two entries on either end (common in Sel'kup architecture) as well as one or two smoke ovens inside (Figure 2). Additionally, open air smoke ovens are also placed around the settlement (Figures 2, 5). These smoke infrastructures function as insect deterrents first and foremost, but they also serve as behavioral conditioning tools, reinforcing herd proximity to the Sel'kup and Khanty families and to encourage herd cohesion. Therefore, the purpose of these reindeer-specific architectures is threefold:

- The smoke houses and smoke ovens provide reindeer with relief from the biting insects that have their high season during the taiga summers.
- 2) The smoke facilities help train the reindeer to voluntarily return to the settlements daily in between grazing, as they associate the settlement with respite from insect harassment.
- 3) The voluntary daily returns are an effective management mechanism, reducing labor associated with searching for animals to return them to the settlement or with confining them through fencing, corralling, etc.

The smoke architectures are strategically placed within the summer settlement area to capitalize on oscillations in the wind. This positioning ensures a nearly continuous insect-free zone within the settlement, enhancing its effectiveness as a refuge for the reindeer. This was demonstrated during the fieldwork with the Sel'kup community when a smokehouse was relocated to a more exposed position in the settlement from its position in the forest where smoke could not disperse. Constructing the smoke fires is a complex task as they require a long, slow and smoke-



producing burn. They should burn long enough to allow the herders to engage in other daily tasks, and low so that they do not produce open flames. The fire should only be intense enough to produce a light smoke. The fuel is chosen accordingly, for example large pieces of fresh pine, wet bark and rotting wood, all of which produce an enduring and smoky fire. Large pieces of wet sphagnum moss can also be used to effectively suppress the fire and reduce the pungency of the smoke. The selection of the fuel is dictated by herders' knowledge of each type of fuel's effectiveness against the insects and in not being too astringent for the reindeer's eyes. Today, these fires are lit mostly in metal containers (old oil barrels etc.) but formerly would have been left open. One of the complementary practices engaged alongside the smoke infrastructure is the placement of troughs of fish by the houses and fires which reindeer can consume throughout the day (Supplementary Figure S1).

By late summer, the mosquitoes start to die off in colder weather. Simultaneously, the mushroom and rutting seasons begin. Both the Khanty and Sel'kup stated that in the late summer to autumn, insect activity declines, which leads to increased herd dispersal, making cohesive management more challenging. As insect activity declines, the reindeer pasturing range increases while they search for mushrooms, and the smoke is not as effective in keeping the deer nearby. Some Taz Sel'kup use extensive corrals to contain the animals, while other families continue to allow the reindeer free range. In order to prevent the dispersal of the herd in the autumn, Sel'kup families rely on implements such as hobbles and shackles (Figure 3), which are fitted to the neck or the legs of the reindeer to slow down their movement. The Khanty use specific wooden shackles fitted to one leg of the reindeer, allowing continued movement but ensuring they do not wander too far now that insect harassment is no longer reinforcing settlement return. It should be able to break if the reindeer is attacked by predators and allow the deer to escape. It is not uncommon for Sel'kup (and other reindeer herding communities, for example Brandišauskas, 2019 and Klokov et al. 2019) to encourage interaction with wild reindeer for breeding purposes during this time, though there is a risk of losing herd members to wild populations, and so this is closely monitored or, amongst the Khanty, discouraged.

## Reindeer management in the Northwest Mongolian taiga

### Insect mitigation through migration

The Tsaatan of the western taiga occupy a range primarily consisting of swamps, dense forest, and mountains. Seasonal camps cluster in lower elevation valleys or on relatively flat terraces at higher elevations (Figure 4). Proximity to water does not seem to significantly impact the location of camps, due to the high density of small streams, rivers, and lakes. However, camps at lower elevations tend to be located on



#### FIGURE 3

Example of Wes Siberian reindeer hobbles, typically used in the late-summer early-fall when insect harassment decreases with temperatures, mushroom and rutting seasons are approaching (A, B). Example of a reindeer stake to keep reindeer in place near the campsite amongst the Tsaatan (C).

forest edges, in more open-canopied and elevated areas. The elevations can be as small as 20–30 cm above the surrounding swamp but terraces several meters above their surroundings are also used. Camps are often located directly on well-used paths, and it is a common occurrence for migrating families to pass directly through occupied or abandoned seasonal camps. Stationary domestic infrastructure is minimal.

One of the primary environmental challenges faced by the Tsaatan and their reindeer is the presence of biting insects, which directly influence herding strategies and mobility patterns. The Tsaatan are acutely aware of how insect harassment affects reindeer, impeding their feeding efficiency, rest, and overall health. Unlike other Indigenous herders, such as the Khanty and Sel'kup, who historically used open-air smoke infrastructures to deter insects, the Tsaatan primarily rely on seasonal movement to avoid peak insect activity. While smoke-based deterrents were once utilized, interviews with herders suggest that the practice has declined, likely due to a decrease in insect populations. Today, mobility remains the central strategy for insect avoidance.

As temperatures rise in late June, substantial swarms of biting insects emerge, reaching their peak in July. This can be unpleasant, like in Siberia, for both the herders and the deer—and fraught with infection and disease risk for the deer. In response, most Tsaatan families undertake a migration of 25–30 km, crossing mountain passes to reach alpine tundra at elevations of 2,200–2,450 m asl. This vertical change in elevation is small, but by moving above the tree line and into the alpine biome, the threat of insects is almost completely mitigated (Figures 4, 5, 7). The alpine valleys are

markedly cooler, with a high level of exposure that allows for consistent wind, both of which are significant insect deterrents.

The most significant infrastructure in reindeer husbandry is the corral, typically located between two or more nearby urts. These corrals, up to a dozen meters in diameter, are shared by multiple families to gather reindeer in the evening, where they are sorted and individually restrained with fabric bridles tethered to wooden stakes (Figure 2). The Tsaatan focus on avoiding insect harassment through strategic mobility, which influences their seasonal movement patterns. Lower forested valleys, at elevations of approximately 1950-2,200 m asl, are inhabited in both spring and fall when insect activity is low despite the wetter conditions. By mid-July, most Tsaatan families, along with their reindeer caravans, cross the mountain passes to reach the alpine tundra at elevations of 2,200-2,450 m asl, a journey of roughly 25-30 km. The modest change in elevation, combined with moving above the tree line into the alpine biome, virtually eliminates insect harassment (Figures 4, 5, 7). The cooler alpine valleys and consistent winds create an environment that deters insects effectively.

# Discussion

## Niche construction and insect synanthropy in multi-agent reindeer herding infrastructure

While the differences in geography and husbandry strategies between the Siberian and Mongolian communities are



#### FIGURE 4

Examples of Tsaatan transitional campsites (A, C) versus the high-altitude mountain tundra summer campsites which provide insect relief (B, D). Also examples of milking and staking in (D).

substantial, a shared driver in the range of reindeer management practices was observed: insects. Insects, particularly mosquitoes (Culicidae), biting midges (Ceratopogonidae), and flies (Diptera, namely Sarcophagidae or 'flesh flies' like horseflies), are an everpresent fixture across North Asia from late spring to late summer, often referred to as a 'plague' by both locals and visitors to these regions. Insects substantially impact how people herd, hunt, and broadly interact with reindeer as we see in both regions explored here. Their impact on reindeer husbandry is significant, influencing how people herd, hunt, and interact with reindeer in both regions examined here. Insect harassment can negatively affect a reindeer herd's health and cohesion, resulting in intense and distinct avoidance behaviors (Colman et al., 2003; Ehlers et al., 2021; Hagemoen and Reimers, 2002; Skarin et al., 2004; Vistnes et al., 2008; Weladji et al., 2003). However, local Indigenous communities do not regard insects solely as a negative factor. For instance, the Khanty herders we consulted explicitly stress that mosquitoes 'help' them herd their animals and that, without them, herding work would be significantly more difficult. During periods when mosquitoes are absent, herds tend to disperse, whereas their presence facilitates gathering and management.

While Sel'kup and Khanty communities utilize nuanced smoking practices within seasonal settlements to provide respite to their herd (Figure 6), Tsaatan engage in altitudinal migrations during the height of the insect plague season, moving up onto the treeless, windy mountain-tundra (Figure 7). These methods, which involve a co-creative relationship with insects, have broader implications for understanding human-animal interactions in the past, particularly due to their nicheconstructing characteristics. Herefore, the social and economic significance of these strategies is best understood within the framework of NCT and its interrelated themes of hunterherder subsistence and landscape modification. Human niche construction is associated with increases in the abundance and predictability of plant and animal resources while reducing labor efforts required to gather, hunt, or manage them (Laland and O'Brien, 2010; Smith, 2011). Like how hunting architecture has been argued as a form of niche construction (Lemke, 2021; Smith, 2013), the strategic use of insect manipulation through smoke,



#### FIGURE 5

Example of the two niche constructing activities: (A) lighting smoke ovens in the summer in West Siberia, and (B) summer migration in Mongolia to higher elevation, insect-free alpine tundra.

hobbling, and fish-feeding infrastructure may also be interpreted as a form of niche construction.

The multi-agent herding infrastructure relies on both a deep understanding of insect and reindeer behavior as well as strategic knowledge of local topography and the environment—key elements that align with the concept of TEK. Reindeer herding among Sel'kup, Khanty, and Tsaatan communities is informed by an in-depth knowledge of reindeer behavior, including their tendency to utilize wide grazing ranges (Åhman and White, 2018), their instinct to seek windy, uphill pastures to avoid predators and insect harassment (Hagemoen and Reimers, 2002; Reckin, 2013), and the trade-offs they make between grazing needs and insect avoidance (Colman et al., 2003; Ehlers et al., 2021). Additionally, herders recognize health risks posed by infectious agents and factor these into their management practices (Carlsson et al., 2018).

The practical application of that knowledge is the deliberate construction of a niche that benefits the multispecies community—and relies on intimate knowledge of and frequent interactions between humans, reindeer, and insects in



daily life. The use of smoke to 'train' and 'tame' reindeer mirrors methods of 'baiting' animals into a human-mediated space (Anderson et al., 2017). This is analogous with strategic grassland burns to improve pastures around bison hunting architectures in the North American Plains (e.g., Oetelaar, 2014) or the cultivation of preferred browse at hunting architectures sites in the Near East which may have served as a pre-cursor to domestication in that region (Svizzero, 2016). The niche that is created in West Siberia is one where the hunterherder seasonal settlement is a symbiotic/mutually beneficial space for both humans and reindeer. It allows for a lower labour output in day-to-day herding of the deer without interfering with daily foraging needs for the family. In the case of Tsaatan migratory practices, vertical transhumance is a



(A) Demonstrates in how insect manipulation through smoke is used in Siberia to reduce insect harassment of a reindeer herd, without intraseasonal migrations whereas (B) demonstrates how insects impact vertical migration in Mongolia as herders move to mitigate insect harassment of reindeer. Lined (--) boxes indicate areas with insects in the spring/summer in the two study areas. Dashed (--) boxes indicate areas with fewer or no insects due to either smoke or higher elevations.

well-established strategy. Herders actively manage reindeer grazing patterns, ensuring that lichen-rich pastures are preserved for the winter season when they are most needed. Insects also play a role in this process, as they help keep reindeer in breezy open areas, preventing them from trampling fragile lichen pastures during the summer. Without such intervention, excessive summer trampling could lead to pasture exhaustion, creating long-term sustainability issues.

Niche enrichment can be a consequence of herd management practises through the propagation of

favourable forage plants and the suppression of unpalatable competitors such as grasses and sedges (Spate, 2019). Reindeer, like other grazers, modify both the quantity and quality of plant litter that forms soil organic matter (Stark et al., 2023). In turn, reindeer can aid in structuring the plant community composition of their habitats through three major mechanisms: food selection (i.e., favoring some plant species over others), trampling, and fertilization. Through this mechanism, reindeer exhibit a major impact on microbially mediated decomposition and mineralization processes in the soil, which in turn feedback to plant nutrient availability and uptake as well as carbon release (Stark et al., 2023). By facilitating and directing herds onto mountain tundra pasture in the Sayan mountains during the summer, the Tsaatan encourage a niche that benefits the reindeer and by extension the herders.

In both regions, herders try to keep reindeer away from lichen-rich pastures in summertime, when the lichen is dry and easily destroyed by the reindeer. Without interference a reindeer herd might trample lichen pastures in summertime, causing pasture exhaustion when kept in a small area. Insects help to keep reindeer in the breezy open spaces away from these important pastures. It is during the snow season that the herders let their herds graze in the lichen-rich forest. The bottleneck in fodder seems to be the late winter for reindeer, and the herders must take care to prevent overgrazing of these winter pastures. Without such intervention, excessive summer trampling could lead to pasture exhaustion, creating long-term sustainability issues.

A key aspect of this niche construction lies in the synanthropic behaviours of mosquitoes, midges, and fly species. These insects, which dominate taiga landscapes in spring and summer, differ from common synanthropes found near human settlements today (e.g., foxes, raccoons, coyotes, mice). However, the species of insects, particularly the mosquitoes, in the study areas are highly synanthropic and often take advantage of human-modified environments to thrive and spread (Andreeva et al., 2017; Khalin and Aibulatov, 2020; Matveyeva and Chernov, 2000; Pestov and Panjukova, 2013; Simard, 2021).

Building on the ethnographic and ecological contexts, the relationship between reindeer herders and insects is a complex, multi-dimensional one that spans cultural, technological, and environmental spheres. The strategies herders employ are shaped not only by ecological needs but also by cultural practices and traditional knowledge. For example, mobility patterns-such as seasonal movement to higher altitudes or specific terrains-reflect a deep understanding of the environment and the insects inhabiting it. These adaptive behaviors are proactive, reflecting the herders' connection to both the land and its creatures (Davydov and Bobrova, 2023; Istomin, 2023; Norum et al., 2021). Through such mobility practices, herders ensure the health of their herds while maintaining a cultural tradition that recognizes the symbiotic relationships between humans, reindeer, and insects (Perevalov, 2022). This dynamic highlights how insects, as active participants in the environment, influence human practices and shape the ecological niche. These interactions likely played a key role in the domestication of reindeer, where human management of insect stressors may have encouraged reindeer behavior that facilitated closer human-reindeer relationships and, ultimately, domestication.

# Insect synanthropy and domestication pathways

Anderson and colleagues (2017) demonstrated that smoke and supporting infrastructure have significant implications for understanding animal domestication. In our observations, smoke and insects were identified as important agents in reindeer husbandry, regardless of the specific infrastructure used. This human-reindeer-insect interface represents a co-created cultural record that reflects niche-constructing activities with significant time depth, potentially shedding light on the ecological dynamics that facilitated reindeer domestication.

Scholars increasingly recognize the importance of ecological relationships in shaping domestication processes (Krajcarz et al., 2020). We propose that the insect interface outlined here constitutes a consistent synanthropic niche in taiga environments-one that has played a beneficial role in the formation of human-reindeer cultural systems. Human responses to insect activity create feedback dynamics: by manipulating insect presence through smoke or migration, humans attract reindeer to habitation areas, generating new incentives and opportunities for interaction. This dynamic of labor reduction and reindeer wellbeing may have encouraged sustained human-reindeer cohabitation, representing a significant domestication pathway warranting further archaeological and archaeozoological research.

## Considering the archaeological footprint

The human-reindeer-insect nexus is embedded in a complex relationship with the local environment, influenced by seasonal conditions (temperature), daily weather patterns (wind and precipitation), landscape features (e.g., elevated terraces, ice patches), and vegetation types (closed or open canopy forest, open tundra, lichen concentrations). Integrating insects into human-animal relationship models enhances archaeological prospection techniques and provides insight into herd management strategies, especially in contexts where architectural markers such as corrals or other built infrastructures are absent. For instance, ideal locations—such as high river terraces where open canopies and wind help deter insects or high-altitude sites with naturally low insect populations—could be examined for settlement traces and insect-related infrastructures.

Although insects themselves are typically invisible archaeologically, there are several ways these reindeer herding systems could be detectable in the archaeological record (ex. Adaev and Zimina, 2016; Groß et al., 2019; Piezonka et al., 2024). In Siberia, the appearance of post-built reindeer houses with one or two smoke ovens as a specific building type, the construction of open-air smoke facilities lined by stake fences to prevent reindeer from getting too close to the hot ovens, and evidence for reindeer husbandry such as bridle parts could be visible archaeologically. Other detectable markers include high concentrations of reindeer dung around smoking places and in reindeer houses, which are regularly cleared of dung and stained soil, leaving a sunken-floor structure with specific soil chemistry and biomolecular markers (ex. phosphate concentrations, fecal biomarkers such as sterols, keratin). As Khanty and Sel'kup communities do not engage in milking reindeer or keeping them bound to one place, only the smoke places would likely be visible archaeologically as infrastructural evidence. The origins of using smoke infrastructure as a herding aid remain unknown, making this an important footprint to explore from a domestication history perspective.

In Mongolia, where shorter-term campsites and vertical migrations are practiced, different infrastructures are associated with reindeer herding. Here, ties are wrapped around the heads of the deer, with each individual attached to a short wooden peg in the evening to keep the reindeer at the settlement at night-a solution employed in the absence of insects at higher-altitude summer sites. While the material evidence of this practice (rawhide or textile ties, wooden pegs) consists of organic materials that would only preserve under specific taphonomic circumstances, the stake holes of the pegs and the biomolecular markers at night sites could still be detectable archaeologically. Using higher-resolution techniques like soil micromorphology (Égüez et al., 2018; 2016), phosphate analysis (Anderson et al., 2019; Seitsonen and Égüez, 2021), as well as biomolecular sciences such as fecal and plant wax biomarkers (Égüez et al., 2022; Égüez and Makarewicz, 2018; Ventresca Miller et al., 2020) and stable isotopic analysis (Fjellström, 2023; Shishlina et al., 2018; Windle et al., 2025) may yield relevant signatures that could give some indication of insect presence in a past multispecies community, allowing for their role to be examined. Further investigation and testing are needed, with accurate interpretation dependent on knowledge of specific herding practices and their broader multispecies context.

## Insects as part of global humananimal systems

The insect interface is not unique to Sel'kup, Khanty, and Tsaatan but appears to be a ubiquitous feature of North Asian reindeer herding, with mosquitoes and other bloodsucking insects acting as key agents in herd management and daily life (Norma et al., 2021). Smoke shelters and fires are used to provide respite for reindeer by south Siberian Evenki and Tuvan reindeer herders (ex. Anderson et al., 2017; Brandišauskas, 2007; Oskal et al., 2009) and herders throughout Taimyr (Perevalov, 2022), and Sakha (Yakutia, Russia) (ex. Magga et al., 2009). This holds true even among more mobile groups that do not rely on fixed infrastructure; for instance, Nenets (tundra sled-pulling herders) suggest that mosquitoes assist in herding reindeer (ex. Oskal et al., 2009; Klokov and Antonov 2022; 2013; Klokov and Mikhaylov, 2017) and play important roles in the mythology of Chukchi reindeer herders as well (Ozheredov et al., 2020). Natural infrastructure, such as the frost and ice patches of eastern Siberia and northern Mongolia, is also used to help reindeer avoid insects while providing heat relief and hydration (Magga et al., 2009; Oskal et al., 2009; Taylor et al., 2019; Vainshtein, 1980; 1961). These examples illustrate how the human-reindeer relationship is embedded in a broader socio-ecological network that includes other nonhumans as well as the wider Arctic and subarctic environment.

Beyond reindeer herding contexts, the manipulation of insects to prevent animal harassment is widely documented in the ethnographic record. In the Nepalese Himalaya, yak herding systems depend on cooperative interactions, one of which involves using smoke from yak dung fires to repel insects from herder campsites (Johnson, 2022). Mongolian steppe pastoralists also burn animal dung to produce smoke as an insect repellent for both herders and livestock (Peemot, 2022), a practice that, like wood smoke fires in Siberia, has transitioned to burning cow and horse dung in metal buckets rather than open fires. Comparable strategies exist outside of Central Asia, such as using smoke to shield cattle from tsetse flies (Diptera: Glossinidae) in Zimbabwe (Torr et al., 2011) and from mosquitoes in India (Gupta et al., 2017). The impact of insects on shared human-animal communities is relevant on a global scale, further underscoring the agential role of this animal class.

While three nonhuman animals—humans, reindeer, and insects—are involved, the environment also actively shapes this interface. Air movement (wind) and temperature play crucial roles in bringing species together, while different tree species and the smoke they produce mediate the process in West Siberia. Thus, what is explored here as a three-way relationship could be conceptualized as a four-way or even five-way interaction (Figure 6). Examining the roles of all members of such systems—whether human, nonhuman, or nonorganic—not only provides insight into the (in)visible impacts of these relationships on the archaeological record but also expands the narrative spectrum of potential pasts.

## Conclusion

In our encounters with reindeer herders in Northern and Inner Asia, we documented a distinctive multispecies dynamic that provides broader insights into human-animal relationships, particularly domestication. This hunter-herder system in the taiga is shaped not only by human activities such as fishing and landscape management but also by interspecies feedback, where insects play a key role in settlement organization, architectural features (houses, ovens), and daily tasks (managing smoke fires, herding, fishing). Herders rely on deep knowledge of reindeer behavior, insect ecology, plant species, and weather patterns to manage their herds within a mobile hunterfisher lifestyle.

Though these practices are often ephemeral, multispecies frameworks and concepts such as synanthropy help illuminate niche-constructing husbandry techniques in which insects are central. This perspective underscores the active roles of nonhuman animals in shaping human-environment interactions. These practices leave archaeologically detectable traces, including seasonally specific settlements, smoke houses, and pegging areas for reindeer. A combined approach—integrating Indigenous knowledge with scientific analysis—is essential for interpreting this evidence and deepening our understanding of the complex multispecies relationships within hunter-fisher-herder communities.

## Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

## **Ethics statement**

The manuscript presents research on animals that do not require ethical approval for their study.

# Author contributions

MW participated in the design of the study. MW, TS, and SD, carried out the ethnographic fieldwork (interviews, participant observations etc.). HP carried out some of the photography and participant observation documentation. HW collected spatial data. in the experiments. MW wrote the majority of the manuscript, with SD contributing especially to Khanty sections. TS, HW, and HP provided comments and editorial contributions to the manuscript. All authors contributed to the article and approved the submitted version.

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# Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

# Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

# Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontierspartnerships.org/articles/10.3389/ past.2025.14081/full#supplementary-material.

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