

Human-Beaver Cohabitation in the Early and Mid-Holocene of Northern Europe: Re-visiting the Material Culture and Ecology of the Mesolithic through a Multispecies Lens

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Abstract (max. 250 words)

The Eurasian beaver (*Castor fiber*) was an important member of Early and Mid-Holocene landscapes and ecosystem communities in Northern Europe. Previous zooarchaeological research has established the alimentary roles of beavers for Mesolithic forager societies and the importance of these animals for fur procurement. We develop an integrated biocultural approach to human-beaver interactions and examine the position of humans and beavers in Mesolithic and Early Neolithic multispecies systems. We contextualize beaver landscape agency in hydroactive environments at the edge of former glaciers with human foraging and landscaping behaviour, especially fish-getting practices, and beaver-related material culture documented in the archaeological record of Northern Europe. This cross-cultural, diachronic analysis reveals previously overlooked facilitations of human behaviour by beaver practices and ecological legacies. We argue that Mesolithic beaver-related material culture is therefore also a result of the cultural keystone status of *Castor fiber* in higher latitude Early and Mid-Holocene landscapes, indicating that post-glacial human settlement in many parts of Northern Europe reflects adaptations to beaver-engineered riverine wetlands and multispecies affordances. We further suggest that long-term trajectories of human-beaver cohabitation differed between northern European regions. While in Southern Scandinavia, human-beaver intersections witnessed major re-organizations during the Mid-Holocene, beavers retained a key role for human societies across the Baltic and Northwestern Russia throughout much of the Holocene and played an important role during the Mesolithic-Neolithic transition in the Dutch wetlands, suggesting that evolved human-beaver systems were unequally affected by developing human lifeways in this pivotal period of human prehistory.

Keywords: *Castor fiber*, hunter-gatherers, human-animal relations, multispecies archaeology, conviviality, mandible tools, fishing

41 **Introduction**

42 Beavers hold deeply ambivalent positions in the Western imaginary. Attitudes have shifted
43 between disdain and open demonization on the one hand and fervent, heartfelt celebration on
44 the other (e.g., Hood, 2011; Liarsou, 2015; Poliquin, 2015). The Eurasian beaver (*Castor fiber*)
45 is currently making a comeback across Eurasia due to successful reintroduction and
46 conservation programmes, yet renewed tensions are particularly prevalent in countries where
47 beaver populations are now thriving (Swinnen *et al.*, 2017; Wróbel and Krysztofiak-
48 Kaniewska, 2020; Halley, Saveljev and Rosell, 2021). To a large extent, the polarized
49 recognition of the beaver as a ‘friend’ or ‘foe’ is rooted in changing perceptions of the effects
50 of beaver activity on landscapes and wider ecologies, and as to whether and how it interferes
51 with human lifeworlds (Liarsou, 2013, 2020). On the one hand, beavers are increasingly
52 celebrated as ‘nature’s architects’ (Crumley, 2015) who can make significant contributions to
53 ongoing efforts of ecosystem restoration (Gorshkov *et al.*, 1999; Müller-Schwarze, 2011; Law
54 *et al.*, 2017), rewilding (Gaywood, 2018; Willby *et al.*, 2018; Gow, 2020; Liarsou, 2020) and
55 climate change mitigation (Lorimer, 2020), and in turn require protection (Rosell and
56 Campbell-Palmer, 2022), for our own sake as well as the sake of the biosphere as a whole. On
57 the other hand, beaver engineering can also be destructive and disruptive to human property
58 and infrastructure, provoking the culling of flourishing beaver populations in some areas
59 (Jansman *et al.*, 2016; Wróbel and Krysztofiak-Kaniewska, 2020).

60 While some of these tensions are unique to the contemporary period and more recent
61 history, human-beaver negotiations as to how to co-inhabit the landscape are not. Relations
62 between humans and beavers have a deep history (Coles, 2006; Liarsou, 2013; Hjørungdal,
63 2019a, 2019b) and both species have crossed paths under different ecological and historical
64 conditions and with varying consequences. Given the recent surge of attention on beavers’
65 conservationist capacities, and the hope they continue to spark in the Anthropocene (e.g.,
66 Woelfle-Erskine, 2019), it is thus informative and timely to revisit the archaeology of human-
67 beaver relations, to interrogate the long-term dynamics and legacies of human-beaver co-living,
68 and to ask what we can learn from the respective interspecies pasts that come into view in this
69 way, as they have been argued to bear important implications for possible and imaginable
70 multispecies futures (Živaljević, 2021).

71 Recentring coupled human-beaver prehistories aligns with current attempts in
72 archaeology to develop more inclusive accounts of the past (Pilaar Birch, 2017; Kay and
73 Haughton, 2019; Hill, 2021; Hussain, 2023b) and to explore the varying contributions of

74 nonhuman animals to human pursuits and projects (e.g., Russell, 2012; Hill, 2013; Mannermaa,
75 2013; Sykes, 2015; Overton, 2016; Harris and Cipolla, 2017; Armstrong Oma, 2018;
76 Brusgaard, Fokkens and Kootker, 2019; Hussain, 2019; Armstrong Oma and Goldhahn, 2020;
77 Marciniak, 2020; Løvschal, 2022). Just as animal historians have proposed to employ a
78 dedicated ‘animal lens’ (Specht, 2016) to disclose new perspectives, insights and
79 understandings of the past, multispecies archaeologists are now beginning to draw attention to
80 the often-underestimated involvement of animal others in the making of prehistory (Hamilakis
81 and Overton, 2013; Pilaar Birch, 2017; Kost and Hussain, 2019; Fredengren, 2021). As Eitler
82 (2014) reminds us, however, the role of animals cannot be cast as invariant and hence as *a priori*
83 given – i.e., as a mere consequence of supposedly essential species-level qualities (see also
84 Haraway, 2003 and Howell, 2018) – there is a pressing need to *historicize* animal behaviour
85 and affect in order to make space for the animals themselves as historical agents and contexts
86 (Hussain, 2022). To qualify the involvement of animals in human material, social, and cognitive
87 pasts arguably requires detailed contextual analysis of historically specific conditions of
88 interspecies encounter, negotiation, and facilitation (Haraway, 2003, 2008; Tsing, 2012), and
89 therefore depends on multi-stranded, synthetic investigations that couple conceptual and data-
90 driven analyses in powerful ways.

91 The intersection between the Eurasian beaver (*Castor fiber*) and post-glacial human
92 foragers in Northern Europe offers a privileged window into such multispecies prehistory, as
93 beavers were among the pioneer species moving into the newly available glacier-freed
94 environments of higher latitude Europe. Beavers have previously been hypothesized to have
95 promoted the first Mesolithic hunter-gatherers to occupy the same northern landscapes (Coles,
96 2006; Liarsou, 2020). Furthermore, beaver remains are prevalent in many north Eurasian
97 Holocene faunal assemblages, suggesting extensive but likely variable interactions between
98 humans and beavers in this time period (e.g., Zeiler, 1987; Enghoff, 2011; Zhilin, 2014a;
99 Schmölcke, Groß and Nikulina, 2017). Liarsou (2020: 39) estimates that beavers were between
100 8 to 50 times more abundant in the European Mesolithic than human foragers, illustrating that
101 beaver activity in the landscape was an important lifeworld context for human behaviour. This
102 broader ecological and archaeological context invites the exploration of how human and beaver
103 worlds were possibly co-configured, and to throw new light on forms of life that emerged at
104 historically specific multispecies gatherings involving both beavers and humans. We thereby
105 contribute to mapping out the dynamics and diversity of human-beaver relations in the past and
106 work towards a deep-historical baseline for discussing beaver relations and impacts in the
107 present.

108 From an archaeological point of view, beavers frame a particularly interesting case of
109 human-nonhuman intersection since they are a paramount example of a species who acts upon
110 and alters the ecology of its human co-inhabitants and in this way intercedes with human
111 endeavours (Hjørungdal, 2019b; Riede, 2019; Hussain, 2022). Another reason for focusing on
112 the beaver is because previous research on the place of animal others in earlier prehistory has
113 mostly privileged larger mammals – what Hjørungdal (2019b) refers to as the ‘big hunter
114 supremacy’ bias – and beavers and their remains, when discussed, are mainly treated as
115 economic resources (see Overton, 2016 and Charles, 1997 for a similar critiques). Little
116 attention has been paid, by contrast, to the socio-ecological dimensions of human-beaver
117 interfaces (Schmölcke, Groß and Nikulina, 2017; Hjørungdal, 2019a). This is despite the fact
118 that the engagement with animal bodies is often of key importance for human social and
119 cosmological sustenance (cf. Eitler, 2014), especially in forager contexts where hunting is a
120 society-making practice (Nadasdy, 2007; Hill, 2019; Hussain, Weiss and Kellberg Nielsen,
121 2022).

122 In what follows, we first outline the archaeological background of human-beaver
123 relations in the first half of the Holocene in Northern Europe, briefly deploy a suit of concepts
124 derived from multispecies studies and geo-sociology to address the dynamics of integrated
125 human-beaver systems in prehistory and then present a synthetic analysis of beaver-related
126 material culture and fish-getting legacies in the Mesolithic and Early Neolithic of the
127 Netherlands, Southern Scandinavia including Northern Germany, and Northeastern Eurasia,
128 comprising the Baltic and Northwestern Russia. We focus on three broader macro-regions as
129 case studies where beaver remains are prevalent in faunal assemblages and where prehistoric
130 landscapes were conducive to facilitating human-beaver interactions, thus providing sufficient
131 data for a cross-cultural and diachronic analysis. We thereby provide new evidence and
132 arguments for the role of the beaver as a ‘cultural keystone species’ (Jacques-Coper, Cubillos
133 and Ibarra, 2019) in post-glacial Northern Europe, who facilitated the expansion and
134 consolidation of human settlement and catalysed regionally divergent trajectories of cultural
135 history across the vast wetland and boreal zones of the region.

136

137 **Beavers in the Early and Mid-Holocene of Northern Europe**

138 The deep prehistory of human-beaver interactions is largely framed by interglacial climate and
139 landscape windows and there is only sporadic archaeological evidence for hominin interference
140 with beaver affairs before the final stretch of the Pleistocene, although this may in part be a

141 research bias (cf. Lebreton *et al.*, 2017; Cuenca-Bescós *et al.*, 2021). Notably, beavers might
142 have played a currently underappreciated role in the sustenance and lifeworlds of at least some
143 interglacial Neanderthals (Müller and Pasda, 2011; Hérissou *et al.*, 2015; Kindler, pers. comm.).
144 Brown and colleagues (2017) have drawn attention to a possible autoecological entanglement
145 of beavers, eels and horses underpinning mobiliary art-making in some European Late Upper
146 Palaeolithic contexts, and beavers have been considered potential high-value prey items of
147 some Late Glacial, especially Allerød, foragers in Northern Europe (Baales and Street, 1996;
148 Charles, 1997; Weber, Grimm and Baales, 2011). Mills (2022: 391) has pointed out that beavers
149 were likely important agents of driftwood procurement within the extensive catchment of the
150 Terminal Pleistocene Channel system. In Northwestern Europe, however, beaver remains and
151 traces of their activity become more frequent in the Early Holocene, when beavers form part of
152 the pioneer fauna re-occupying higher latitude Europe after the Younger Dryas climatic
153 downturn (Coles, 2006).

154 In Britain, beaver impacts and their geohydrological shaping of Early Holocene
155 landscapes is well-documented (Coles, 2001, 2006). Archaeological sites such as Star Carr
156 (Milner, Conneller and Taylor, 2018b) and Thatcham (Wymer and King, 1962; Evans, 1975:
157 88; Coles and Orme, 1983: 95-102; Overton, pers. comm) demonstrate that beaver activity
158 comprising woodland modification, dam and channel building, and lodging *precedes* the
159 earliest Mesolithic settlement. Beaver ecosystem modification may have thus been a locational
160 factor in the re-occupation of Northern Europe (Coles, 2006). In the British Mesolithic, there is
161 no evidence of beaver remains outside of their habitat (Coles, 2008). This may in part be a
162 selection bias of archaeological excavation but could to some extent also suggest that human
163 foragers engaged with beavers directly where they lived – in beaver country. Beaver-framed
164 locales and landscapes may have therefore constituted vibrant ‘contact zones’ where humans
165 and beavers were drawn together (Hjørungdal, 2019b; sensu Haraway, 2008: 216). Coles (2000)
166 has prominently argued that Mesolithic people were probably attracted by beaver-infused
167 localities because of the pre-procured and ready-made wood resources of various kind made
168 available by beaver activity at these places.

169 As in Star Carr, the earlier Mesolithic site of Järingsholm 2 in Northern Skåne, Sweden,
170 has produced evidence for beaver presence at a lakeshore environment before humans settled
171 there (Kjällquist, 2005). Hjørungdal (2019a) has further drawn attention to the interesting
172 observation that some Early Mesolithic dwellings currently interpreted as anthropogenic
173 resemble collapsed beaver architecture – circular structures with a simple opening. It has been

174 suggested that because beavers and Mesolithic people were critically exposed to one another's
175 rhythms and practices and in some cases might have literally *inhabited* them, they have likely
176 exercised mutual influence and perhaps imitated each other (Coles, 2008; Overton, 2018;
177 Hjørungdal, 2019b). Yet this nascent perspective on human-beaver relations in the Mesolithic
178 of Northern Europe not only requires further qualification and contextualization, it also remains
179 a fairly marginal perspective, as archaeologists overwhelmingly continue to picture the beaver
180 as 'good to eat' and/or 'good to use' (cf. Hussain, 2022), foregrounding the animals'
181 supplementary caloric value and role in early fur-getting economies (e.g., Price, 1991; Zhilin,
182 2014). This especially holds true for the interpretation of the abundant beaver remains recovered
183 from continental Northern Europe. In addition, while the socio-ecological facets of human-
184 beaver interactions have been comparatively well-studied for prehistoric Britain (Wells,
185 Hodgkinson and Huckerby, 2000; Coles, 2006; Overton, 2014, 2016, 2018), the same can
186 certainly not be said for continental Northern Europe, nor for higher-latitude Europe as a whole.

187 Osseous remains of beavers are a recurrent feature of the Mesolithic across continental
188 Northern Europe, encountered from the Netherlands in the Northwest via Denmark and
189 Northern Germany to the Baltic and Western Russia in the East (e.g., Price, 1985; Zeiler, 1987,
190 1997; Zhilin, 2004; Schmölcke and Nikulina, 2015; Groß, 2017; Lõugas, 2017). In the
191 Northeastern Mesolithic, beaver remains in many cases quantitatively make up a substantial
192 portion of the recovered faunal assemblages and are often only outnumbered by elk (*Alces*
193 *alces*) bones (Zhilin, 2014a; Lõugas, 2017). Similarly, in the Dutch wetlands, beaver remains
194 are frequent in faunal assemblages from the Late Mesolithic and Early Neolithic, together with
195 other freshwater fauna, such as otter (*Lutra lutra*), wild boar (*Sus scrofa*), waterbirds, and fish
196 (Lauwerier, van Kolfschoten and van Wijngaarden-Bakker, 2005; Çakırlar *et al.*, 2019). In
197 southern Scandinavia, by contrast, beaver remains tend to be few in number and the handful of
198 later Mesolithic assemblages with higher counts of beaver bones are typically interpreted as
199 specialized hunting or trapping stations linked to delayed-return fur extraction systems
200 (Rowley-Conwy, 1998). Enghoff (2011: 295) notes a geographical pattern in the Danish
201 material, with beavers being considerably more common at Mesolithic sites on Zealand than on
202 their counterparts on the Jutland peninsula, and Schmölcke and colleagues (2017) have
203 suggested that beavers were of little economic relevance in this part of Europe given the
204 generally small number of sites with significant beaver bone shares.

205 Zhilin (2020) has recently also drawn attention to the extensive record of organic tools
206 made of beaver remains including mandible and incisor tools that form an integral part of the

207 larger Mesolithic interface within the Eastern European forest zone. Similar beaver-procured
208 tools have been reported from a few Mesolithic sites in Northern Germany (Schuldt, 1961;
209 Schacht and Bogen, 2001; Schmölcke, Groß and Nikulina, 2017), the Netherlands (Coles and
210 Kooijmans, 2001) and Denmark (Broholm, 1924: 133; Hatting, 1970), but previous work has
211 paid surprisingly little attention to this beaver-related material culture and its possible
212 significance (but see Hjørungdal, 2019a). Although ethnographic parallels have been invoked
213 to interpret these beaver-sourced tools, scholars have mainly highlighted the functionality of
214 these objects and the *capacity* of Mesolithic people to make use and take advantage of the
215 animal materials available to them. Hatting (1970: 126), for example, symptomatically
216 concludes that ‘it must [thus] be held with certainty that the idea of this kind of tool making
217 was known in the Stone Age of Denmark.’ In the Mesolithic of Northeastern Europe, beaver
218 body-parts such as teeth and ankle bones sometimes also made their way into human burials
219 (see e.g., Grünberg, 2013; Mannermaa *et al.*, 2020; Kashina, Ahola and Mannermaa, 2021) yet,
220 again, this material has so far hardly been considered and further contextualized, partly also
221 because Mesolithic scholarship has focused on other, supposedly more symbolically potent
222 nonhuman animals such as various bird and deer species, but also suids, and their role in
223 Mesolithic identity construction (e.g., Price, 1985; Bridault, 1992; Tilley, 2003; Conneller,
224 2004, 2011; Kashina, 2005; Kashina and Zhulnikov, 2011; Mannermaa, 2013; Zagorska,
225 Meadows and Iršénas, 2018; Mannermaa *et al.*, 2019; Lozovskaya, 2021).

226 In the extensive wetland and boreal zones associated with the earlier Holocene in
227 Northern Europe, beaver remains thus appear in archaeological sites linked to the Preboreal,
228 Boreal and early Atlantic chronozones, and generally span the whole period, from the earlier
229 Mesolithic to the later Mesolithic and earliest Neolithic, even though some notable
230 spatiotemporal patterns can be discerned. For the purposes of this paper, we distinguish between
231 three chronocultural phases in Northern Europe (see **Tab. 1** for an overview of the
232 corresponding chronozones and time ranges). For the Baltic and Northwestern Russia, we
233 follow the literature (Hartz, Terberger and Zhilin, 2010; Lõugas, 2017; Zhilin, 2020) and
234 subdivide the period into an ‘Early Mesolithic’ phase including complexes such as Early Kunda
235 and Butovo, a ‘Middle Mesolithic’ harbouring the later Kunda and Botovo phases, and a ‘Late
236 Mesolithic/Early Neolithic’ consisting of the Mid-Holocene Early Comb Ware complex
237 featuring entities such as Narva and Valday. The same chronological scheme is applied to
238 Northwestern Europe, where the Early Mesolithic comprises the earlier phase of the Maglemose
239 complex as recently defined for Southern Scandinavia, Northern Germany and Britain (Milner,
240 Conneller and Taylor, 2018a; Sørensen, Lübke and Groß, 2018), the Middle Mesolithic is more-

241 or-less synonymous with the later phase of Maglemose complex (Groß, 2017), and the Late
242 Mesolithic/Early Neolithic accommodates the Dutch Swifterbant Culture (Raemaekers and De
243 Roever 2010, Dreshaj et al. 2022) and the Ertebølle complex (EBK) in Southern Scandinavia
244 and northern Germany (Price, 2000, 2015).

245 We collected all accessible faunal datasets from these periods. We recorded mammal
246 and fish Number of Identified Specimens (NISP) for all regions and periods, except for the
247 Early and Middle Mesolithic in Southern Scandinavia and Northern Germany where only
248 Minimum Number of Individuals (MNI) was readily available (**Supplementary Information**
249 **M and F**). For the Ertebølle complex, we made a selection of sites due to the sheer number of
250 relevant instances. Thus we selected sites documenting >1000 NISP of mammals supplemented
251 by sites with fish remains >1000 NISP, which assures a relatively representative sample, as
252 suggested by Gron (2013). This provides a total sample of 116 archaeological sites with faunal
253 information encompassing modern day Denmark, Sweden, Northern Germany, the
254 Netherlands, Poland, Latvia, Lithuania, Estonia, and Northwestern Russia. We additionally
255 review, synthesize and re-contextualize instances of beaver-related material culture published
256 from across the study region.

257 Against this archaeological background of human-beaver relations in the Northern
258 Mesolithic, we attempt a new synthesis and offer a re-interpretation of the record based on
259 multispecies thinking, stressing the importance of human-beaver entanglements as a history-
260 making dynamic. Before doing so, we briefly outline our conceptual point of departure,
261 deploying a ‘beaver lens’ and shifting attention to the assembly and long-term development of
262 human-beaver systems in the past. This perspective, we argue, supplies the necessary
263 conceptual resources to re-examine the potential formative but context-dependent role of
264 beavers throughout the earlier Holocene of northwestern Eurasia.

265

266 **Integrated human-beaver systems as a generative dynamic of European** 267 **prehistory**

268 Multispecies thinking challenges overly human-oriented approaches to the archaeological
269 record (Hamilakis and Overton, 2013; Boyd, 2017; Kay and Haughton, 2019; Kost and Hussain,
270 2019; Hill, 2021), as the various worlds inhabited by past people are recognized as
271 fundamentally co-constituted by a broad array of possible beings and entities, many of which
272 are nonhuman (Harris and Cipolla, 2017; Pilaar Birch, 2017). Although the contribution and
273 influence of these variegated denizens of the past tends to differ vastly and is highly context-

274 dependent, it is their ‘becoming-with’ – to speak with Haraway (2003, 2008) – that calls for
275 particular attention. The multispecies past in this way becomes a story of the diversity of life,
276 including the situated struggles and possibilities that emerge at the interstices and intersections
277 of species. Rather than emphasizing capacities and concerns of individual beings and isolated
278 actors, multispecies archaeologies highlight the creative potential for stability and change that
279 emerges from the *orchestration* of life in all its heterogeneity. In Haraway’s (2016: 58) terms,
280 the past is *sympoietic* and hence lived and made ‘in company’. Tsing (2021) similarly maintains
281 that ‘[s]taying alive – for every species – requires liveable collaborations’, necessarily entailing
282 ‘working across difference’. The challenge for coming to terms with multispecies pasts,
283 therefore, is to recognize and theorize *difference* across species while nonetheless not losing
284 sight of their historical *malleability* and *inter-relationality*. Which species meet and under
285 which conditions is crucial for what becomes possible – social, material or otherwise – and for
286 what *matters*. This principle of ‘horizontality’, which is now increasingly recognized as a
287 conceptual key across the environmental humanities (Cabral, 2021), also begins to feature more
288 and more prominently in life-oriented accounts of natural evolution (Margulis, 1998; Corning,
289 2005; Walsh, 2015).

290 Working through beaver difference requires to foster a ‘beaver lens’ and to look at the
291 past from the perspective of beaver practices and autoecologies. Beavers have been qualified
292 as ‘nature’s architects’ (Crumley, 2015) because they build structures such as lodges and dams
293 and engage in earth-working by digging canals and gullies. Their woodworking activities also
294 alter the dynamics of vegetational successions, thin out forest patches and create openings in
295 woodland landscapes. Beavers are potent ‘niche constructors’ and ‘ecosystem engineers’
296 (Johnston, 2017; Brazier *et al.*, 2021), so that their continued presence and varied activities
297 within a landscape quickly develop significant impact on the broader ecosystem. Beavers are
298 agents of disturbance (Tape *et al.*, 2018) and through their interference with hydrological and
299 geomorphological systems foster dynamic wetlands (Crumley, 2015; Liarsou, 2015; Poliquin,
300 2015). Practices such as dam, lodge and canal-building change water regimes and create new
301 habitats such as ponds of varying size and microecology as well as extended littoral zones,
302 which support a diversity of aquatic and terrestrial life (Larsen, Larsen and Lane, 2021), thus
303 reconfiguring ecosystem structure and functioning in riparian landscapes across scales. By
304 altering freshwater physical habitat, biotic composition and habitat connectivity (Macfarlane *et*
305 *al.*, 2017), this beaver-promoted regime change facilitates the ‘invasion’ of new species such
306 as riverine plants, a range of invertebrates, and various fish (Bunn and Arthington, 2002).

307 Notably, beaver-engineered freshwater habitats experience local shifts toward anaerobic
308 biochemical cycling and nitrogen accumulation and encourage higher rates of sediment,
309 nutrient and detritus trapping (eutrophication: Naiman, Melillo and Hobbie, 1986; Krylov,
310 2002). The result is often an associated shift from lotic (moving water) to lentic (standing water)
311 fish communities (Larsen, Larsen and Lane, 2021) and the promotion of species thriving under
312 eutrophic conditions (O'Hare *et al.*, 2018), including plants such as *Nymphaeaceae* (water
313 lilies). As opposed to rivers, sustained beaver-activity in lakes does not tend to substantially
314 change aquatic species composition but conserves lentic assemblages and generally increases
315 habitat quality, probably incurring extensive long-term legacy effects (Bashinskiy, 2020).
316 Dynamic beaver-powered wetlands attract and promote waterbird breeding and diversity (e.g.,
317 Nummi and Pöysä, 1997; Nummi and Hahtola, 2008; Nummi and Holopainen, 2014) and have
318 been shown to increase localized mammal richness (cf. Wright, Jones and Flecker, 2002;
319 Gauvin *et al.*, 2020). Beavers co-regulate biodiversity, often locally increasing it (Stringer and
320 Gaywood, 2016; Law *et al.*, 2019), and they typically complexify ecological networks and
321 interactions where they are active (Naiman, Melillo and Hobbie, 1986). Fedyń and colleagues
322 (2022) have shown that beaver-impacted habitats in temperate forest environments form
323 hotspots of seasonal mammalian aggregation, especially for small and large carnivores but also
324 deer. Beaver-modified landscapes therefore harbour resource patches of high potential foraging
325 value and predictability.

326 Because of these disproportional ecological impacts of beaver practices measured by
327 the overall abundance of the animals, the beaver emerges as a 'keystone species' in riverine and
328 boreal environments (Janiszewski, Hanzal and Misiukiewicz, 2014). Beavers are a resident
329 species yet can rapidly colonize new landscapes as they become available (Swinnen *et al.*,
330 2017), and also commonly abandon lodges when water and wood supply become insufficient.
331 Because of this dynamic, beaver activity tends to inscribe itself into the life-history of its host
332 landscapes and beaver effects can be charted through four broad stages of impact, from the
333 initial flooding of river banks after colonization to the formation of legacy meadow complexes
334 after site abandonment (Polvi and Wohl, 2012; Westbrook, 2021). Based on satellite time-series
335 data from the Canadian Arctic, Tape and colleagues (2018) have established that beaver
336 colonization and its attended landscape transformations not only happen on the scale of decades
337 but also accelerate climate change as beaver landscape engineering promotes permafrost
338 thawing, among other things contributing to thermokarst formation. Beavers are thus likely a
339 key agent of coupled climatic, environmental and geomorphological change at the Pleistocene-
340 Holocene transition in Northern Europe, where the retreating glaciers provided ideal,

341 hydroactive habitat for incoming beaver populations, conditions that were subsequently
342 reinforced by beaver activity.

343 The ecosystem impacts of the beaver not only frame the animal as a prominent and
344 dynamic agent in the environment, potentially garnering special human attention, some of the
345 above enlisted consequences of beaver behaviour enact profound ‘ecosystem services’ (sensu
346 Balvanera *et al.*, 2017) for foragers inhabiting the same landscapes. Beaver-propelled landscape
347 dynamics thus cater alluring possibilities and affordances for human life, while human
348 behaviour in turn may similarly shape the action-space of beavers – for the better or worse. This
349 coming together, and possible coordination, of human and beaver practice in situated historical
350 contexts as ‘becoming-with’ can be examined as a *systemic articulation* likely involving
351 assembly, consolidation and disintegration. Following Schroer (2022), we can explore such
352 articulations from the perspective of a general ‘geosociology’. Sociality, in this view, emerges
353 from the ‘geopraxis’ of all life as it contributes to the creation of serviceable living spaces,
354 shared lifeworlds and efforts of world-building in general. All animals, accordingly, ‘organize,
355 constitute and inform’ the world in their own way (Castoriadis, 2010: 156), and beavers are
356 beings *par excellence* who directly act upon the geo- and biosphere and by means of the
357 incurring consequences co-constitute the sociality of other species, including humans.
358 Geopraxis, then, as performed by beavers, becomes a *life-service* supporting the sustenance of
359 humans in the landscape as well – a service primarily conditional on two factors: i) human
360 practice must not undermine beaver ecosystem engineering, for example through overhunting;
361 and ii) human life must be predicated on practices and modes of occupation that can benefit and
362 take advantage of beaver practice or even rely/depend on it (see Liarsou, 2013, 2015 for similar
363 arguments). By analysing and comparing different human-beaver systems in time and space,
364 these issues can be scrutinized and addressed empirically and supported by data-driven
365 analyses, yielding important insights for the possibilities and challenges of present and future
366 human-beaver co-living.

367 Mustering this ‘beaver lens’ thus allows to tackle the historicity and contingency of
368 human-beaver systems. Importantly, the human acceptance and cultivation of beaver-provided
369 life services can provide ‘impetus for new practices of multispecies hospitality and conviviality’
370 (Rigby, 2020: 110), and may thus ultimately lead to novel or unique but frequently tangible,
371 archaeologically observable forms of beaver-related socio-material negotiation. As Eitler
372 (2014) points out, animal materialities and materializations should not be approached as mere
373 products or representations of their associated human-animal relationships but instead as

374 partaking in the ongoing *production* of these relationships. Materializations such as
375 Palaeolithic, Mesolithic or Neolithic animal-rendering visual culture or animal-sourced
376 material culture are in this view misunderstood as an ‘output’ of either culture, cognition or
377 ecology, or *representational* forms (representationalist fallacy). These materializations rather
378 help to generate and secure relations of ‘becoming-with’ and variously crystallize an/or
379 synthesize ‘natural’ and ‘cultural’ conditions of human-animal arrangements. Haraway’s
380 (2008: 216) notion of the ‘contact zone’, inspired by Pratt’s (2008) original human-oriented
381 concept, aligns with this view, highlighting that historical subjects are never given, but always
382 ‘constituted in and by their relations to each other’, which are in turn devised in terms of co-
383 presence, intra-action, and interlocked understandings and practices, although typically within
384 unbalanced power-relations. From such ‘contact zones’, then, historically specific forms and
385 systems of ‘conviviality’ can emerge.

386 *Conviviality* describes the ability of humans to interact creatively and autonomously
387 with others in their environment and to satisfy their needs while thriving in the social company
388 of these nonhuman others, thus framing prolific modes of multispecies cohabitation (Rigby,
389 2018, 2020; Straughan, Phillips and Atchison, 2022). Conviviality is not to be confused with
390 living-in-harmony, however, and does therefore not re-introduce or revive the problematic
391 notion of the ‘noble savage’. Conviviality is expressed in the adoption and cultivation of
392 practices that promote species co-living – frequently *despite* or *because of* tension and conflict
393 – and these practices are often materially generative and foster heightened attentiveness to
394 others’ presences, affordances and life services. Such attentiveness can be directly investigated
395 archaeologically, for example through the many ways animal materialities including bodies and
396 material culture were handled by past people. Systems of conviviality are expected to vary
397 considerable in time and space, however, and not all human-animal systems promote long-term
398 or even short-term conviviality. Convivial systems may lay foundation to what is sometimes
399 referred to as the ‘multispecies commons’ (Satsuka, 2014; Bresnihan, 2015; Centemeri, 2018;
400 Haldrup, Samson and Laurien, 2022) – a notion recently also mobilized by Woelfle-Erskine
401 (2019) to frame human-beaver collaboration in the context of ecosystem restoration and
402 stewardship. To what extent integrated human-beaver systems in the earlier Holocene of
403 Northern Europe may be qualified as an expression of deep-time conviviality and interspecies
404 ‘commoning’ is an open but increasingly relevant question and will be explored in the
405 following.

406

407 **A new synthesis of human-beaver intersections in the Northern Mesolithic**

408 *Macro-patterns in zooarchaeological beaver assemblages*

409 In contrast to the Terminal Pleistocene of higher latitude Europe where beaver remains are
410 rarely encountered in archaeological contexts (cf. Weber, Grimm and Baales, 2011; Veil *et al.*,
411 2015: 661), the Eurasian beaver becomes an important and recurrently encountered component
412 of faunal assemblages from the Early and Mid-Holocene of Northern Europe (**Fig. 1;**
413 **Supplementary Information M**). Altogether, beaver remains in the Early Holocene (Early and
414 Middle Mesolithic; Greenlandian: c. 9700-6300 cal. BC) constitute 5-18% of recorded mammal
415 MNI in Northwestern continental Europe. In Northeastern Europe, beaver remains are more
416 frequent during this period and NISP percentages reach an upper sealing of almost 50%. In the
417 Mid-Holocene (Late Mesolithic/Early Neolithic; Northgrippian: c. 6300-2250 cal. BC), this
418 picture only slightly changes, although regional signatures start to crystalize. In Northwestern
419 Europe, beaver contributions to mammalian faunas remain small but show some notable
420 chronospatial peaks and differentiations, ranging from 1 up to 49%. In the Northeast,
421 penecontemporary assemblages contain between c. 3 and 60% beaver NISP and generally retain
422 a higher level of beaver remains than in the Northwest, even though differences in inter-regional
423 faunal histories similarly emerge from the record.

424

425 Northeastern Europe

426 The Early and Middle Mesolithic in the Baltic and Russian Northwest are represented by the
427 Early Kunda, Veretje, and earlier Butovo complexes (Zhilin, 1996; Hartz, Terberger and Zhilin,
428 2010; Damlien, 2016; Manninen *et al.*, 2021), while the Late Mesolithic/Early Mesolithic
429 comprises Late Kunda, later Butovo, and Janislawice as well as the regional variants of the
430 emerging Early Comb Ware complex of Northeastern Europe (Zvelebil, 1994; Oras *et al.*, 2017;
431 Piezonka, 2021). Site types and conditions of archaeological recovery vary greatly between and
432 within regions. In the earlier Mesolithic, sites are mainly located above river and lake terraces
433 or in extended wetlands and are often represented by small flint scatters or mixed deposits,
434 while in the later part of the Mesolithic settlement systems become more structured and a
435 duality between habitation and extraction sites as well as between coastal and inland
436 occupations begins to take shape (Piezonka, 2021). For the Russian Northwest, well-preserved
437 faunal assemblages are mainly associated with the many bog and wetland sites of the Volga-
438 Oka interfluvium (Zhilin, 1996, 2004, 2007, 2014b), and the record may thus be biased towards
439 specific localities and forager activities in the landscape.

440 A directly dated beaver-gnawed piece of wood from the important Ivanovskoye peat
441 bog dated to around 10,000 years ago (Zhilin, 2019) provides evidence for prolonged histories
442 of human-beaver co-residence in the Russian Northwest. In the Early and Middle Mesolithic,
443 beaver makes up between 5 and 47% of total mammalian NISP in the Baltic and 19 to 36% in
444 Northwestern Russia, while the Late Mesolithic/Early Neolithic is characterized by beaver
445 NISP frequencies between 3 and 61% in the Baltic and 9 to 34% in Northwestern Russia (**Fig.**
446 **2a**). In the Early Mesolithic of Northwestern Russia and the Baltic, beaver is often the second-
447 most frequent mammal after the elk, pointing to the beaver's economic relevance and, possibly,
448 elevated abundance in the ecosystem. Muskrats (*Ondatra zibethicus*) and martens (*Martes* sp.)
449 are also an important faunal component in this period.

450 From the Middle Mesolithic onwards, the importance of elk diminishes in the area,
451 while wild boar and red deer (*Cervus elaphus*) become increasingly important in the Baltic and
452 the water vole (*Arvicola amphibius*) in Northwestern Russia. Interestingly, the increasing
453 importance of water vole in the Northeastern inland Mesolithic, reaching up to 61% of recorded
454 NISP at individual archaeological sites, corresponds to a general trend of decreasing faunal
455 representation of the beaver during the Middle and Late Mesolithic of the region, and this may
456 be related to long-term beaver-modulated changes in riverine-lakeland habitats, strongly
457 promoting water vole populations on a local scale.

458 In the Baltic, beaver frequencies are overall less stable across archaeological sites and
459 the pattern is more punctuated than in Northwestern Russia: some sites harbour fairly low
460 beaver abundances (c. 3-7%), while others show increased beaver yields (c. >20-60%), pointing
461 to functional differences in site formation and perhaps more diverse human-beaver interactions.
462 The Late Mesolithic/Early Neolithic site of Dąbki 9 in Northern Poland, for example, has been
463 argued to represent a seasonal special purpose locality mainly geared towards fur-extraction
464 and possibly exchange (Schmölcke and Nikulina, 2015). It is notable that among the other
465 species from Dąbki 9, the otter makes up c. 6% of the documented mammalian NISP, thus
466 representing the third-most frequent animal in the whole assemblage. Although otter remains
467 are not generally frequent at beaver-bearing sites, they are often a common yet low-abundance
468 feature. This association is conspicuous since otters and beavers are known for their sympatric
469 relationships, as otters benefit from beaver-engineered and disturbed habitats, especially in
470 riverine higher latitude woodland environments (Tumlison, Karnes and King, 1982; Reid, 1984;
471 LeBlanc *et al.*, 2007).

472 The possible presence of muskrat (28%) alongside beavers (30%) in Early Mesolithic
473 Stanovoye 4 at the Volga-Oka interfluvium in Northwestern Russia (Zhilin, 2004) is notable and
474 may similarly indicate that foragers took advantage of the facilitative effects of beavers on their
475 animal co-inhabitants (cf. Crego, Jiménez and Rozzi, 2016).

476

477 Northwestern Europe

478 The Early and Middle Mesolithic of Southern Scandinavia including parts of Germany is
479 characterised by the Maglemose complex (9500-6400 BC) and the earlier part of Kongemose
480 (6800-5400 BC), known in particular from the many well-preserved bog sites across Denmark
481 and Northern Germany. Two types of sites are known from the Early Mesolithic: so-called
482 deposition sites and habitation sites (Sørensen, Lübke and Groß, 2018). The respective lithic
483 and faunal assemblages are often very small and fragmented, indicating short-term visits. Well-
484 preserved faunal material only derives from deposition sites in Southern Scandinavia, while in
485 Northern Germany habitation sites also occur (Sørensen, Lübke and Groß, 2018).
486 Archaeological sites associated with the large glacial valleys and the moraine landscapes of the
487 region are generally better preserved than sites from the Northeuropean sand belt (Groß, 2017:
488 123). The included Middle Mesolithic sites from Southern Scandinavia are well-preserved,
489 derive from wetland deposits, and have mostly been described as habitation sites ('base camps':
490 Schuldt, 1961; Gramsch, 2000; Groß, 2017: 185), but we may miss the more ephemeral sites
491 from the period. Early and Late Maglemose sites from Jutland and Eastern Denmark show
492 patterned differences in preservation and depositional context (Blankholm, 1996; Nielsen,
493 2006). In the Netherlands, only a few archaeological sites with faunal remains are known from
494 the Early and Middle Mesolithic. The zooarchaeological assemblages are small and beaver
495 remains number only a handful, making the comparison with Northeastern Europe and Southern
496 Scandinavia difficult for the Early Holocene.

497 In Early Mesolithic Southern Scandinavia and Northern Germany, beaver remains make
498 up an average of 8% of total MNI, ranging between 5 and 14% (**Fig. 2b**). Most assemblages
499 from this period are very small (<50 total MNI), making it difficult to draw firm conclusions
500 from species compositions. At Sværdborg, where several excavations have yielded larger faunal
501 assemblages, beavers are clearly present (between 5 and 9%), as are other fur-bearing mammals
502 such as otter (5-8%) and badger (*Meles meles*) (2-5%). In general, otters are relatively common
503 in the Early Mesolithic of Southern Scandinavia (2-33% of MNI), supporting the observations
504 made for Northeastern Europe. Overall, however, there is a greater emphasis on largefauna,

505 such as wild boar and roe deer (*Capreolus capreolus*). Despite the noted differences in faunal
506 preservation for habitation and deposition sites between Southern Scandinavia and Northern
507 Germany, there is no apparent divergence in beaver MNI representation. In the here considered
508 Middle Mesolithic faunal assemblages from Southern Scandinavia, beaver remains continue to
509 be present but in consistently small numbers. They average c. 9% of total mammalian MNI,
510 ranging between 2% and 18% respectively. Larger mammals are again found in greater
511 numbers, but, as noted above, most of the respective assemblages are unfortunately too small
512 and fragmented to draw broader inter-site conclusions.

513 The Maglemose and Kongemose complexes are succeeded by the Ertebølle Culture
514 (EBK; 5400-3950 BC), identified first and foremost by the famous coastal shell-midden sites.
515 The EBK represents the end of the Mesolithic in Southern Scandinavia and many sites reflect
516 transitional phases to the Funnel Beaker Culture (TRB) marked by the appearance of
517 domesticated animals and cereals (Gron and Sørensen, 2018). EBK zooarchaeological
518 assemblages derive from a variety of site contexts, such as bogs, submerged/waterlogged sites,
519 and shell middens, introducing systematic taphonomic and recovery biases (Gron and Robson,
520 2016). Beavers decrease to an average of only 0.4% in EBK, with values ranging between 0
521 and 2% at individual sites (cf. **Fig. 2b**). Other fur-bearing animals, in particular marten and wild
522 cat (*Felis silvestris*), make up a more substantial part of the faunal assemblages than beavers,
523 while large fauna continue to be important. In EBK, marine mammal shares increase
524 significantly in abundance and together with marine fish become a key part of the human diet
525 (Rowley-Conwy, 1999).

526 In the Netherlands, the Late Mesolithic/Early Neolithic has produced a wealth of faunal
527 data from Swifterbant Culture (ca. 5500-3400 BC) sites in the Dutch wetlands. The Swifterbant
528 Culture has long been considered a transitional archaeological complex at the forager-farmer
529 interface, but recent evidence demonstrates that from 4250 BC on these communities had
530 established agricultural practices while also relying on diverse natural resources (Huisman and
531 Raemaekers, 2014; Raemaekers *et al.*, 2021; Brusgaard *et al.*, forthcoming). Swifterbant
532 Culture sites are all habitation sites, some seasonal and some year-around. In the Early
533 Neolithic, Linearbandkeramik (LBK) farming communities also inhabited the southernmost
534 zone of what is now the Netherlands, but faunal remains from these sites are few in number (8
535 total identified mammal NISP), so we restrict the discussion to the Swifterbant Culture in this
536 region.

537 Beaver remains are altogether abundant at Swifterbant Culture sites, averaging c. 20%
538 of total NISP, but the numbers are highly variable between sites, ranging between 0.4 and 49%.
539 Beaver remains are predominant at the oldest sites, Hardinxveld-Giessendam Polderweg and
540 De Bruin (5500-4250 BC) (34% and 49% of total NISP, respectively) and Schokland P14
541 (4900-3300 BC) (37%), where they rival or even outnumber larger ungulates such as wild boar
542 and red deer. At the Hardinxveld-Giessendam sites, the total percentage of beaver NISP masks
543 the notable increase in beavers over time, reaching frequencies of 83% at Polderweg and 51%
544 at De Bruin in the final occupation phases, while the number of large fauna decreases
545 (Oversteegen *et al.*, 2001; van Wijngaarden-Bakker *et al.*, 2001). This is possibly a result of
546 increasingly wet conditions due to the sea level rise in the area – conditions in which beaver
547 would have flourished and foragers may have become increasingly reliant on aquatic resources
548 (Brusgaard, Dee, *et al.*, 2022).

549 At the Swifterbant type sites S2, S3, and S4 (4300-4000 BC), where domesticated
550 livestock are also present (Zeiler, 1997; Brusgaard *et al.*, forthcoming), beaver makes up
551 between 12 and 23% of total NISP. Beaver-gnawed willow branches were found at S3 (Casparie
552 *et al.*, 1977) and Prummel (2017) has highlighted that the Swifterbant environment would have
553 been ideal for human exploitation due to beaver engineering. In contrast, at the sites Tiel, Hoge
554 Vaart, and Nieuwegein, beaver represents less than 5% of the total NISP, and there is more
555 emphasis on large fauna. Otter remains fluctuate almost on par with beaver remains at each site,
556 ranging between 29% at Hardinxveld-Giessendam Polderweg (where beavers are abundant)
557 and <1% at Tiel (where beavers are few). The only exception to this pattern is Schokland where
558 the NISP of beaver is high but only few otter remains were recovered.

559 From an environmental perspective, the prevalence of beaver remains at many of the
560 Swifterbant Culture sites is not surprising considering their location in freshwater riparian
561 landscapes. The Dutch data discussed here is generally biased towards such locations because
562 faunal remains from archaeological sites on the sandy (drier) soils have not been preserved and
563 no coastal sites are known due to erosion (Vos, 2015). It is therefore presently unknown which
564 wild fauna was exploited in these other landscapes. While the presence of beaver at Mesolithic
565 and Early Neolithic wetland sites is thus not unanticipated, the relative abundance of beaver
566 remains points to some form of concentrated exploitation of these animals (and of otters) by
567 Swifterbant communities. The main trends in beaver remains between archaeological sites and
568 over time appear to be negatively structured by the frequency of large prey animals such as
569 cervids and wild boar, suggesting a strategic trade-off between either beaver and otter or

570 targeting of such larger species. There is, however, *not* a switch to other fur-bearing animals
571 such as martens, as often observed in more recent periods and for example appears to be
572 reflected in the faunal evidence from EBK hunting locales in Southern Scandinavia (see below).

573

574 *Macro-patterns in beaver-related material culture*

575 Beaver-related material culture has been recovered from across the Northern European wetland
576 and boreal zones in the Early and Mid-Holocene (cf. **Fig. 1; Supplementary Information 1**).
577 This material culture can be grouped into four primary groups: i) incisor tools, ii) mandible
578 tools, iii) tooth pendants, and iv) other modified bones not directly tied to food-getting or
579 tooling endeavours, such as ankles. Incisor tools are made from the front teeth of beavers
580 without their associated bone sockets, either by manipulating the teeth or by using and/or
581 subsequently re-sharpening them. Mandible tools consist of completely or partially removed
582 beaver mandibles including the front teeth, often modified and roughly shaped to facilitate
583 instrumentalization. Tooth pendants are defined as beaver teeth that are either grooved or
584 perforated for suspension.

585

586 Incisor and mandible tools

587 Incisor tools are found across the entire region, from the Early Mesolithic to the Late
588 Mesolithic/Early Neolithic, whereas mandible tools are mainly known from the Baltic and the
589 Russian Northwest, where they are abundantly found at Mesolithic sites of all ages (Zhilin,
590 2001, 2020; Lozovskaya and Lozovski, 2015; Lozovskaya, Leduc and Chaix, 2017). For the
591 Russian North alone, Zhilin (2020) reports more than 1400 beaver mandible and incisor tools
592 dated to the Mesolithic, mostly from the wetland sites. Most of these objects are prepared and/or
593 used mandibles (n=1388) and only a handful represent modified frontal teeth (n=34). The
594 number of such objects varies greatly among archaeological sites, ranging from sites with only
595 a small amount of such tools to archaeological sites such as Ozerki 5/IV and Veretje 1 bearing
596 more than 100 objects. Mandible tools are least frequent in the Early Mesolithic and increase
597 from the Middle to the Late Mesolithic/Early Neolithic (Zhilin, 2020). Incisor tools are
598 currently unknown from the Early Mesolithic and most of these artefacts derive from Middle
599 Mesolithic contexts within the region.

600 In Northwestern Europe, beaver-sourced tools from the Mesolithic are much less
601 abundant but they have been reported in the literature (**Fig. 3; Tab. 2**). A single worked

602 mandible has been described from the Early Mesolithic occupations of Star Carr in Britain
603 (Knight *et al.*, 2018), attributed to the Maglemose complex. In Southern Scandinavia and
604 Northern Germany, mandible tools are presently also known only from Maglemose contexts,
605 including some of the classic Maglemose localities from Zealand in Eastern Denmark
606 (Broholm, 1924; Hatting, 1970; Lautsen Lomborg, 2021). They mainly date to the
607 Boreal/earliest Atlantic ('Middle Mesolithic' in the here-adopted terminology) and thus likely
608 belong to the later part of the Early Holocene, even though this material should be radiocarbon
609 dated to confirm this placement. Beaver incisor tools, even though mostly isolated pieces, were
610 found at the Middle Mesolithic sites of Holmegård, Ørgård and Sværdborg (Hatting, 1970;
611 Lautsen Lomborg, 2021) and at Hohen Viecheln I (Schuldt, 1961; Schmölcke, Groß and
612 Nikulina, 2017) and Rothenklempenow 17 (Schacht and Bogen, 2001) in Northern Germany.
613 Beaver-sourced tools, both mandibles and incisors, were also found in a likely EBK context
614 from Heidemoor in the German Northeast (Ewersen, 2011), but this attribution similarly awaits
615 corroboration in the future.

616 No mandible tools have been found in the Netherlands. Only incisor tools are known
617 and they derive from the two Late Mesolithic Hardinxveld-Giessendam sites (Coles and
618 Kooijmans, 2001; Louwe Kooijmans *et al.*, 2001; Louwe Kooijmans, Oversteegen and van
619 Gijn, 2001). These tools bear a remarkable similarity to the incisor tools recovered from the
620 Danish Middle Mesolithic sites. Esser *et al.* (in prep.) further draw attention to the circumstance
621 that at Tiel-Medel, while beaver mandibles have been recovered, only a very small number of
622 teeth occur in the assemblage, which is taphonomically unlikely, and may thus point to
623 anthropogenic selection and filtering. It is for example possible that the missing beaver teeth
624 have been removed for use or ornamentation elsewhere or were exported from the site but this
625 hypothesis requires future empirical substantiation.

626 The evidence from the Northwestern Europe is thus extremely sparse, despite
627 researchers being keenly aware of such finds and thus on the lookout for them (e.g., Enghoff,
628 2011; Esser *et al.*, in prep.), suggesting this is most likely not due to researcher bias. The
629 Northwestern earlier Mesolithic record thus appears to be structurally different from what is
630 observed in the Northeast. Most relevant beaver-related material culture from the region either
631 dates to the Middle Mesolithic or is associated with the earlier part of the Mid-Holocene, even
632 though the precise dating of some of the objects remains problematic. It is worth noting that for
633 the EBK specifically, tools made from animal bone are rare overall, so this difference may have
634 less to do with the role of beavers in particular and more with the status of animal-related

635 material culture in general. In Swifterbant Culture contexts, by contrast, a wide diversity of
636 species appear to have been involved in tool production – from wild boar to swans to caprines
637 (Louwe Kooijmans *et al.*, 2001; Kranenburg and Prummel, 2020; Aal and van Gent) –
638 suggesting little species-level discrimination. More detailed analysis, for example with regard
639 to body part selectivity (see e.g., Hill, 2019 and Hussain, Weiss and Kellberg Nielsen, 2022 for
640 the key importance of the latter), may be warranted, however.

641 The function of beaver-sourced tools has been discussed extensively in the literature
642 (e.g., Zhilin, 1997, 2020; Coles, 2006; Lozovskaya, Leduc and Chaix, 2017; Schmölcke, Groß
643 and Nikulina, 2017). At Middle Mesolithic Veretje 1, the first ever securely identified beaver
644 mandible tool was reportedly still bound with a strip of bark, revealing its tool character and
645 the way it was instrumentalized (Oshibkina, 1983; Zhilin, 1997). Similar mandible tools
646 attached to wooden handles are for example known from Indigenous people from Alaska who
647 used them as scrapers, the molars functioning like a rasp (Osgood, 1940; Schmölcke, Groß and
648 Nikulina, 2017). Following Zhilin (2014, 2020), Mesolithic instances of such beaver-sourced
649 tools were mainly used as scrapers, knives and chisels or as pressure flaking devices.
650 Woodworking was an important task of many of these tools but some scraper-like mandible
651 tools were apparently also used for bone-working (Zhilin, 2020). The utilization of these objects
652 therefore largely mirrors the capacity of the respective body-parts in a living beaver, which has
653 led Schmölcke and colleagues (2017: 8) to suggest that ‘perhaps by observing these animals
654 prehistoric people got the notion that they have built-in woodworking tools.’ We return to this
655 point below and take it up again in the discussion.

656 The in-depth techno-functional analyses of these object performed by Zhilin (2020)
657 have further shown that beaver-sourced tools were not deployed *ad hoc*, as might perhaps
658 hastily be inferred from a pragmatic copy-paste logic *vis-à-vis* beaver woodcutting practices.
659 The *chaîne opératoire* of these objects is often surprisingly complex and demonstrates distinct
660 stages of reworking, suggesting not only that many of these tools were probably in use for quite
661 some time, but also that they were actively curated and thus generally *cared* for. We must
662 assume that Mesolithic people generally had the capacity and means to acquire beaver bodies
663 to replenish tool stocks if they had wished to, and the extended life-histories of beaver-sourced
664 tools thus strongly suggest that the objects *mattered* to people, and keeping the same items in
665 human systems was a conscious concern. Furthermore, using and handling these tools would
666 have brought beaver bodies to the centre of human ‘horizons of concern’ (sensu Bird-David,
667 2017), promoting understanding of and *sympathy for* the beaver, and thus bringing human and

668 beaver perspectives closer together, with human and beaver bodies and phenomenological
669 horizons literally merging, if only temporally.

670

671 Tooth pendants and other invested beaver objects

672 Beaver tooth pendants are relatively rare and currently confined to the eastern Boreal zone,
673 where some examples have been reported from the Middle Mesolithic site of Ozerki 17 (Zhilin,
674 1996: 218), Late Mesolithic Okajomovo 5 and Nushpoli 11 at the Dubna River (Zhilin, 2007),
675 Late Mesolithic Kubenino at the Onega River (Kashina, Ahola and Mannermaa, 2021), and
676 >1200 beaver teeth in total were found in human burial contexts within the extensive Late
677 Mesolithic/Early Neolithic hunter-gatherer cemetery of Oleniy Ostrov in what is today Karelia
678 (Grünberg, 2013; Mannermaa and Rainio, 2020), making up about 20% of all animal tooth
679 pendants originally published by Gurina (1956) for the site. Some of these were cut into plates,
680 show macroscopic use-wear traces and bear notches and/or grooves, suggesting that they were
681 worn extensively (Grünberg, 2013: 235; Mannermaa *et al.*, 2019), perhaps by more than a single
682 person. Beaver tooth pendants seem to be rare at Early Mesolithic sites but (Zhilin, 2014a) has
683 recently reported several such objects from the Preboreal site of Ivanovskoye 7/IV (cf.
684 Schmölcke, Groß and Nikulina, 2017: 5). Beyond the importance of the species origin for
685 understanding these objects, Grünberg (2000) has suggested that beaver incisors were probably
686 significant because of their unique orange-brown colouring. In addition, some of the beaver
687 pendants were probably made from former mandible or incisor tools (Zhilin, 2001, 2020: 10)
688 and thus represent the final life-history stage of beaver-sourced material culture, so that placing
689 these objects into burials may be significant itself. In the Baltic, a small number of beaver tooth
690 pendants were recovered from Early Mesolithic Pulli and the Early Neolithic site of Kudruküla
691 in Estonia (Jonkus and Rannamäe, 2018), and there are likely more examples from this region
692 that either await publication or escaped our literature survey.

693 Beaver astragali (ankle bones), perforated or not, have been found in greater numbers
694 in human interments at the important Early-to-Late Mesolithic/Early Neolithic burial ground of
695 Zvejnieki in Northern Latvia (Eriksson, Lougas and Zagorska, 2003), where most of the animal
696 bone pendants associated with the more than 100 buried human individuals represent beaver
697 astragali (Zagorskis, 1987; cf. Grünberg, 2013: 237). The number of bone pendants at Zvejnieki
698 generally increases from the Early to the Late Mesolithic/Early Neolithic. Interestingly, both
699 beaver tooth pendants and astragali seem to be associated mainly with female-sexed human
700 bodies (Fehner, 1963; O'Shea and Zvelebil, 1984), pointing to the involvement of beavers in

701 the construction of social *persona*, and perhaps gender, in this hunter-gatherer context. Some
702 Mesolithic burials in Northeastern Europe, for example at Oleniy Ostrov, are associated with
703 other unmodified beaver bones such as ulnae (Grünberg, 2013), but it is presently difficult to
704 establish how important, selective or wide-spread specific bone-burial patterns and their linked
705 cultural practices were.

706 There is thus a gradual diversification of beaver-related material culture and practices
707 of materialization in the course of the Northeastern Mesolithic (Mannermaa *et al.*, 2019). In
708 this context, it is notable that Zagorska and colleagues (2018) have recently re-interpreted a
709 fragmented zoomorphic antler staff head from Late Mesolithic/Early Neolithic Zvejnieki as
710 rendering either beaver or otter, linking the object to the distinct tradition of zoomorphic
711 figurine-making which spans the Baltic and parts of Western Russia in their well-defined
712 Middle Neolithic at the end of the Mid-Holocene. This tradition features exceptional beaver
713 and/or otter-like figurines, either plastically carved or rendered in bird's-eye profile, for
714 example from the settlement of Valma at Lake Võrtsjärv in Estonia (Jaanits, 1965), where an
715 amber figurine from a female burial is now interpreted as a beaver (Ots, 2010).

716 In contrast, no ornaments and/or grave goods made from beaver remains have been
717 documented in Northwestern Europe. This is despite the fact that pendants made from animal
718 teeth are relatively common at Swifterbant Culture sites for example, both in settlement and
719 burial contexts, including perforated teeth of cattle (*Bos* sp.), wild boar, pig (*Sus domesticus*),
720 horse (*Equus ferus*), dog (*Canis familiaris*), and otter (Devriendt, 2008; Kranenburg and
721 Prummel, 2020). These differences between eastern and western North Eurasia indicate
722 divergent histories of human-beaver interaction and cohabitation, and may point to important
723 differences in how beavers were negotiated, which place they were assigned in multispecies
724 systems and, possibly, how significant they were for human livelihoods.

725

726 Two trajectories of beaver-related material culture

727 Two different trajectories of beaver-related material culture development can therefore be
728 discerned. In the Northwest of Europe, beaver-related material culture appears to be mainly
729 confined to the instrumentalization of beaver body parts as tools, documented in different areas
730 at different time intervals. In the Baltic and in Northwestern Russia, by contrast, beaver-related
731 tool-making practices are joined by evidence for the use of beaver teeth as pendants and the
732 special treatment of other body parts, especially astragali. These large scale inter-regional
733 differences are interesting, as they suggest, together with the faunal data reported above, that

734 human-beaver exposition and cohabitation was more stable and consequential in the Northeast,
735 developing in own distinct historical dynamic reflected in material culture diversification over
736 time, while the significance of beavers in the northwest may have been more situational and
737 context-specific without a notable long-term dynamic.

738

739 *Ichthyofaunal patterns*

740 Fish remains from the Northern Mesolithic provide important information on human landscape
741 use and exploited aquatic ecologies, and may further disclose hitherto overlooked evidence for
742 human-beaver cohabitation and encouragement in wetland and freshwater environments.
743 Similarly as the data on mammalian faunal compositions, the available evidence on human-
744 procured fish during the Mesolithic indicates a broad distinction between ichthyofaunal
745 assemblages in Northwestern Europe on the one hand and the Baltic and the Russian Northwest
746 on the other (**Fig. 4a, 4b; Supplementary Information F**).

747

748 Northeastern Europe

749 In Northwestern Russia, northern pike (*Esox lucius*) dominates the ichthyofauna from the Early
750 to the Late Mesolithic (mean NISP% = c. 50-70) but the relative importance of pike decreases
751 slightly over time, while other large freshwater predators such as the European perch (*Perca*
752 *fluviatilis*) become more frequent throughout the Middle and Late Mesolithic (**Fig. 4a**). Early
753 Mesolithic assemblages tend to be more monospecific, focusing either on the pike or, in one
754 case, on the predatory zander/pike-perch (*Sander lucioperca*: 95%). From the Middle
755 Mesolithic onwards, the ichthyofauna not only becomes more diverse, it is also notably enriched
756 in carps and ground-feeders in general. Wels catfish (*Silurus glanis*), occasionally found already
757 in the Early Mesolithic, emerges as a regular although low-frequency component of Late
758 Mesolithic/Early Neolithic assemblages. The vast majority of represented species forms part of
759 lentic communities (**Fig. 5**) and some of the notable later Early Holocene and Mid-Holocene
760 species suggest that eutrophic conditions must have been well-established in the landscape by
761 then. The eel (*Anguilla* sp.) remains exceptionally rare even in the Late Mesolithic, when the
762 Littorina Sea was already well developed (Kostecki, 2014) and eel has been shown to be present
763 in Baltic waters (Enghoff and Ediger, 2016).

764 In the Baltic, the evidence is sparser and some patterns are repeated. In the Early and
765 Middle Mesolithic, the ichthyofauna is dominated by both northern pike and zander/pike-perch,

766 which together make up at least >60% and often >90% of recorded fish NISP. Yet in contrast
767 to Northwestern Russia, northern pike becomes more frequent in the Late Mesolithic/Early
768 Neolithic, often at the expense of zander, and the Middle and Late Mesolithic are again
769 characterized by a notable catfish input (up to NISP%=28 in the Late Mesolithic). Interestingly,
770 Wels catfish seems to supplant carps in the course of the Mesolithic but the dataset is not robust
771 enough to securely establish this trend. Kõpu I in Estonia presents a rare example of notable
772 marine fish input during the Late Mesolithic/Early Neolithic, but the fish assemblage is too
773 small (n=6) to extrapolate from this so far isolated context. Given that the site's mammalian
774 fauna is dominated by seal (Lõugas, 2017), the marine fish component is likely the result of the
775 specific foraging activities linked to targeted phocid hunting at the emerging Baltic Sea, and is
776 thus not necessarily reflective of a systematic practice and/or well-established marine fishing
777 economies (cf. Boethius *et al.*, 2017 for similarly cautionary arguments regarding another Baltic
778 Early Holocene context).

779

780 Northwestern Europe

781 In Southern Scandinavia, the Early Holocene fish record strongly differs from its Mid-Holocene
782 counterpart. Early and Middle Mesolithic fish assemblages from Northern Germany and
783 Denmark are strongly dominated by northern pike (mean NISP%= >80), while carps are also
784 common, especially in the Middle Mesolithic, and some pike-heavy assemblages feature a few
785 catfish remains (**Fig. 4b**). These Early Holocene assemblages attributed to the Maglemose
786 complex are exclusively freshwater-oriented. Bølling Sø in Jutland is the only site featuring
787 marine fish, the catadromous (migrating down-river) European eel (Robson and Ritchie, 2019).
788 Even though Mesolithic people in the area had undoubtedly access to the sea, they did thus
789 mostly exploit freshwater habitats and overwhelmingly focused on larger lentic fish, in
790 particular predators and cyprinids, even though other species were available. Future
791 investigations may complement this picture as most former Early Holocene coastal sites, if they
792 existed, are submerged today (Astrup, 2018, 2020). This being said, a similar emphasis on pike,
793 perch (*Perca fluviatilis*), and carps has recently been established for the Early Mesolithic site
794 complex at Lake Flixton in Northern England including the important occupations at Star Carr
795 (Robson *et al.*, 2018).

796 This picture changes in the Mid-Holocene and the ensuing EBK complex, which mostly
797 spans the later Atlantic (cf. Enghoff, 1994; Enghoff, MacKenzie and Nielsen, 2007). The focus
798 is then shifted towards eel, cods (*Gadidae*), and flounder (*Pleuronectidae*), and thus to deep sea

799 and/or transitional fish species (Ritchie, 2010). Whereas eels (NISP%=1-73), cods (NISP%=2-
800 74) and flounders (NISP%=1-58) compete for the top-ranking spot in the early Mid-Holocene
801 fish record in Jutland, cods (NISP%=44-86) dominate the record in Zealand, followed by
802 flounders (NISP%=2-71) and eels (NISP%=1-9), who are much less important in this part of
803 Mesolithic Denmark (Ritchie, 2010). Carps remain significant in some Danish Mid-Holocene
804 contexts, notably on the Jutland peninsula, but overall there is a transition to marine fisheries.
805 This change in human subsistence is broadly concomitant with emerging sea mammal and
806 dedicated ocean-bound economies developing during the Atlantic chronozone (Price, 1985;
807 Rowley-Conwy, 1999; Price *et al.*, 2018).

808 The Mid-Holocene fish record from the Dutch wetlands is also governed by lentic fish
809 communities, albeit with more lotic and marine fish representation than in the Northeastern
810 Mesolithic (cf. **Fig. 4b, 5**). Together, northern pike and carps dominate the Late
811 Mesolithic/Early Neolithic assemblages and it has been suggested that the migratory patterns
812 of pike may have been critical in establishing the seasonal mobility of the communities using
813 the Hardinxveld-Giessendam environments (Beerenhout, 2001a, 2001b). Pike becomes less
814 frequent through time and carps show the reverse trend. At the Early Neolithic site Hoge Vaart
815 A27, cyprinids contribute more than 69% of recorded fish NISP (Laarman, 2001). Pike is
816 overall less abundant than in the Northeastern Mesolithic and there is a general shift from an
817 initial focus on large predatory freshwater fish such as pike and European perch to an emphasis
818 on carps and catfish, which can reach up to 13% ichthyofaunal NISP representation in the Early
819 Neolithic (Kranenburg and Prummel, 2020). Salmonids are always very rare. Interestingly, eel
820 only becomes a factor at around 4000 cal. BC (c. 3-14% of NISP) and this parallels a notable
821 increase in lentic fish, many of which also thrive in freshwater environment with reduced or
822 locally disrupted riverine connectivity. Notable is also the occasional occurrence of a small
823 component of sturgeons (*Acipenseridae*), a coastal species which is anadromous (migrates
824 river-up). The marine fish component is otherwise negligible, even though people must have
825 also had direct access to the coast, so this is unlikely a question of availability alone. The Late
826 Mesolithic/Early Neolithic evidence from the North European wetland zone thus clearly
827 bespeaks of a unique and highly complex aquatic ecology at the mouth of the young Holocene
828 River Rhine and the Swifterbant river system with different coexisting flow regimes. This
829 complexity of riverine habitats within a vast, braided river network supporting varied levels of
830 hydrological connectivity and eutrophication is at least in part the co-product of the activities
831 of beaver populations in the region, who were probably present in the wider area from at least
832 the Early Holocene onwards.

833 **Discussion**

834 The onset of the Holocene in Northern Europe may be framed as a ‘beaver event’ setting the
835 scene for post-glacial human history above 50° latitude north. Beavers were among the pioneer
836 species moving into the newly available high-latitude environments released by the retreating
837 glaciers at the end of the Pleistocene. These novel environments with their rich and dynamic
838 hydrologies, including many glacial legacy lakes, were not only suitable for beavers to establish
839 themselves as prominent keystone agents in the north, these environments were also rapidly
840 transformed by beaver geopraxis, which promoted wetlands, riverine heterogeneity, distinct
841 lake and pond-invested ecosystems, as well as unique patterns of plant and animal biodiversity
842 across landscape scales. As Tape and colleagues (2018) have shown, beaver colonization of
843 Arctic tundra landscapes can accelerate the thawing of permafrost and may thus quicken the
844 transformation of periglacial into post-glacial ecosystems. At the onset of the Holocene in
845 Northern Europe, beavers were not just widely present and recognizably important agents in
846 the landscape (Liarsou, 2020) – documented well-before human foragers left any tangible traces
847 in the archaeological record – they were probably *co-responsible* for shaping the kinds of
848 environments that we today readily identify as earlier Holocene, from the extensive riverine
849 wetlands of Northwestern Europe to the mosaic of lake-rich boreal and tundra environments in
850 the Baltic and Northwestern Russia (Wohl, 2021).

851 The combined archaeological and zooarchaeological evidence from the Northern
852 Mesolithic reviewed and synthesized here (c. 9000-4000 cal. BC) opens up the interesting
853 possibility that transformative beaver ecosystem agency provided an important framework and
854 generative context for human foraging lifeways and ecocultural identities at the edge of former
855 glaciers. The persistence of beaver remains through large parts of the Mesolithic across the
856 study regions suggests that human-beaver intersections were likely more consequential than
857 previously recognized, and long-term developments in material culture and society appear to
858 have been critically interlaced with the changing dynamics of human-beaver systems.
859 Deploying a ‘beaver lens’, the archaeological record and spatiotemporal patterns in mammal
860 remains, fish fauna and beaver-related material culture in the Mesolithic of Northern Europe
861 drawn together here thus motivate re-evaluation and re-contextualization with beaver agency,
862 ecological engineering, and changing human historical registers.

863 As a whole, the available archaeological evidence points to notable differences in the
864 long-term development of human-beaver systems between the Northwest and Northeast of
865 Europe but also *within* the Northwestern region. In the boreal and taiga zone of the Baltic and

866 Northwestern Russia, beaver remains form a substantial and stable component of the species
867 composition throughout the Mesolithic. Beaver-related material culture is abundant, and
868 represents a significant and diversified corpus of beaver-related materialization, with beavers
869 becoming increasingly important in ornamental and burial practices through time. In contrast,
870 only a few beaver-material tools and no pendants are known from Southern Scandinavia and
871 Northern Germany. Here, beaver remains are far fewer than in the Northeast in the Early and
872 the Middle Mesolithic, but they are a steady component of Maglemose and Kongemose
873 assemblages. This changes significantly in the Late Mesolithic, when beavers all but disappear
874 from the zooarchaeological record. In the Dutch Late Mesolithic and Early Neolithic, in
875 opposition, beaver remains are abundant, rivalling Northeastern beaver percentages. While
876 there is notable variation between sites, beaver appears to have been an important component
877 of Swifterbant Culture subsistence and remains so at wetland sites until well into the Dutch
878 Neolithic (cf. Lauwerier, van Kolfschoten and van Wijngaarden-Bakker, 2005). Yet only a few
879 incisor tools have been found and none of the many animal tooth pendants derive from beavers.
880 The lack of sites from the Early and Middle Mesolithic makes it currently impossible to assess
881 developments through time, however.

882 We suggest that the divergence of regional trajectories between Northwestern and
883 Northeastern Europe is bound to the varying nature of human-beaver relationships, pertaining
884 to modes of cohabitation and the shifting *significance* of beavers for human affairs. Querying
885 these differences in human-beaver expositions in the Mesolithic of Northern Europe requires to
886 unsettle current orthodoxy and to methodologically invert the direction of inquiry – to ask what
887 beavers could do for human societies and how the animals would have framed human affairs,
888 thus investigating possible *life-services* for human societies provided by beavers. It is here that
889 the other mammalian and the ichthyofaunal evidence from the Mesolithic is of particular
890 relevance (cf. Liarsou, 2013: 174, 2015, 2020: 38-42), opening up renewed conversations on
891 the supportive role of beavers for earlier Holocene human occupations of the northern wetland
892 and boreal zones of continental Europe.

893

894 *Mammal hunting affordances*

895 A ‘beaver lens’ reveals interesting patterns in species co-associations and possible long-term
896 dynamics in multispecies assemblages related to beaver agency. In Northeastern Europe, for
897 example, the predominance of elk alongside beaver is noteworthy as beaver-elk ecosystem
898 associations are reflective of incipient colonization scenarios where beaver-powered wetlands

899 create a mosaic of standing water bodies and promote the growth of riparian or edge vegetation
900 such as willow (Gibson and Olden, 2014), in turn attracting elk (Ripple and Beschta, 2004;
901 Baker *et al.*, 2005; Nummi *et al.*, 2019). Beavers and elk also display a high degree of dietary
902 overlap (Hoy *et al.*, 2019). As previously argued by Pedersen (2009: 46), beaver-elk
903 interactions are often beneficial for human foragers and the beaver may have come into view
904 as a ‘faunal regenerator’ because of this. Similar dynamics are harder to trace in Northwestern
905 Europe, in part because elk is much less frequent there. In Southern Scandinavia, for instance,
906 elk altogether disappears from the zooarchaeological record in the course of the Mesolithic,
907 even though, puzzlingly, the species remains culturally important (Bridault, 1992) – but these
908 processes may in fact be interrelated. In the Dutch wetlands, elk is consistently present only in
909 small numbers, despite wetlands being among the preferred habitats of the species (cf. Janík *et*
910 *al.*, 2021), opening up the possibility that Swifterbant Culture communities culturally opted not
911 to hunt elk systematically. This scenario is not in principle inconceivable for the later Mesolithic
912 of Southern Scandinavia as well.

913 A recent ecological study conducted in Denmark has shown that red deer and roe deer
914 avoid water in areas with high beaver proximity, and that these cervids tend to occur in higher
915 numbers in areas with fewer beavers (Pejstrup, Andersen and Mayer, 2023). This is noteworthy
916 because the Dutch Mesolithic and Early Neolithic record contains few *Cervidae* and high
917 number of beavers – precisely the predicated pattern. In Northeastern Europe, the pattern is
918 overall the same, and the few sites with abundant red deer (Zvidze and Zemaitiskes) yielded
919 few beaver remains. In Southern Scandinavia and Northern Germany, by contrast, red deer and
920 roe deer are very common and, as noted earlier, beaver less so than in the other regions. Pejstrup
921 and colleagues (2023) also note that human impact likely plays a formative role in these recent
922 interspecies dynamics, so it remains an open question as to what extent such dynamics can be
923 extrapolated back in time, but they are in any case worth considering and should further be
924 explored in the archaeological record.

925 The faunal record of Northwestern Europe hosts a diversity of megafauna, including
926 cervids, horse, wild boar, and aurochs. *Cervidae* and horse indicate a more open wetland zone
927 interspersed with deciduous and mixed woodland already very early in the Holocene. Over the
928 course of the Mesolithic, these animals would have played a role in opening up the dense
929 alluvial forests through extensive grazing (e.g., Noe-Nygaard, Price and Hede, 2005). In the
930 Baltic, the documented increase of wild boar, red deer and eventually aurochs may also have
931 been encouraged by well-established openings at the edge of mature beaver habitats and the

932 role of beaver hotspots as landscape attractors for these animals (Fedyń *et al.*, 2022) – probably
933 fuelled by early low-level human woodland impact and perhaps management (cf. Poska, Saarse
934 and Veski, 2004). This may point to an easily overlooked interplay – with notable feedback
935 potential – between beaver woodland engineering and clearance on the one hand and ungulate
936 suppression of woodland regeneration on the other hand – a dynamic possibly consequential
937 for Northwestern Europe and its specific Late Mesolithic/Early Neolithic human histories.

938 Unlike deer, wild boar are strongly attracted to beaver-engineered landscapes and in
939 particular aged beaver ponds provide ideal foraging and wallowing locales for them (Nitsche,
940 1997; Rosell *et al.*, 2005). Their co-occurrence with beaver remains in the zooarchaeological
941 record in all of the study regions is therefore interesting and probably influenced by the
942 interspecies co-facilitation, in turn providing human foragers with the possibility to target boar
943 in beaver country. Wild boar forms an important element of subsistence across Mesolithic
944 northern Europe, for meat – and for teeth, tools and pendants, as discussed earlier. It is important
945 to note that that wild boar appears to acquire a new role in human economies in the Late
946 Mesolithic and Early Neolithic (e.g., Magnell, 2006), probably due to local anthropogenic
947 encouragement and/or incipient management strategies (Rosvold *et al.*, 2010; Maring and
948 Riede, 2019; Brusgaard *et al.*, forthcoming). This latter process may not be unrelated to the
949 likely facilitation of wild boar in beaver landscapes, as humans foraging in these landscapes
950 would also intersect and increasingly interact with wild boar, perhaps laying the foundation for
951 subsequent management, taming, and domestication.

952 Some smaller mammals in the dataset may also signal beaver-related ecological
953 promotion. In Northwestern Russia, the Early Mesolithic is characterized by the importance of
954 muskrat and marten, animals which have been argued to form an early colonizer assemblage
955 within formative beaver landscapes (Crego, Jiménez and Rozzi, 2016; Nummi *et al.*, 2019).
956 The case of the muskrat may be especially instructive as this semiaquatic rodent is known to
957 parasitize beaver lodges (Mott, Bloomquist and Nielsen, 2013), so that knowledge on beaver
958 landscapes can promote muskrat foraging and generally supports integrative foraging strategies
959 in Boreal ecologies (cf. Winterhalder, 1981; see below). The relationship between the beaver
960 and the water vole in this region, as noted earlier, is of further interest because of the common
961 ecological association, and succession, of the two species, which is also an important concern
962 of contemporary restoration projects (cf. Stringer and Gaywood, 2016). This interspecies
963 relationship is also reflected in geoarchaeological findings from Grabow 15 in Northern
964 Germany, where an early Atlantic beaver burrow system was documented in conjunction with

965 a later, possibly Late Holocene, water vole-gnawed piece of wood (Tolksdorf *et al.*, 2017),
966 supporting the idea that water vole is an indicator species of developed-matured beaver
967 wetlands.

968 Otter is consistently present in Mesolithic assemblages in which beavers are also
969 prevalent, probably because of the earlier outlined facilitation of otters through beavers
970 geopraxis (Tumlison, Karnes and King, 1982; Reid, 1984; LeBlanc *et al.*, 2007). In the
971 Netherlands, the exploitation of both beaver and otter has been shown to be a key feature of
972 Swifterbant Culture sites, as well as Middle Neolithic sites attributed to the so-called
973 Vlaardingse Culture (c. 3500-2600 BC) (Zeiler, 1987; Lauwerier, van Kolfschoten and van
974 Wijngaarden-Bakker, 2005; Brinkkemper, Drenth and Zeiler, 2011). This pattern supports the
975 observations from Northeastern Europe where these two species tend to converge in the faunal
976 record, and therefore the idea that integrated low-level beaver and otter foraging was often
977 opportune and possibly sustainable.

978 In Southern Scandinavia and Northern Germany, marten, mink (*Mustela* sp.), and otter
979 are a recurrent but low-abundance faunal component in the Early and Middle Mesolithic, which
980 may similarly be indicative of foraging affordances within beaver habitats. It is not clear,
981 however, whether the decrease in beaver remains documented in the Late Mesolithic of the
982 region denotes a principal change in hunting practices and logics with regard to beavers or
983 instead signals a switch to other animals occurring in beaver landscapes at the expense of
984 beavers, or both. For example, some sites feature hardly any beaver remains but have yielded
985 abundant fur-bearing animals like pine marten (*Martes martes*) and wild cat, which were
986 probably targeted separately within specialized/dedicated fur-getting economies (Trolle-
987 Lassen, 1987; Price, 1991; Richter and Noe-Nygaard, 2003; Richter, 2005). Otter in the EBK
988 was likely targeted in the context of coastal and marine activities (e.g., Price *et al.*, 2001),
989 signalling a reorganization of foraging affordances and perhaps even their partial disintegration,
990 and this may indicate subtle but relevant changes in the role of beaver affordances in regulating
991 larger hunting/forager systems.

992 Taken together, these successional and interspecies faunal dynamics may point to the
993 importance of integrated foraging systems in the Mesolithic of Northern Europe, centred on
994 animal resources directly accessible at hotspots of beaver activity or at sites of former beaver
995 occupation (legacy sites). This changed in Southern Scandinavia and Northern Germany
996 towards the end of the Mesolithic while demonstrating substantive continuity in the other study
997 regions. This would have granted beaver landscapes special significance for human foragers

998 and it is tempting to conceptualize such ‘beaver country’ in analogy to notions of *Country*
999 perpetuated by Indigenous groups across Australia, emphasizing reciprocity and nourishment
1000 through human care (Urwin *et al.*, 2022). Either way, these dynamics of human-beaver
1001 cohabitation would have drawn the beaver closer to the centre of forager lifeworlds and
1002 ‘horizons of concern’ (sensu Bird-David, 2017), fostering people’s attentiveness to the animals
1003 and their resource provisioning work as well as the attendant multispecies rhythms. Beavers,
1004 then, hold a double status as ecological and phenomenological cornerstones of Northern
1005 Mesolithic more-than-human landscape ‘dwelling’ (sensu Ingold, 2022). In this optic, the
1006 beaver, furthermore, quickly acquires the status of a *collaborator* – a feral partner – in the
1007 pursuit of human sustenance. The ecological keystone status of beavers in Northern Europe –
1008 their capacity to anchor and assemble animal ecologies and ecosystem processes – therefore
1009 arguably laid the foundations for the *ecological facilitation* of Mesolithic human foragers living
1010 in the same landscapes, who in turn integrated a large suite of beaver landscape affordances
1011 into their behavioural repertoire. As Kikvidze and Callaway (2009) point out, facilitation can
1012 be a powerful but often overlooked evolutionary factor, structuring multispecies communities
1013 and shaping long-term dynamics of history.

1014

1015 *Fish-getting affordances*

1016 The possibility of beaver facilitation is substantiated by the Mesolithic fish record. The striking
1017 feature of the fish record from the earlier part of Holocene Northern Europe is its strong
1018 emphasis on larger predatory freshwater fish such as pike, zander, and perch in conjunction
1019 with a growing importance of lentic bottom-dwellers through time, such as carps and Wels
1020 catfish. This accentuation is consistent with some known effects of beaver-fish interactions,
1021 while the observed regional variability similarly points to important differences in hydrological
1022 systems and aquatic ecologies across Northern Europe – especially the relative importance of
1023 larger lakes *vis-à-vis* riparian corridors – and the changing impacts of the beaver on these
1024 systems. Beaver activity generally fosters habitat heterogeneity over larger spatial scales by
1025 creating patches of lentic habitat within a corridor of lotic habitat, thus altering and framing
1026 new niches for both ‘stream species’ and ‘pond species’ (Snodgrass and Meffe, 1999; Collen
1027 and Gibson, 2000: 452). In warm water ecosystems, beaver ponding, eutrophication and lentic
1028 shallow-water/edge-habitat engineering mainly promote potamodromous (i.e., freshwater-
1029 only) species such as pike and perch, who can over time outcompete and replace smaller bodied
1030 cyprinids (e.g., Rosell *et al.*, 2005; Pliūraitė and Kesminas, 2012; Gaywood, 2018). Pike is

1031 found to benefit from beaver ecosystem modification especially when larger ponds or lakes are
1032 available (Collen and Gibson, 2000), while perches are generally attracted by beaver lodge
1033 debris (Gibson, 1969). As conditions within ponds become increasingly anaerobic, larger carps
1034 and species such as catfish increasingly benefit and typically grow in abundance. Wels catfish,
1035 once promoted, can further impact freshwater ecologies due to induced alterations of the trophic
1036 chain and physiochemical modifications of the water content (Rodriguez-Labajos *et al.*, 2009),
1037 sometimes leading to the displacement and near-disappearance of other species such as the
1038 common carp (*Cyprinus carpio*) (Snodgrass and Meffe, 1998), whilst attendant algae growth
1039 may complicate the spearing of larger fish such as pike.

1040 In all study regions, the fish evidence often reveals a gradual re-configuration of lentic
1041 fish communities in the course of the Mesolithic – a successional sequence starting with an
1042 emphasis on pike and other large freshwater predators leading to increased attention to
1043 cyprinids and eventually catfish. This, then, is unlikely to be reflective only of human foraging
1044 preferences but probably also records a latent beaver legacy effect, as these changes are a
1045 consequence of consolidating and aging beaver landscapes including ponds, some of which are
1046 ultimately abandoned, offering distinct fishing opportunities. Fish-getting practices during the
1047 Mesolithic were thus likely influenced, and dynamically modulated, by the specific *fish-getting*
1048 *affordances* emerging from long-term beaver activity in the hydroactive wetland and boreal
1049 environments of Northern Europe at the edge of former glaciers.

1050 Beavers almost never fully disrupt riparian connectivity (Schlosser, 1995) but they can
1051 severely impede the capacity of river migrating species such as salmon and eels to traverse
1052 across riparian landscapes (cf. Kemp *et al.*, 2012). Mitchell and Cunjak (2007) found that
1053 beaver dams in coastal rivers prevent upstream migration of salmonids and simultaneously,
1054 through competitive exclusion, increase fish diversity upstream. This dynamic may apply to,
1055 and in part explain, the ichthyofaunal patterns of the Late Mesolithic/Early Neolithic from the
1056 Dutch wetlands, where salmonids are conspicuously rare. This pattern indeed continues at
1057 Middle Neolithic wetland and coastal sites in the area, where seal and other marine mammals
1058 increase in importance, yet the ichthyofaunal emphasis remains on pike, sturgeon, eel, and
1059 cyprinids (Lauwerier, van Kolfschoten and van Wijngaarden-Bakker, 2005). This could suggest
1060 long-lived beaver legacies, hunting affordances, and the resulting cultural practices. A highly
1061 similar pattern emerges from the Middle Mesolithic of the Baltic, where beaver-supported lentic
1062 fish including pike, perch, and cyprinids remain the focal target of fish-getting practices, even
1063 though human foragers begin to engage in specialised seal hunting (Lõugas, 2017). The

1064 increasing importance of the sea does therefore, contrary to common assumptions, not lead to
1065 a dramatic shift in ichthyofaunal acquisition patterns, and lotic fish continue to form only small
1066 portions of human-foraged fish. Boethius *et al.* (2017) have explicitly argued that freshwater
1067 fish derived from eutrophic lakes remained a key subsistence staple even in the context of the
1068 initial Early Holocene occupation of Gotland in the Baltic basin, while marine mammal hunting,
1069 especially the targeted pursue of younger seals, was secondary and probably mainly oriented
1070 towards raw material acquisition.

1071 Salmonids and eel inputs to Mesolithic fish assemblages remain generally negligible,
1072 perhaps indicating some level of amensalism (cf. Arthur and Mitchell, 1989) between earlier
1073 Holocene beaver-powered environments and migratory, lotic fish requiring access to the open
1074 sea. This idea may be supported by the faunal evidence from Mesolithic Ireland, where the
1075 beaver is *not* part of the native mammal fauna, while salmonids and eel are important in
1076 the anthropogenic fish assemblages (Kelly, 2005; Warren, 2022), contrasting the data from
1077 Mesolithic mainland Europe and Britain where these species are virtually absent (Zhilin, 2014a;
1078 Robson *et al.*, 2018; Robson and Ritchie, 2019). This again suggests that beaver agency co-
1079 structured anthropogenic fish assemblages. Alternatively, or complementarily, lentic fish,
1080 especially larger predatory species and fast-growing carps, offered more attractive, more
1081 reliable and easier to access food resources as to their predictable association with beaver-
1082 fabricated ponds and wetlands.

1083 In this context, a few comments on the evolution of fishing technologies in Northern
1084 Europe are useful. Sophisticated and curated fishing installations such as fish weirs, fences
1085 and/or proper fisheries only emerge in the course of the Mesolithic and typically date the later
1086 part of the Middle Mesolithic or the Late Mesolithic/Early Neolithic in the study regions (e.g.,
1087 Fischer, 2007; Amkreutz, 2013; Lozovski and Lozovskaya, 2016). In the Early Holocene, fish
1088 was thus probably often acquired via spearing and/or bowing, sometimes but not always in
1089 conjunction with angling, and these practices can easily take advantage of fish trapped in ponds,
1090 and the shallow water habitats engineered by beavers can greatly facilitate the spotting, spearing
1091 and/or bowing of larger freshwater fish such as pike. Eutrophic lakes and ponds have
1092 consequently been invoked as potent landscape attractors for Early Holocene foragers in
1093 Northern Europe (Boethius *et al.*, 2017) and Welinder (1978) specifically suggested that
1094 overgrown lakes formed central elements of Maglemose adaptations.

1095 Contrasting with the Dutch and Northeastern European data, the Late Mesolithic and
1096 Early Neolithic record from Southern Scandinavia and Northern Germany shows a clear break

1097 in the fish species composition (cf. **Fig 4b**). EBK sites demonstrate an increased emphasis on
1098 both marine mammals and marine fish. The emergence of coast-bound and increasingly marine
1099 economies in the EBK may have considerably weakened the probiotic effect of the beaver on
1100 human livelihoods and drawn human attention away from beaver habitats, thus simultaneously
1101 defusing the reliance on beaver-engineered, inland foraging affordances. To over-exaggerate,
1102 Early and Middle Mesolithic foragers in this region encountered the beaver as a key society-
1103 sustaining agent – as a nonhuman fishing aid or *more-than-human fishing technology* – whereas
1104 Late Mesolithic/Early Neolithic humans increasingly relied on their own fishing infrastructure
1105 and self-devised fish-getting technologies at coast-inland interfaces, yet perhaps nonetheless
1106 inspired by the transgenerational experience of beaver geopraxis. The nature and significance
1107 of a human-beaver ‘contact zone’ as envisioned by Hjørungdal (2019b, 2019a) for the Southern
1108 Scandinavian Mesolithic thus likely depended on the intersection of lived human and beaver
1109 geographies and, perhaps more importantly, the extent to which beaver habitats were routinely
1110 visited, and thus *integrated* into broader forager landscapes. In analogy to other documented,
1111 integrated human foraging strategies such as ‘garden hunting’ in the Americas (Linares, 1976;
1112 Stahl, 2020; Guiry *et al.*, 2021), we may refer to this strategy as ‘pond hunting’ or ‘wetland
1113 foraging’. The development of coastal and open-water economies in the course of the Late
1114 Mesolithic in Southern Scandinavia and Northern Germany would have contributed, then, to
1115 the disruption of these foraging systems centred on the diverse resource opportunities in and
1116 close to beaver habitats.

1117

1118 *Other multispecies affordances*

1119 Other indirect ecosystem effects of beaver geopraxis with benefits for hunter-gatherers include
1120 waterfowl encouragement and promotion (Brown, Hubert and Anderson, 1996; Nummi and
1121 Hahtola, 2008; Nummi and Holopainen, 2014) as well as beaver ‘gardening’. Waterfowl
1122 encouragement is a notable life service for human co-inhabitants as waterfowl was an important
1123 subsistence good for meat and feathers (e.g., Zhilin and Karhu, 2002) and this bird category is
1124 prevalent in the Mesolithic archaeozoological record of the study regions (e.g., Lauwerier, van
1125 Kolfshoten and van Wijngaarden-Bakker, 2005; Zhilin, 2014a; Lõugas, 2017; Çakırlar *et al.*,
1126 2019). Water birds are also occasionally rendered in the visual art of the Mesolithic of
1127 Northwestern Russia (Lozovskaya, 2021), similarly suggesting their prominence and potential
1128 abundance in earlier Holocene environments. Waterfowl presence draws in and sustains larger
1129 birds of prey such as ospreys and sea eagles and these birds have often received special attention

1130 by Mesolithic foragers across Northern Europe (Amkreutz and Corbey, 2008; Mannermaa,
1131 2013; Hussain, 2023a), again indexing the crucial role of beaver habitats in framing human
1132 forager life, perception, culture and possibly cosmology in the European North. Another
1133 example of the important and consequential role of beavers in modulating larger multispecies
1134 communities is provided by the pond turtle (*Emys orbicularis*), who is strongly promoted by
1135 beaver wetland engineering and pond-making (Janiszewski, Hanzal and Misiukiewicz, 2014)
1136 and is well-represented in the earlier Mesolithic of Northwestern Europe (Groß, 2017: 18). Pond
1137 turtles notably make an appearance in the Dutch Late Mesolithic at the Hardinxveld-
1138 Giessendam sites (Oversteegen *et al.*, 2001; van Wijngaarden-Bakker *et al.*, 2001) and equally
1139 occur at some Southern Scandinavian Middle Mesolithic sites (Groß, 2017). Interestingly, these
1140 reptiles disappear from the archaeological record again during the Atlantic, and this may be
1141 linked to a shift in beaver preponderance, landscape impact and/or proximity to human
1142 habitation sites in some northern areas at the end of the study period.

1143 In addition, beaver behaviour effectively conforms to a form of *landscape gardening* –
1144 encapsulated in the notion of a ‘beaver meadow complex’ – which promotes distinct plant
1145 community successions (Westbrook, 2021), and can notably encourage aquatic plants that grow
1146 and proliferate under eutrophic conditions. Water lilies (*Nymphaea*) and water chesnuts (*Trapa*)
1147 both benefit from beaver-induced damming and pond formation (Benke, Ward and Richardson,
1148 1999; Law, Bunnefeld and Willby, 2014; Kukuła and Bylak, 2017) and the remains of both
1149 plants have been found in Northern Mesolithic sites as well as in human coprolites (e.g., Price,
1150 1991; Zvelebil, 1994; Bakels, van Beurden and Vernimmen, 2001; Kubiak-Martens and van
1151 der Linden, 2022). Beavers are known to strategically feed on white water lilies (*Nymphaea*
1152 *alba*) while promoting them ecologically (Law, Bunnefeld and Willby, 2014), and beaver
1153 habitats therefore not only signal the potential availability of high-value plant resources,
1154 Mesolithic people may have actually *discovered* this specific resource potential of wetland-
1155 lakeland ecosystems by observing and learning from beavers. Beaver-directed *mimicry* (sensu
1156 Bhabha, 1984; GoGwilt and Holm, 2018), in this optic, may not only be an expression of
1157 relating to beavers as socially relevant others, but could reflect human attempts to literally
1158 assume a beaver gaze, as the beaver come into view as a nonhuman guide and tutor of the North
1159 (see e.g. Stobiecka, 2022 for a general exposition of these latter notions), disclosing unique
1160 possibilities of navigating and using the landscape. This perspective brings us close to an
1161 understanding of Mesolithic beavers as a *nonhuman landscaping technology*, even though
1162 reducing beavers to purely instrumental roles would obviously undermine the gist of the here
1163 proposed arguments.

1164 All of this being said, beaver-shaped landscapes clearly invite particular foraging
1165 behaviours and offer exceptional possibilities for integrated food-getting strategies, but to
1166 exploit these efficiently requires intimate knowledge on beavers and their geopraxes. We thus
1167 propose that adapting to earlier Holocene environments in Northern Europe in many cases
1168 involved *human adaptation to beaver behaviours and landscapes*. The beaver, in line with
1169 Cole's (2006) previous arguments for Britain, was thus likely a key agent in the Early
1170 Mesolithic (re-)occupation of high-latitude Europe as a whole, and 'landscape learning' (sensu
1171 Rockman, 2003) was promoted by attunement to and familiarization with beaver activity,
1172 drawing the beaver into human affairs and fostering human respect and care for beavers, as
1173 'thinking with' and 'acting with' the animals emerged as an important touchstone of Mesolithic
1174 forager life in different parts of northwestern Eurasia.

1175

1176 *Human-beaver cohabitation*

1177 The Mesolithic data reviewed and synthesized here may thus be taken to suggest that exploiting
1178 the attractive foraging grounds curated by ongoing beaver ecosystem engineering was a central
1179 pillar of the earlier Holocene human occupation of Northern Europe, suggesting that forager
1180 lifeways were at least in part predicated on beaver agency. Human-beaver cohabitation and its
1181 associated behavioural possibilities, in other words, emerged as an important precondition for
1182 human sustenance and livelihood within the vast wetland and boreal zones of the European
1183 North, only to be disrupted when Late Mesolithic and Early Neolithic societies turned their
1184 attention to the sea. The Dutch wetland Mesolithic/Early Neolithic, interestingly, shows notable
1185 similarities in overall beaver-related ecosystem relations with the Baltic and the Russian
1186 Northwest, rather than Southern Scandinavia as may be expected based on geographic
1187 proximity. This convergence may be in part be a consequence of the rich delta landscapes in
1188 these regions, acting as biodiversity contraptions with extensive wetlands and catalysing beaver
1189 habitation as well as the attendant successional dynamics for human foragers (cf. e.g., Giosan
1190 *et al.*, 2014; Richardson, Michalski and Becu, 2021). Beavers have been shown to play key
1191 roles in the maintenance of these landscapes and the provisioning of attendant deltaic wetland
1192 resources (Hutchings and Campbell, 2005) The cognitive and less tangible aspects of human-
1193 beaver cohabitation in these regions are more difficult to glean and clearly open up a host of
1194 new questions. Compellingly, however, the here-adopted beaver perspective suggests that
1195 geographically close regions in the European Northwest appear to have embarked on divergent
1196 ecocultural trajectories, with notable differences in the place of beavers in multispecies systems.

1197 In contrast to the Northwest, the European Northeast stands out in the richness and
1198 diversity of beaver-related material culture. The productive co-habitation and cross-fertilization
1199 of humans and beavers in the Early and Mid-Holocene has thus arguably laid the foundation
1200 for an increasingly diverse beaver-related material culture, understood here as a consequence
1201 of fostered human-beaver intimacies throughout the Mesolithic. Extended life-histories of
1202 beaver-sourced tools and the human care put into them (Zhilin, 2020) as well as the association
1203 between the teeth and astragali of beavers on the one hand and human bodies on the other
1204 strongly suggest that beavers participated in the making of the human social world and became
1205 entangled with human bodies. The evidence is therefore consistent with the idea that beaver
1206 landscape significances became deeply sedimented into cultural memory systems as beavers
1207 and humans curated relatively stable neighbourhoods.

1208 The observation that beaver-related material culture appears in the archaeological record
1209 of Northwestern Europe less frequently than in the Baltic and Northwestern Russia and tend to
1210 postdate the Early Mesolithic is important, potentially showing that beaver knowledge took
1211 more time to crystallize in the respective human societies, although the comparison may be
1212 hampered by the lack of sites from the Dutch Early and Middle Mesolithic. In all regions, there
1213 is, however, some evidence for the co-optation of beaver capacities through the use and
1214 transformation of selected body parts, embodying the environmental agency of the animals.
1215 This again underscores human attempts to *mimick* beaver geopraxis, in turn showcasing
1216 elevated awareness, attentiveness, and care in relation to beaver others.

1217 Animal body-part selectivity is a common feature of forager zoo-materialities, often
1218 linked to broader concepts of trait fluidity and bodily transposition rooted in relational
1219 epistemologies and zooontologies emerging from lived interspecies intimacies (Hill, 2011, 2019;
1220 Hussain, Weiss and Kellberg Nielsen, 2022; McNiven, 2022). Beaver-related materializations
1221 linked to human instrumental, ornamental and burial practices, from this perspective, arguably
1222 helped to *produce* human-beaver co-sociality, acknowledging the socio-historical efficacy and
1223 lived significance of beaver neighbourhoods for Mesolithic people. Beaver-related material
1224 culture can then be interpreted to reflect the recognition of beavers as ‘co-workers’ and as
1225 ‘community’ (sensu Welden, 2022), and thus as symptomatic feature of what Bird-David
1226 (2017) has termed ‘plurispecies’ societies. Against this broader background, it may be
1227 significant that the beaver is one of the few animal species *not* drawn upon for ornamentation
1228 in the Dutch Swifterbant Culture, perhaps signifying the importance of animals facilitated by
1229 beaver-engineered landscapes at the expense of beavers themselves, even though this is

1230 challenging to unpack archaeologically. More research on the Swifterbant Culture bone and
1231 tooth artefacts is certainly needed to interpret these patterns.

1232 The systems-perspective on human-animal interactions pursued here places particular
1233 emphasis on the relational assembly, integration, consolidation and disintegration of humans,
1234 beavers, landscapes and material culture in the course of the Early and Mid-Holocene. It queries
1235 the changing ‘intra-actions’ (Barad, 2007; cf. Kirksey, 2015) within these systems, relationships
1236 such as conflict, tension, synergy, cross-pollination and possibly co-constitution. **Figure 6**
1237 attempts to outline the central place of the beaver in these systems, in human world-making
1238 during the Mesolithic of Northern Europe as suggested by our analysis and discussion. In total,
1239 we argue that the beaver’s role as a potent ecological keystone species in the Early and Mid-
1240 Holocene of Northern Europe provided the larger context for a broader prehistory of *sympoiesis*
1241 (sensu Haraway, 2016). The status of the beaver as a socially significant other in the Northern
1242 Mesolithic was thereby not given but *made*, and it emerged out of an extended history of human-
1243 beaver co-habitation in the region. Beaver remains and beaver-related material culture, in this
1244 view, trace the millennial-scale transformation of the beaver into a ‘cultural keystone species’
1245 (Garibaldi and Turner, 2004; Platten and Henfrey, 2009; Jacques-Coper, Cubillos and Ibarra,
1246 2019). The timing and trajectory of this process differs between Northwestern and Northeastern
1247 Europe and *within* Northwestern Europe, and articulates with other documented patterns in the
1248 archaeological record. This cultural keystone status of the beaver appears to be conserved in
1249 the Northeast and in the Dutch wetlands in the course of the Mesolithic, while human-beaver
1250 relationships in Southern Scandinavia and Northern Germany appear to be re-configured, and
1251 perhaps lose their former significance, as human practices are subject to dramatic changes and
1252 other animals such as wild boar (e.g., Magnell, 2006; Maring and Riede, 2019) and marine
1253 mammals including killer whales (Andersen, 1996) rise to prominence during the Mid-
1254 Holocene.

1255 Based on historical data, Liarsou (2013, 2015) has suggested that the relationship
1256 between humans and beavers is often re-tailored as humans introduce and invest into new
1257 landscape practices such as pastoralism and farming. There are several reasons for this tendency
1258 and many of them have to do with human encroachment and/or destruction of beaver habitat.
1259 Increasing population pressure, intensification of economic activities in aquatic areas,
1260 deforestation, and cereal cultivation in sync with growing infrastructural and environmental
1261 fingerprints, including expanded riparian transportation, often have detrimental effects on the
1262 size and distribution of beaver populations, in addition to curtailing and fragmenting beaver

1263 habitat and mobility. Changing human relations to the landscape, especially claims to and early
1264 annexation or ‘proportization’ of particular places, also provoke changes in the perception and
1265 conceptualization of beavers, frequently shifting human attitudes, as the readily attention is
1266 drawn to interactive tension and possible conflict. The beaver’s landscape-altering capacities
1267 are then easily cast as ‘destructive’. This is particularly the case when humans become
1268 cultivators themselves since beavers may flood and/or severely damage fields and larger
1269 agricultural landscapes, so changing the conditions and context of interaction. Unsurprisingly,
1270 this is also one of the major sources of present-day beaver-landowner tensions in reintroduction
1271 areas, such as Britain, the Netherlands, and Denmark ((Jansman *et al.*, 2016; Coz and Young,
1272 2020; Naturstyrelsen, 2020) .

1273 It is therefore possible that the arrival of agricultural life in Northern Europe marks an
1274 important turning point in human-beaver relations, and there is indeed evidence for substantial
1275 human population growth in this period (Shennan and Edinborough, 2007; Shennan, 2013),
1276 coupled with increasing evidence for aquacultural investment in the form of fishing
1277 infrastructure and extractive freshwater economies (Price, 1985, 2000, 2015; Beerenhout,
1278 2001b; Amkreutz, 2013) as well as expanded riverine and oceanic transportation, at least in
1279 some areas such as Southern Scandinavia, and new systems of livestock management (Gron *et*
1280 *al.*, 2016; Brusgaard, Çakırlar, *et al.*, 2022). In Southern Scandinavia and Northern Germany,
1281 the transition to agropastoral systems occurs around 4000 BC (Gron and Sørensen, 2018).
1282 However, a decrease of beaver within faunal assemblages can already be observed from the
1283 Middle to Late Mesolithic onwards, well before this transition. In the Netherlands, sites with
1284 the first clear evidence for crop and animal management date to around 4250 BC and continue
1285 to yield relatively high percentages of beaver remains. While beaver numbers decline later in
1286 the Dutch Neolithic, this is the case for wild animals in general, in tandem with the increase of
1287 domesticated livestock (Lauwerier, van Kolfshoten and van Wijngaarden-Bakker, 2005;
1288 Çakırlar *et al.*, 2019). Wetland landscapes and natural resources remain generally important
1289 throughout the Dutch Neolithic and even the Bronze Age, with specialised sites continuing to
1290 be used for fur-animal extraction (Zeiler, 1987; Dusseldorp and Amkreutz, 2020).

1291 At first glance, therefore, our dataset reveals no clear indications for a correlation
1292 between the transition to agricultural practices and human-beaver relations. Full-blown farming
1293 systems do not become established in the region before the later part of the Mid-Holocene and
1294 perhaps even later, so these changes may occur later. It is also important to note that the
1295 expected developments in human-beaver relations may manifest themselves in different ways

1296 in the (zoo)archaeological records. Agricultural conditions may for example greatly favour the
1297 classification of beavers, together with other wildlife, as ‘pests’ (Liarsou, 2013: 177) and may
1298 thus foster concerns to remove them from human landscapes and lifeworlds, in turn motivating
1299 targeted ecological suppression or even overhunting. For example, agro-horticulturalist in
1300 Mexico carry out subsistence hunting of species that otherwise pose a threat to crops (Santos-
1301 Fita, Naranjo and Rangel-Salazar, 2012), which ironically occur at the edges of human-shaped
1302 habitat in turn providing attractive habitat for these species. Therefore, other lines of evidence,
1303 such as harvesting profiles which can inform on the sustainability of hunting practices may
1304 offer additional insights here in the future. Çakırlar *et al.* (2019) have for example concluded
1305 that there is currently no indication for beaver overhunting at Dutch Late Mesolithic sites as the
1306 corresponding harvesting profiles indicate mostly adult-oriented hunting, which they interpret
1307 as being consistent with a stable source population. However, these profiles are based on a now
1308 outdated method of age-determination for beavers (Iregren and Stenflo, 1982) and thus need to
1309 be revisited. It is furthermore important to consider that forager hunting patterns may have been
1310 less influenced by utility-oriented decision-making predicated on universal, neoclassical
1311 notions of ‘rational choice’ than by situated animal ethologies and lived predator-prey
1312 responses, including so-called ‘ecologies of fear’ (Brown, Laundré and Gurung, 1999; Holmern
1313 *et al.*, 2006; Zanette and Clinchy, 2019; Brusgaard *et al.*, 2022; Hussain, 2022). To account for
1314 such dynamics requires to acknowledge the ‘bounded rationality’ (Simon, 1957; Wheeler,
1315 2020) of human behaviour, drawing attention to a possible role of diverse nonhuman agents in
1316 steering and stabilizing human foraging systems and their rationalities. Beaver agency in
1317 Mesolithic hunting practices thus certainly demands further investigation, which may in turn
1318 shed novel light on the influence of emerging agricultural systems and other landscape practices
1319 on beaver relations and populations.

1320 All of this being said, the introduction of livestock as part of the diverse forms of
1321 agriculture and pastoralism developed by Mid-Holocene people in Northern Europe may
1322 nonetheless signify an important landmark in human-beaver engagements. Developed beaver
1323 landscapes where the animals’ activity has turned formerly flooded areas into meadows
1324 (Westbrook, 2021) provide localised grazing opportunities for livestock. Meadows can act as
1325 ‘alluvial grasslands’ (Hejcman *et al.*, 2013) and demarcate pockets of open, grazable land
1326 within otherwise hydrologically textured and wooded areas (see esp. Ritchie, 2017 for an
1327 illuminating historical account). Patchy grassland formation is thus part of the larger package
1328 of beaver landscape legacies and, in conjunction with the clearance activities of larger
1329 herbivores, contributes to nonhuman geopraxes that can set the stage for early forms of animal

1330 husbandry. Aged beaver landscapes, from this perspective, promote high-quality *natural*
1331 *pastures* (Liarsou, 2013: 175) and thus provide land-use affordances which differ from the kind
1332 of beaver-supplied affordances for foragers without livestock (cf. Coles, 1992). Eriksson (2020)
1333 has illustrated how meadows, once created, recruit novel human-animal entanglements and
1334 become central places or even focal points in the landscape. The ramifications of this
1335 successional dynamic within developed Holocene beaver landscapes for the architecture and
1336 development of human-beaver relations are potentially substantial. It is therefore interesting to
1337 ask whether and to what extent human intersections with beavers were critically re-configured
1338 as landscape affordances became *mediated by domestic livestock* and the focus shifted to
1339 localities where beavers were no longer present as living beings or were suppressed by grazing
1340 livestock and people, in turn reinforcing grassland and pasture formation and setting processes
1341 in motion that further altered beaver habitat, accelerated ‘meadowing’, and no longer favoured
1342 beaver neighbourhoods.

1343 This configuration would have fundamentally transformed the place of beavers in
1344 human lifeworlds and gradually removes them as embodied agents from agropastoral ‘horizons
1345 of concern’, projects and deeds – undermining or at least complicating their status as cultural
1346 keystone species. The development of agropastoralism at the end of the Mesolithic may
1347 therefore have eventually provoked consequential re-negotiations of human-beaver relations in
1348 some parts of Northern Europe, a perspective that imposes itself especially for Denmark,
1349 Northern Germany and the Netherlands but not for Northeastern Eurasia where foraging
1350 lifestyles persisted. Put more provocatively, the North European proclivity for early
1351 agropastoral systems may in itself represent a consequence of beaver landscape curation – a
1352 way of life based on thousands of years of beaver work without recognizing the workers. Even
1353 though these ideas need to be explored and tested in more detail in the future, they suggest that
1354 systems of human-beaver conviviality that have developed from the Early to the Middle
1355 Mesolithic might have been disrupted by the conditions and requirements of agropastoral life,
1356 especially in Northwestern Europe, and this could explain some of the patterns observed in the
1357 archaeological record, especially from the Mid-Holocene onwards. Liarsou (2013: 175), for
1358 example, discusses archaeological evidence for a possible preference of human settlement
1359 locations in or close to environments previously managed and transformed by beavers during
1360 the French Middle Neolithic (cf. Pétrequin and Pétrequin, 1989). In Northwestern Europe and
1361 Britain, beaver legacies may similarly *live on* in some of the pastures used and further modified
1362 by Neolithic, Bronze Age, and Iron Age communities. Archaeological research is highly
1363 significant here as the vast majority of these beaver legacies remain undocumented, and this

1364 even though the cumulative ecosystem and geomorphological impacts of the hundreds of
1365 millions of beavers who once modified rivers and floodplains across the northern hemisphere
1366 can hardly be underestimated (see esp. Wohl, 2021).

1367 When contrasted with these possible later structural transformations in human-beaver
1368 systems, Mesolithic engagements with beavers can be described as ‘commensal’ (Liarsou,
1369 2013: 178; see O’Connor, 2013 for a general account of commensalism) – with human foragers
1370 being commensal *to beavers*. This divergence suggests important changes in the status of
1371 beavers as ‘companion species’ in the sense of Haraway (2008), linked to important changes in
1372 human lifeways and behavioural regimes. Contextualizing the available archaeological data for
1373 human-beaver interactions from the Early and Mid-Holocene of Northern Europe indicates that
1374 beavers offered different affordances and life services for different types of human societies
1375 and beaver landscapes were likely unequally perceived, valued and imagined because of these
1376 differences. While beaver agency in the earlier Mesolithic helped to anchor and spatially
1377 organize forager lifeways, beavers were gradually excluded from the centre of Southern
1378 Scandinavian lifeworlds in the course of the later Mesolithic, while mutually conducive
1379 relationships were seemingly maintained in the Dutch and Northeastern Late Mesolithic, with
1380 the latter resulting in the diversification and promulgation of beaver-related material culture
1381 with continuities at least into the developed Neolithic. In general, the documented dynamics
1382 clearly expose the fragility of systems of human-beaver conviviality that have evolved over
1383 millennia and that greatly depend on human practices that allow beavers to enter the realm of
1384 social significance and to garner human concern and care. These archaeological insights on the
1385 millennial-scale dynamics of multispecies systems – echoing Liarsou’s (2013, 2020) earlier
1386 arguments – are important sources of information for the ecological management and
1387 restoration of beavers in the present, as they demonstrate the inseparability of human lifeways
1388 and the functioning and implicit normativity of human-animal systems.

1389

1390 **Conclusion**

1391 The archaeological evidence drawn together and re-contextualized in this paper from a
1392 multispecies perspective points to an important role of the beaver in the making of Early and
1393 Mid-Holocene forager societies in Northern Europe. The evidence is consistent with a role of
1394 beavers as important life-service providers for human hunter-fisher-gatherers trying to establish
1395 themselves in the wetland and boreal-taiga zones of higher latitude Europe, and showcases the
1396 material generativity and vibrancy of human-beaver relations. We have argued that beaver-

1397 related material culture is rooted in evolved modes of human-beaver cohabitation characterized
1398 by facilitation and mutuality, insofar as human life relied on and took advantage of beaver
1399 presence and beavers, in turn, were acknowledged and belaboured as autonomous but
1400 significant social others. We therefore suggest that much of human prehistory in the earlier part
1401 of the Holocene in Northern Europe can be re-framed as the result of developing human-beaver
1402 convivialities and human practices drawing on, and increasingly acknowledging, a broader
1403 ‘beaver commons’ – i.e., beaver-provisioned resources shared with human foragers to sustain
1404 the latter in the landscape. This not only exposes the multispecies constitution of the Northern
1405 Mesolithic, it also suggests that *becoming-with* beavers was a foundational condition of human
1406 life in the period. Beavers, in this view, contributed in distinct ways to Mesolithic developments
1407 across Northern Europe, as embodied agents but also through co-shaping mammalian and
1408 ichthyofaunal assemblages. The latter also calls for more critical zooarchaeological attention to
1409 possible and hitherto underrated (or unrecognized) animal ecological legacies in faunal datasets.

1410 We further suggest that the archaeology of Early and Mid-Holocene continental
1411 Northern Europe reveals divergent co-occupational histories of humans and beavers, and that
1412 important re-negotiations as to the place of beavers in larger multispecies systems of Southern
1413 Scandinavia can be linked to the emergence of coast-oriented lifeways and disruptions of
1414 evolved human-beaver intersections incurred by agropastoral systems. These disruptions are
1415 not a historical necessity, however, but appear to be context-dependent, as the impact of
1416 agropastoralism on Northern European human-beaver relations varies greatly across different
1417 regions. We propose that these dynamics, in need of further empirical qualification, yield
1418 valuable information for contemporary concerns of beaver restoration, rewilding, ecosystem
1419 management and biodiversity stewardship, as they contribute to a better understanding of the
1420 human dimensions and requirements of living together with beavers. The ‘beaver lens’
1421 deployed in this paper thus not only provides a new perspective on the Northern Mesolithic and
1422 its ecocultural fabric by centring an archaeologically often underestimated animal, it also
1423 showcases the unique role that archaeology can play in elucidating the long-term, millennial-
1424 scale contributions of animals to human deep history by highlight the conditions in which they
1425 can play key roles in securing human livelihoods.

1426

1427 **Author contributions**

1428 STH and NOB have contributed equally to this research.

1429 **Acknowledgements**

1430 We thank the participants of the academic conferences on which aspects of this paper were
 1431 presented for their valuable feedback and comments. Kamilla Laustsen Lomborg helped with
 1432 bibliographic research in an early stage of this project and provided some important input. Nick
 1433 Overton, Ben Elliot and Jörg Ewersen offered their expertise on and excitement about beavers.
 1434 We thank the archaeological companies Archeoplan Eco, BAAC, and RAAP for providing their
 1435 unpublished data from recent excavations. STH acknowledges funding received through the
 1436 CLIOARCH CoG project from the European Research Council (ERC) under the European
 1437 Union’s Horizon 2020 research and innovation programme (grant agreement No. 817564).
 1438 NØB was funded by the Dutch Research Council (NWO), as part of the EDAN project (grant
 1439 no. 406.18.HW.026).

1440

1441 **Tables and captions**

1442 **Tab. 1.** Three-stage chrono-cultural scheme of the Northern European Mesolithic adopted in
 1443 this study.

Stages of the Northern Mesolithic	Technocomplexes and archaeological cultures	Chronozones	Absolute radiocarbon years	Corresponding Holocene Age	Absolute radiocarbon years
Early Mesolithic	Early Maglemose, Early Kunda, Veretye, Butovo	Preboreal, early Boreal	c. 10-9k cal. BP (c. 8-7k cal. BC)	Greenlandian (Early Holocene)	c. 11.7-8.2k cal. BP (c. 10-6.2k cal. BC)
Middle Mesolithic	Late Maglemose, Early Kongemose, Late Kunda, Butovo	Boreal, incipient/early Atlantic	c. 9-8k cal. BP (c. 7-6k cal. BC)	Greenlandian (Early Holocene)	
Late Mesolithic/Early Neolithic	Late Kongemose, Janislawice, Ertebølle, Swifterbant, Western Funnel Beaker, Eastern Funnel Beaker, Early Comb Ware (Narva, Valday, etc.)	Atlantic, later	c. 8-5k cal. BP (c. 6-3k cal. BC)	Meghalayan (Middle Holocene)	c. 8.2-4.2k cal. BP (c. 6.2-2.2 cal. BC)

1444

1445 **Tab. 2.** Overview of published beaver-related material culture from Mesolithic and earliest
 1446 Neolithic of continental Northwestern Europe.

Site	Country	Dating/chronology	Period	Description	References
Star Carr	England	Preboreal, Early Maglemose, c. 9500-8500 BC	Early Mesolithic	A single worked beaver mandible half	Knight <i>et al.</i> , 2018;

				associated with a few other beaver bones remains in the earliest Mesolithic occupation	Milner <i>et al.</i> , 2018
Hardinxveld-Giessendam Polderweg	Netherlands	Atlantic, c. 5500-4650 BC	Late Mesolithic/Early Neolithic	Six modified beaver incisors, probably for use as chisels. The site also has produced >1000 NISP of beaver remains	Coles and Kooijmans, 2001; Louwe Kooijmans <i>et al.</i> , 2001; Dreshaj <i>et al.</i> , 2023
Hardinxveld-Giessendam De Bruin	Netherlands	Atlantic, c. 5450-4250 BC	Late Mesolithic/Early Neolithic	Eight modified beaver incisors, probably for use as chisels. The site also yielded >1000 NISP of beaver remains	Coles and Kooijmans, 2001; Louwe Kooijmans <i>et al.</i> , 2001; Dreshaj <i>et al.</i> , 2023
Lundby	Denmark, Zealand	Boreal/early Atlantic, Late Maglemose	Middle Mesolithic	A single beaver mandible with traces of anthropogenic removal and potential use, associated with a small number of beaver bones (quantity unknown)	Hatting, 1970
Spjellerup	Denmark, Zealand	Boreal/Atlantic	Middle Mesolithic?	Isolated beaver mandible with traces of anthropogenic use recovered from a bog	Hatting, 1970
Ravnsbjerggård	Denmark, Zealand	Boreal/Atlantic	?	Two beaver mandibles with traces of anthropogenic use.	Hatting, 1970
Holmegård	Denmark, Zealand	Late Boreal/early Atlantic, Late Maglemose, c. 6500 BC	Middle Mesolithic	A single split and worked beaver incisor within an assemblage of 70 beaver remains including skull	Hatting, 1970; Lautsen Lomborg, 2021

				fragments, mandibles and isolated teeth	
Øgårde	Denmark, Zealand	Boreal/early Atlantic, Late Maglemose	Middle Mesolithic	A single incisor with polish and reworking traces as well as a few worked beaver mandibles associated with >200 beaver remains including some beaver mandibles and a few isolated teeth	Hatting, 1970; Lautsen Lomborg, 2021
Sværdborg	Denmark, Zealand	Boreal/early Atlantic, Late Maglemose	Middle Mesolithic	Two removed and used beaver incisor tools within a larger assemblage of beaver remains including mandible and tooth (n=219)	Hatting, 1970; Lautsen Lomborg, 2021
Hohen Viecheln I	Germany	Boreal, Maglemose	Middle Mesolithic	A few used pairs of frontal beaver incisors (n=3) and isolated incisors with use marks (n=3) within a small assemblage of beaver remains. The frontal part of one such incisor tool is recorded to have been attached to wooden stick	Schuldt, 1961; Schmöcke, Groß and Nikulina, 2017
Rothenklempenow 17	Germany	Boreal, Maglemose	Middle Mesolithic	A single pair of frontal incisors glued together with birch tar, found in association with a few beaver remains (exact number	Schacht and Bogen, 2001; Schmöcke, Groß and Nikulina, 2017

				unknown), otter bones and a notable quantity of fish, especially carps, pike, perch and zander	
Heidemoor	Germany	Later Atlantic, Ertebølle?	Late Mesolithic/Early Neolithic	Six modified (polished) beaver mandibles and characteristic chipping of used incisors on mandibles; assemblage contains are large assemblage of mandibles and mandible fragments and 53 isolated lower jaw beaver incisors	Ewersen, 2011

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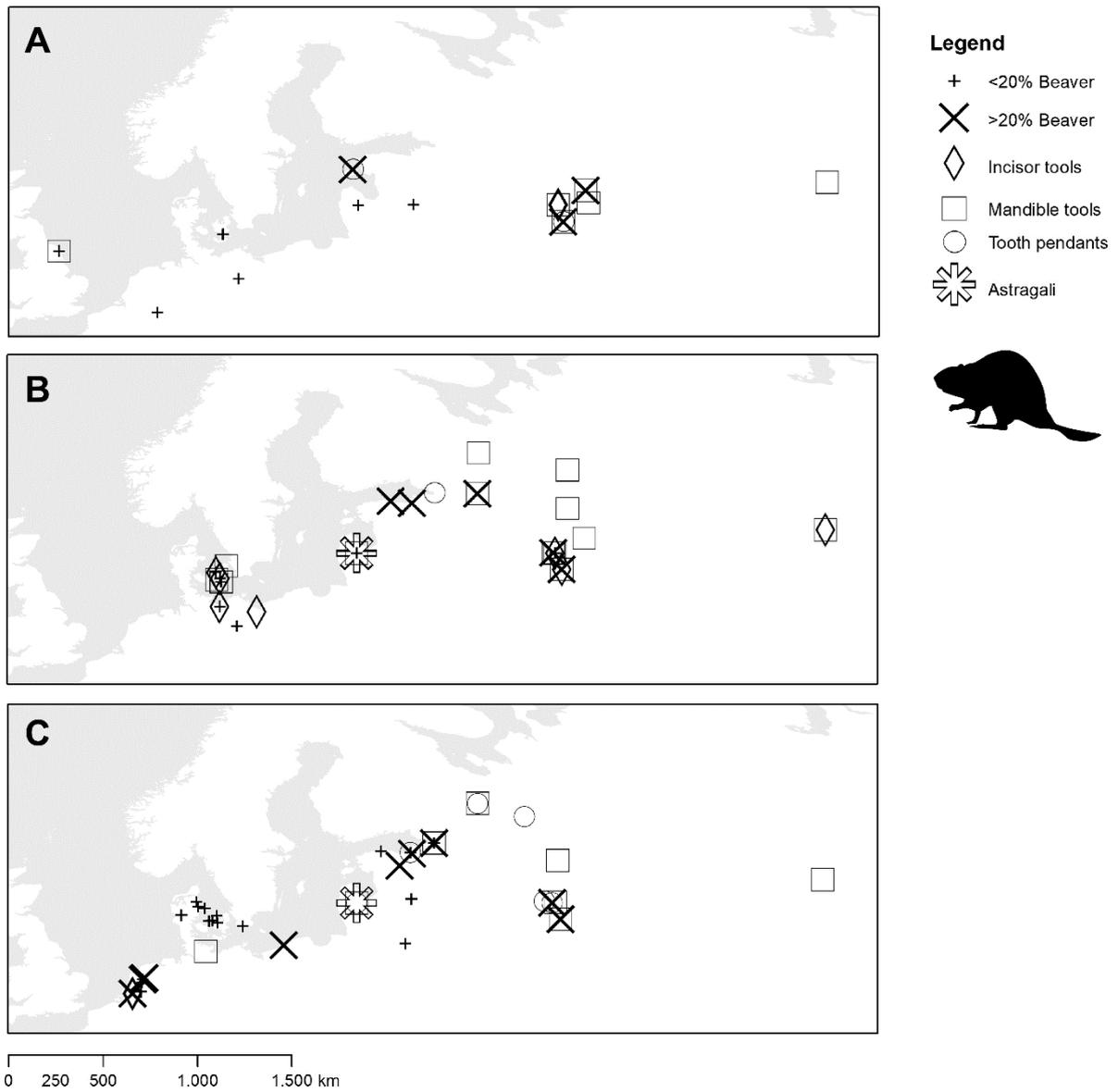
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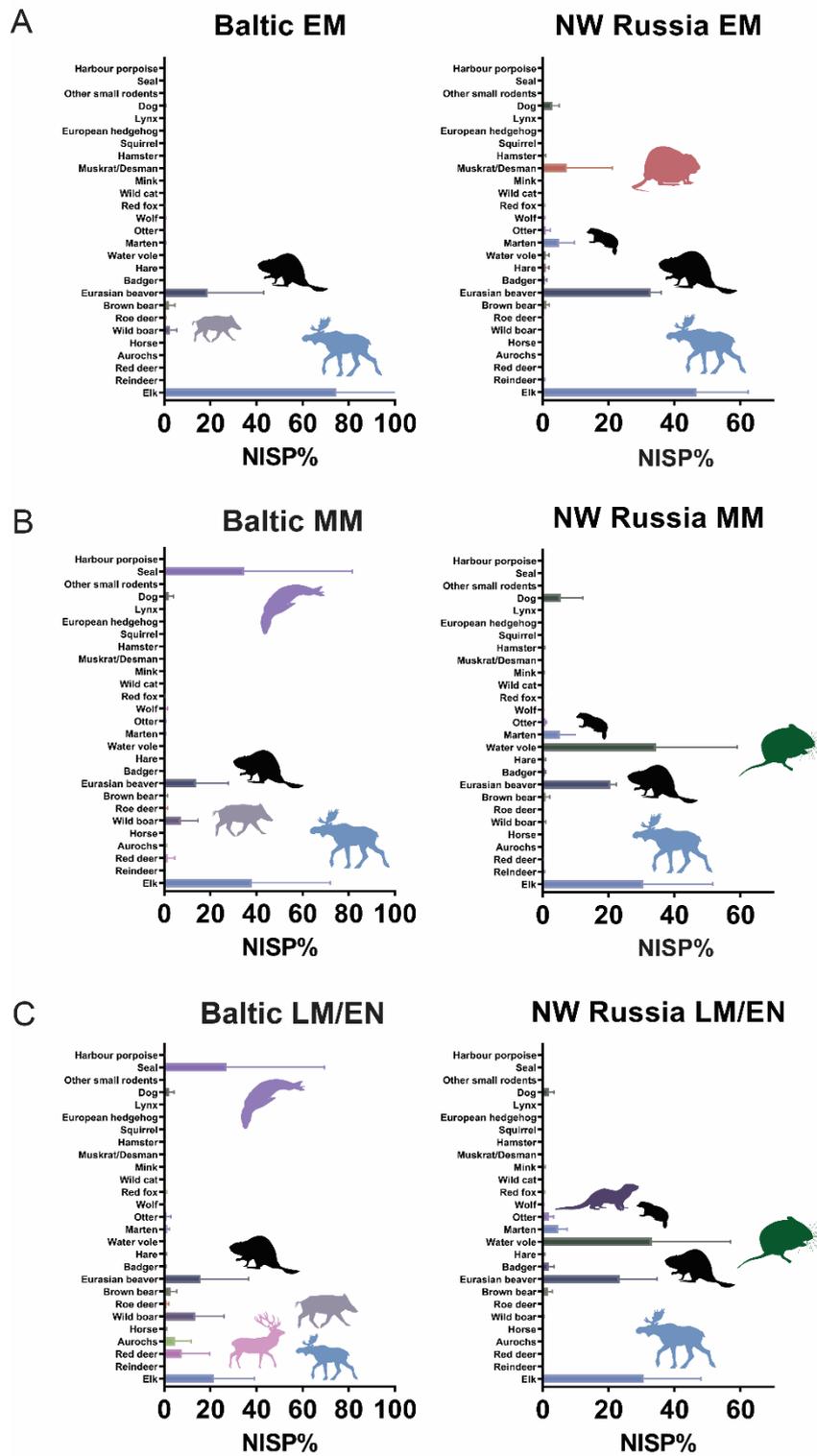
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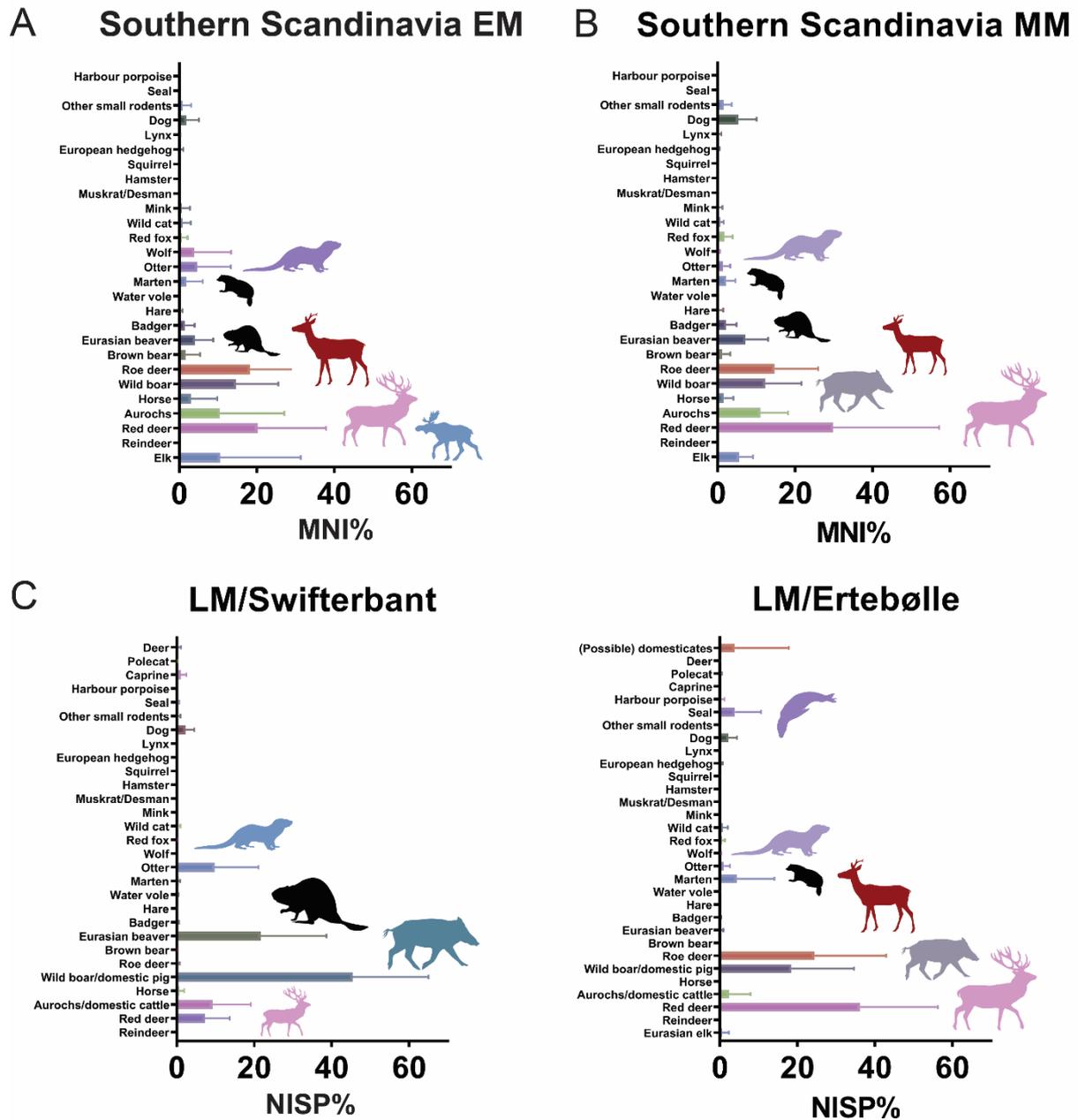
1463 **Fig. 1.** Overview of key sites from the Northern Mesolithic and their associated beaver remains and
1464 beaver-related material culture. A: Early Mesolithic; B: Middle Mesolithic; C: Late Mesolithic/Early
1465 Neolithic. Data provided in **Supplementary Information 1**.



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1467 **Fig. 2a.** Number of reported mammal species frequencies (NISP%) from the Baltic countries and
 1468 Northwestern Russia from the Early to the beginning of the Mid-Holocene (A: Early Mesolithic; B:
 1469 Middle Mesolithic; C: Late Mesolithic/Early Neolithic). Horizontal bars represent median values with
 1470 standard deviations. Animal silhouettes have been retrieved from <https://www.phylopic.org/> under CC
 1471 licensing. Raw data are provided in **Supplementary Information M Tab. 1 and 2.**

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1474 **Fig. 2b.** Number of reported mammal species frequencies (NISP%/MNI%) from Southern
 1475 Scandinavia and the Dutch wetlands from the Early to the first part of the Mid-Holocene (A: Early
 1476 Mesolithic; B: Middle Mesolithic; C: Late Mesolithic/Early Neolithic). Note that data for the latter
 1477 region is only available for the final phase. Horizontal bars represent median values with standard
 1478 deviations. Animal silhouettes have been retrieved from <https://www.phylopic.org/> under CC
 1479 licensing. Raw data are provided in **Supplementary Information M Tab. 3 and 4.**

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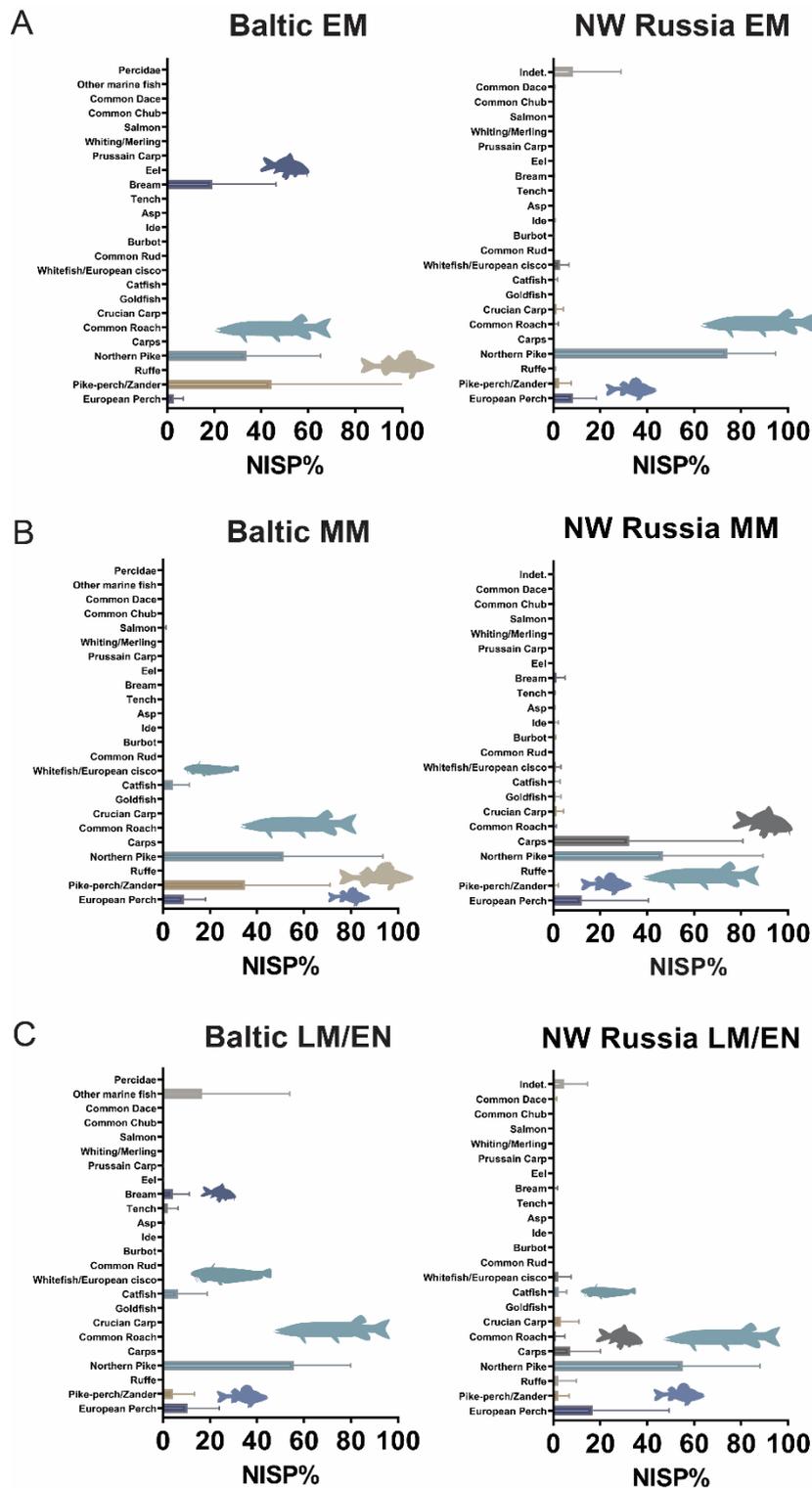
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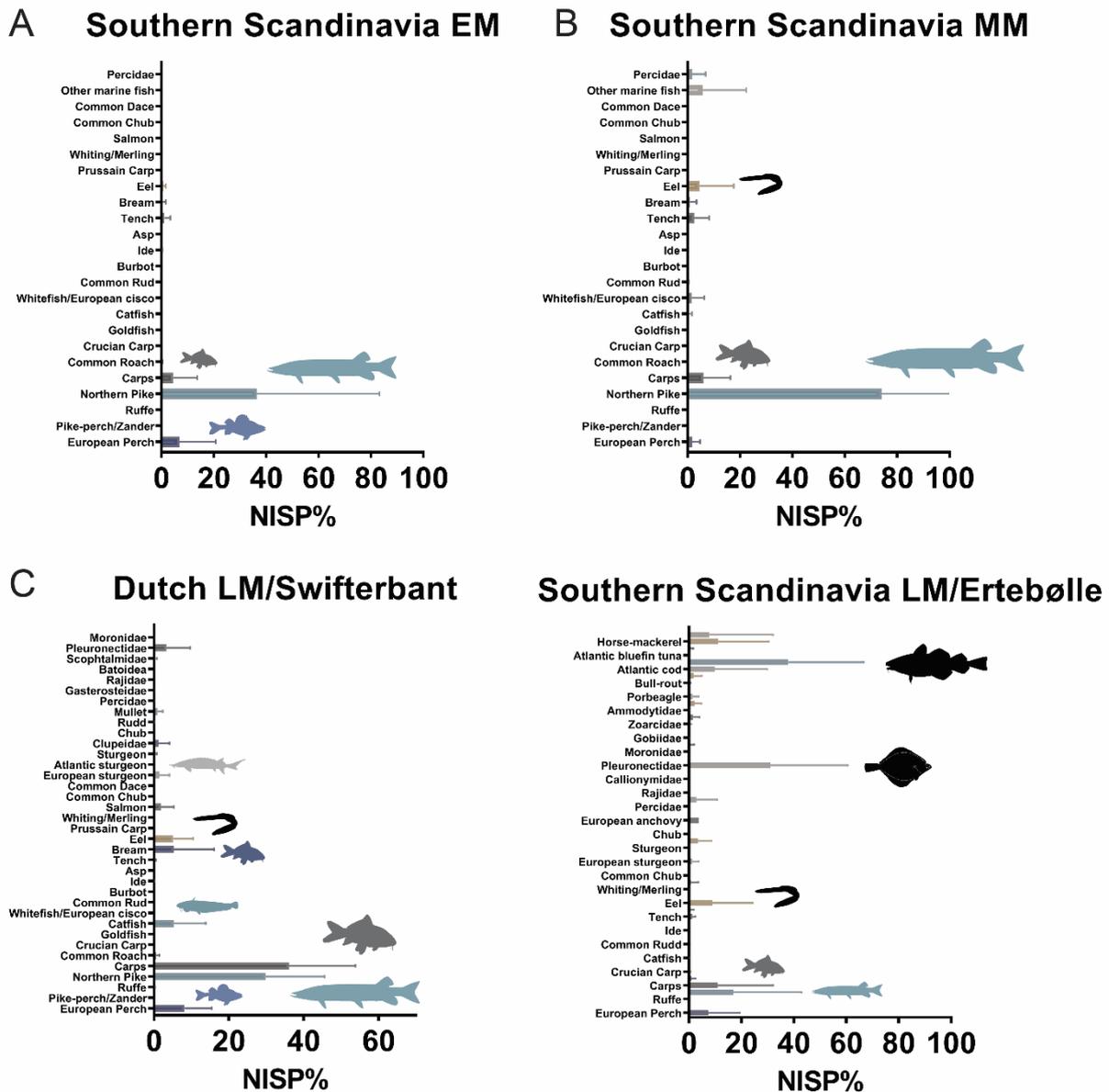
1484 **Fig. 3.** Selected beaver-sourced tools from the Mesolithic of Northwestern European wetland zone. 1-
 1485 4: beaver incisor tools; 6-7: beaver mandible tools. 1: Hohen Viecheln (Germany), Middle Mesolithic
 1486 (Schmölcke, Groß, and Nikulina 2017: Fig. 6; photograph: H. Lübke, ZSBA Schleswig); 2:
 1487 Hardinxveld-Giessendam Polderweg (the Netherlands), Late Mesolithic (Coles and Kooijmans 2001:
 1488 Figure 2); 3: Holmegård (Denmark), Middle Mesolithic (Hatting 1970: Fig. 10); 4: Øgårde (Denmark),
 1489 Middle Mesolithic (Hatting 1970: Fig. 9b); 5: Spjellerup (Denmark), Middle Mesolithic? (Hatting
 1490 1970: Fig. 4); 6: Lynby (Denmark), Middle Mesolithic (Hatting 1970: Fig. 8b).

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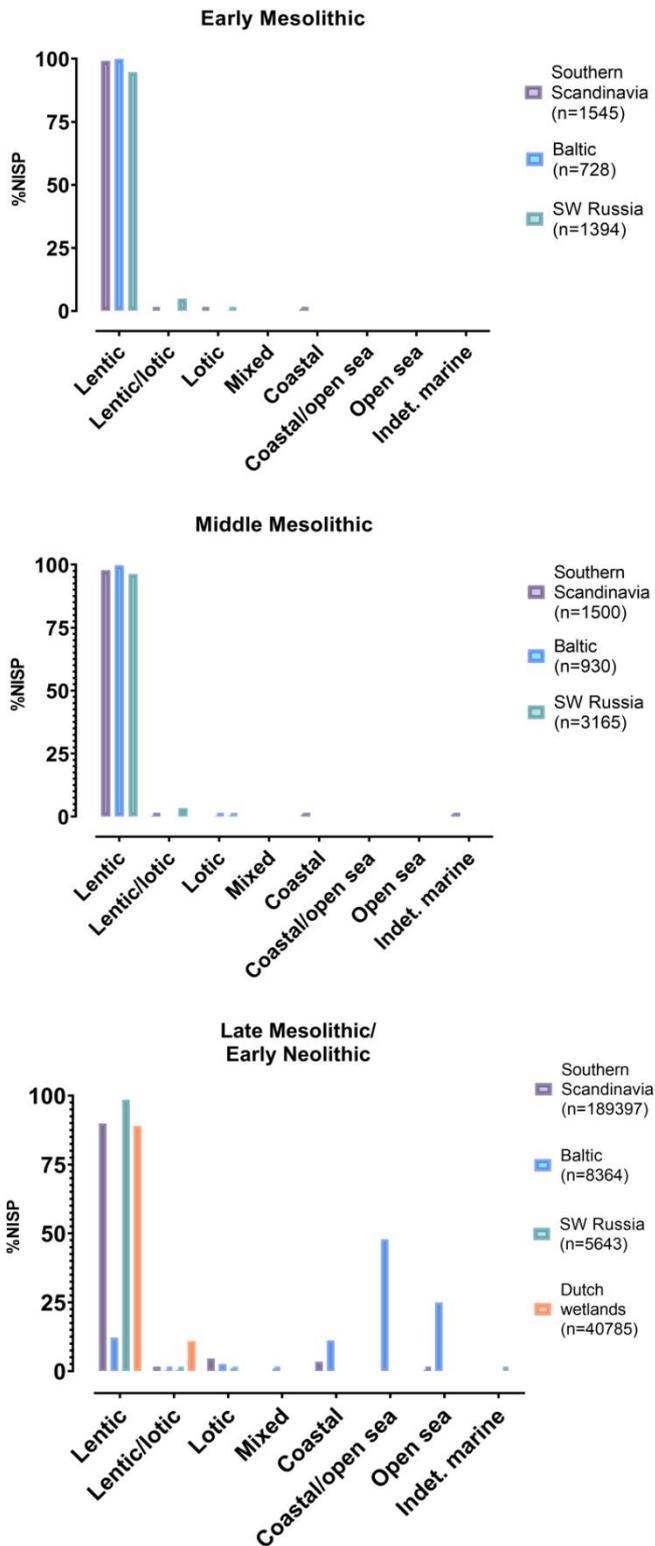
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1493 **Fig. 4a.** Number of reported mammal species frequencies (NISP%) from the Baltic countries and
 1494 Northwestern Russia from the Early to the first part of the Mid-Holocene (A: Early Mesolithic; B:
 1495 Middle Mesolithic; C: Late Mesolithic/Early Neolithic). Horizontal bars represent median values with
 1496 standard deviations. Animal silhouettes have been retrieved from <https://www.phylopic.org/>
 1497 under CC licensing. Raw data are provided in **Supplementary Information F Tab. 1 and 2.**



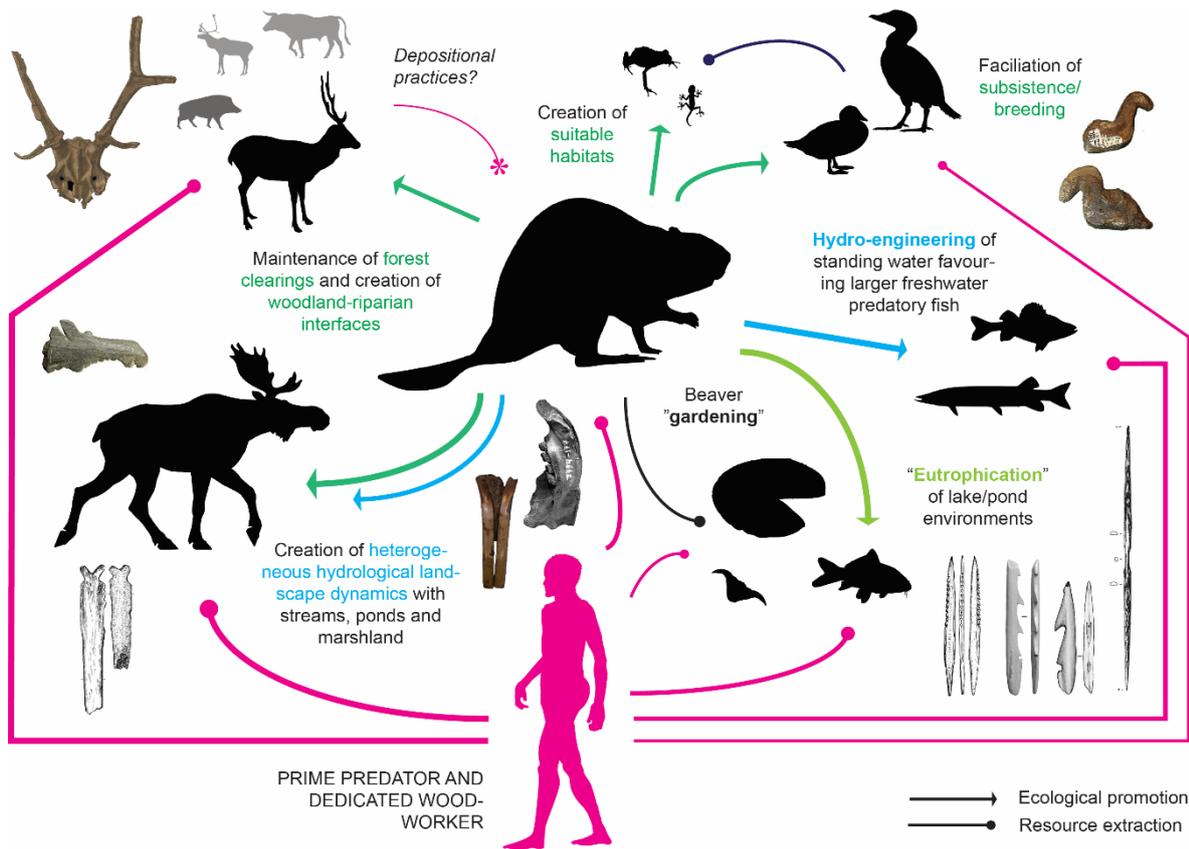
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1499 **Fig. 4b.** Number of reported fish species frequencies (NISP%) from Southern Scandinavia and the
 1500 Dutch wetlands from the Early to the first part of the Mid-Holocene (A: Early Mesolithic; B: Middle
 1501 Mesolithic; C: Late Mesolithic/Early Neolithic). Note that data for the latter region is only available
 1502 for the final phase. Horizontal bars represent median values with standard deviations. Animal
 1503 silhouettes have been retrieved from <https://www.phylopic.org/> under CC licensing. Raw data are
 1504 provided in **Supplementary Information F Tab. 3 and 4.**



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1506 **Fig. 5.** Marine vs. freshwater fish ecologies within ichthyofaunal assemblages as represented by NISP
 1507 shares in different regions and periods. Species classification and summary data table are provided in
 1508 **Supplementary Information 2.**



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1510 **Fig. 6.** Tanglegram of human and beaver practice in the Northern Mesolithic. Beaver agency and
 1511 geopraxis structure human behavioural systems and provide key affordances for subsistence (hunting,
 1512 fishing, fowling and wetland gardening) as well as the production, curation, and signification of
 1513 material culture. Human-beaver co-living provides a key adaptive background for human forager life
 1514 in the European North of the Early and Mid-Holocene. Human practices and materialities, in this view,
 1515 cannot be properly understood outside of their attendant multispecies systems.

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