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1 **Deglacial landscapes and the Late Upper Palaeolithic of Switzerland**

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27 **Abstract:**

28 The presence of people in Switzerland in recently deglaciated landscapes after the
29 Last Glacial Maximum represents human utilisation of newly available environments.
30 Understanding these landscapes and the resources available to the people who exploited
31 them is key to understanding not only Late Upper Palaeolithic settlement in Switzerland, but
32 more broadly human behavioural ecology in newly inhabited environmental settings. By
33 applying bone collagen stable isotope analysis ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$) to faunal remains from
34 Late Upper Palaeolithic localities in Switzerland, we investigate animal ecology and
35 environmental conditions during periods of human occupation. High and relatively uniform
36 $\delta^{34}\text{S}$ values indicate that landscapes north of the Jura Mountains provided comparatively
37 stable environmental conditions, while lower and more variable $\delta^{34}\text{S}$ values on the Swiss
38 Plateau suggest a dynamic landscape with diverse hydrological and pedological conditions,
39 potentially linked to regionally different patterns of permafrost thaw. This contrasts with the
40 archaeological record that appears relatively uniform between the two regions, suggesting
41 people were employing similar subsistence behaviours across a range of environmental
42 settings. The pattern of change in $\delta^{15}\text{N}$ across the deglacial period appears consistent
43 between areas that remained ice-free throughout the LGM and those that were glaciated.
44 Most notable is a period of exclusively low $\delta^{15}\text{N}$ values between 15,200 and 14,800 cal. BP,
45 which could relate a regional expansion of floral biomass in response to environmental
46 change.

47

48 **Keywords:** Magdalenian, collagen, sulphur isotopes, nitrogen isotopes, carbon isotopes,
49 Pleistocene, palaeogeography, Europe, horse, reindeer

50

51 **1. Introduction**

52 The period after the Last Glacial Maximum (LGM) in Switzerland saw significant
53 expansion of human settlement into previously ice-covered landscapes. This was facilitated
54 by the rapid development of pioneer floral and faunal communities, and most likely by
55 changes in the range dynamics of key prey species, such as horse (*Equus* sp.) and reindeer
56 (*Rangifer tarandus*) (Leesch et al., 2012; Cupillard et al., 2015). Understanding the
57 environmental developments that drove such changes is key to interpreting the subsistence
58 and settlement patterns of the human populations in this region and, more broadly, to
59 investigating human behavioural ecology in newly available landscapes. Here we examine
60 post-LGM paleoenvironmental conditions at two archaeological localities; Kastelhöhle-Nord
61 (Figure 1), which is situated north of the Jura Mountains and remained ice-free throughout
62 the LGM, and Monruz and Champréveyres (Figure 1), which are situated on the Swiss
63 Plateau and became ice-free before 17,500 cal. BP (Ivy-Ochs et al., 2004). Bone collagen
64 stable isotope analyses ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$) are applied to the archaeological faunal
65 assemblages from these sites to provide a direct record of past prey species ecology and
66 environmental conditions during the period of human activity. New radiocarbon dates are
67 also obtained from the fauna to better contextualise the chronology of human occupation. By
68 combining this data with other published results, the pattern of post-LGM environmental
69 change is compared between regions that remained ice-free throughout the LGM and those
70 that were glaciated.

71

72 **1.1 Post-LGM environment and archaeology in Switzerland**

73 Switzerland during the LGM was almost entirely covered by ice with only a small
74 region north of the Jura Mountains remaining unglaciated (Ivy-Ochs et al., 2004; Bini et al.,
75 2009; Ivy-Ochs 2015;). While a brief phase of human occupation during the LGM occurred in
76 the ice-free region (Terberger and Street, 2002; Reade et al., 2020), it is not until after the
77 LGM that evidence of widespread and sustained Late Upper Palaeolithic human activity
78 becomes apparent (Leesch et al., 2012). Post-LGM ice sheet decay in Switzerland was
79 rapid, and the entire central Swiss Plateau was ice free before the onset of Greenland
80 Stadial 2.1a (GS-2.1a, c.17,450 – 14,650 BP, Figure 2; Ivy-Ochs et al., 2004; Rasmussen et
81 al., 2014). The exposure of new landscapes during Greenland Stadial 2.1b (GS-2.1b, c.
82 20,850 to 17,450 BP, Figure 2; Rasmussen et al., 2014) was quickly followed by the
83 development of pioneer floral communities. Vegetation on the northern margins of the Jura
84 Mountains was dominated by *Poaceae*, *Artemisia*, *Juniperus* and *Hippophae* (Cupillard et
85 al., 2015), while species-rich treeless steppe tundra had developed on the Swiss Plateau by
86 around 18,700 cal. BP (Rey et al., 2017). This was followed by an increase in herbaceous
87 vegetation (e.g. Ammann and Lotter, 1989; Lotter, 1999; Wehrli et al., 2007) that allowed

88 large herbivores to recolonise deglaciated regions by around 17,000 cal. BP (Morel and Hug,
89 1996; Hajdas et al., 2007).

90 There is some evidence for a relatively early phase of post-LGM human activity early
91 in GS-2.1a, but the main expansion of settlement in Switzerland did not occur until the latter
92 part of GS-2.1a (Weniger, 1989; Napierala, 2008; Leesch et al., 2012; Maier, 2015). These
93 sites, associated with the Magdalenian culture, are characterised by a dominance of horse
94 and reindeer in their faunal assemblages (Leesch et al., 2012; Nielsen, 2013; Maier, 2015).
95 Attributed to Magdalenian techno-complexes D and E, the sites cover a wide geographic
96 distribution across the Swiss Plateau and Jura region, indicating the exploitation of a variety
97 of landscapes (Leesch et al., 2012). Archaeological evidence comes from both caves and
98 rockshelters, such as at Kesslerloch and Kastelhöhle-Nord, and open-air localities, such as
99 the sites of Monruz and Champréveyres (Leesch et al., 2019). Coleoptera-based
100 temperature estimates suggest summer and winter mean air temperatures on the Swiss
101 Plateau during GS-2.1a were around 9°C and –20°C respectively (Coope et al., 2000; Thew
102 et al., 2009), while summer temperatures of around 12°C are estimated for the region north
103 of the Jura mountains (Cupillard et al., 2015). Pollen and plant macrofossil evidence attest to
104 vegetation rapidly increasing in diversity, but still dominated by cold-tolerant herbaceous
105 species (Thew et al., 2009; Cupillard et al., 2015).

106 The onset of Greenland Interstadial 1 (GI-1, c. 14,650 to 12,850 BP, Figure 2;
107 Rasmussen et al., 2014) corresponds to a rapid rise in temperatures on the Swiss Plateau
108 and the expansion of juniper and birch vegetation into open shrub and grasslands (Thew et
109 al., 2009). It is currently not clear whether Magdalenian activity continued into this early
110 phase of GI-1e or ended with the onset of this warm period, but by c. 14,400 cal. BP Azilian
111 occupation of the Swiss Plateau was established (Leesch et al., 2012). During this time,
112 mean summer and winter temperatures are estimated to have been around 15°C and 0°C
113 respectively, with vegetation composed of a mosaic of open birch woodland, patches of
114 dwarf birch and shrubs, and areas of grasses and sedges (Leesch, 1997; Thew et al., 2009).
115 These more temperate conditions are reflected in the change in subsistence focus, with red
116 deer (*Cervus elaphus*) and horse being important prey species (Leesch et al., 2004; Nielsen,
117 2013; Maier, 2015).

118 Considering the availability of different prey species and the ecologies and
119 environments they represent is key to understanding the landscapes past people would have
120 experienced. Whilst there is a wealth of Swiss Lateglacial palaeoenvironmental data from
121 numerous lake and mire archives (e.g. Lotter, 1999; Coope et al., 2000; Wehrli et al. 2007;
122 Lotter et al., 2012; Cupillard et al., 2015; Rey et al., 2017), analysis of the archaeological
123 faunal assemblage provides the means to directly link inferences on habitat, ecology, and
124 palaeoenvironmental conditions, to human hunting, settlement and subsistence practices.

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1.2 Palaeoenvironmental records from faunal stable isotopes

Palaeoenvironmental and ecological data can be obtained directly from skeletal remains of prey species from archaeological contexts through stable isotope analyses (e.g. Stevens and Hedges, 2004; Stevens et al., 2008, 2014; Drucker et al., 2011a; 2011b; 2012; Bocherens et al., 2015; Jones et al., 2018; Reade et al., 2020). In this study we use carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$) and sulphur ($\delta^{34}\text{S}$) isotope ratios in bone collagen to explore post-LGM environments and prey species ecology in Switzerland. The measured isotopic signals are underpinned by dietary specialisation, animal behaviour and environmental conditions.

Bone collagen $\delta^{13}\text{C}$ values are largely determined by species-specific dietary behaviours, such as grazing versus browsing, or specific dietary specialisations, such as the consumption of lichens by reindeer, which leads to systematically higher $\delta^{13}\text{C}$ values in comparison to other herbivore species (Drucker et al., 2010; Bocherens et al., 2015). However, dietary $\delta^{13}\text{C}$ values also reflect atmospheric CO_2 concentration and $\delta^{13}\text{C}$, environmental variables such as temperature and moisture availability, and vegetation density and type (Heaton, 1999; Stevens and Hedges, 2004; Drucker et al., 2008; Kohn, 2010). Faunal $\delta^{15}\text{N}$ values are linked to both dietary specialisation/niche position and to climatic parameters, such as temperature and precipitation, mediated through soil processes (Amundson et al., 2003; Stevens et al., 2008; 2014; Drucker et al., 2011b; 2012; 2018; Craine et al 2015; Rabanus-Wallace et al., 2017). In particular, nutrient availability and microbial activity may be reflected in herbivore bone collagen $\delta^{15}\text{N}$ values, parameters that were likely strongly influenced by the presence of permafrost and ice sheets in the European Lateglacial (Stevens and Hedges, 2004; Stevens et al., 2008; Drucker et al., 2011b). Collagen $\delta^{34}\text{S}$ values relate to the soil environment upon which the animal fed. Bioavailable sulphur can be derived from sulphates in groundwater and rain, atmospheric sulphur, and from mineral weathering of the underlying geology (Nehlich, 2015). As such, bone collagen $\delta^{34}\text{S}$ values are spatially variable and often considered a tool for exploring mobility and landscape utilisation (e.g. Drucker et al., 2012; 2018; Jones et al., 2018; Wißing et al., 2019). However, bone collagen $\delta^{34}\text{S}$ values may also hold significant promise as a palaeoenvironmental proxy, as soil-bedrock interactions, mineral weathering, and sulphur cycling in the soil are driven by hydrological and microbial processes (Thode, 1991). These are dynamic systems influenced by climatic and environmental conditions, such that $\delta^{34}\text{S}$ values in the local landscape are unlikely to have remained static across major environmental transitions, for example the last deglaciation.

2. Materials and Methods

161 In this study we present $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ data generated from horse, reindeer,
162 red deer and *Bos/Bison* bone collagen samples from the Swiss sites of Kastelhöhle-Nord,
163 Monruz and Champréveyres to explore animal ecology and environmental conditions after
164 the LGM.

165

166 **2.1 Archaeological samples**

167 The faunal assemblage from Kastelhöhle-Nord provides a record from the ice-free
168 region of Switzerland, on the north edge of the Jura Mountains. Excavation of the cave
169 between 1948 and 1954 revealed an 'intermediate' horizon associated with a Badegoulian
170 phase of occupation, dated to the latter part of the LGM (Terberger and Street, 2002; Reade
171 et al., 2020), and a 25cm-thick 'upper' horizon associated with the post-LGM Magdalenian
172 (Leesch et al., 2012). This upper horizon contained a rich lithic assemblage that certainly
173 represents more than one phase of Magdalenian activity at the site and most likely
174 comprises more than one techno-complex (Magdalenian D-a and E; Leesch et al., 2012). A
175 relatively long duration of accumulation for this horizon was confirmed by three faunal
176 radiocarbon dates, which range from 16,350–15,965 cal. BP (ETH-45024) to 14,265–13,967
177 cal. BP (ETH-45026) (Leesch et al., 2012; Figure 2, Table 1). We sampled the large
178 herbivore species found within the upper horizon (Schweizer, 1959); reindeer (n=10), horse
179 (n=5) and *Bos/Bison* (n=6). Of these, one reindeer bone displayed evidence of
180 anthropogenic impact (cut marks). To investigate the chronology of this horizon, 3
181 specimens (two horse and the cut-marked reindeer bone) were selected for radiocarbon
182 dating. The three specimens that had previously been dated (two reindeer, one *Bos/Bison*)
183 were also re-dated to ensure methodological consistency between laboratories.

184 Comparative post-LGM samples from the Swiss Plateau, which was glaciated during
185 the LGM, come from the open-air localities of Monruz and Champréveyres. Excavated
186 between 1984 and 1992, both sites produced Late Upper Palaeolithic Magdalenian and
187 Azilian occupation horizons, with rich faunal, botanical and lithic assemblages. Phases of
188 Magdalenian activity at the sites date to the later part of GS-2.1a and were focused primarily
189 on the exploitation of horse, together with a broad spectrum of smaller mammals, birds and
190 fish, particularly in spring and summer (Müller et al., 2006; Müller, 2013). Three horse bones
191 from these assemblages have previously been radiocarbon dated, producing age
192 determinations between 15,874–15,349 cal. BP (OxA-20699) and 15,585–15,053 cal. BP
193 (OxA-20701) (Figure 2, Table 1). We selected five reindeer and 12 horse samples from
194 Monruz (all from Magdalenian sector 1) and 7 red deer samples from Champréveyres (four
195 from Magdalenian sector 2, two from Azilian sector 1, and one from sector 2 where the
196 association to the Magdalenian or Azilian was uncertain) for stable isotope analysis. While
197 the specimens do not bear direct traces of anthropogenic action, the large herbivore faunal

198 assemblage from the sites is confidently interpreted as the product of human action (Müller
199 et al., 2006; Müller, 2013). While Magdalenian activity has been dated both from faunal and
200 charcoal remains, dating of the Azilian phase has so far relied solely on charcoal samples.
201 Therefore, one bone from the Azilian concentration at Champréveyres was selected for
202 radiocarbon dating as part of this study.

203

204 **2.2 Sample pre-treatment**

205 A small sample of bone (0.2 to 1.3g) was collected from each specimen using a
206 dental drill with either a small cutting wheel or tungsten burr attachment. Samples were
207 prepared at University College London (UCL) using a modified version of the Oxford
208 Radiocarbon Accelerator Unit (ORAU) collagen extraction procedures (AF and AG methods;
209 Brock et al., 2010), which is based on a modified version of the Longin (1971) method. All
210 samples were treated with 0.5M hydrochloric acid (HCl) at 4°C until fully demineralised and
211 then thoroughly rinsed with ultrapure water. Some samples were then also treated with 0.1M
212 sodium hydroxide (30mins), and 0.5M HCl (1hr) to remove humic contaminants (Szpak et
213 al., 2017), again being thoroughly rinsed with ultrapure water between reagents. All samples
214 were then gelatinised in pH3 HCl solution at 75°C for 48hrs and filtered using a pre-cleaned
215 Ezee-filter. For most samples, including all those to be radiocarbon dated, the filtrate was
216 then passed through a pre-cleaned 15–30 kD ultrafilter, with the >30 kD fraction collected
217 and freeze-dried (AF method). For some samples the ultrafiltration step was omitted (AG
218 method); while ultrafiltration has been shown to successfully improve the removal of
219 contaminants that can influence radiocarbon determinations (Higham et al., 2006), it also
220 significantly reduces collagen yield, while at the same time producing little difference in
221 measured stable isotope compositions (Sealy et al., 2014; Szpak et al., 2017). Details of pre-
222 treatment methodology are given for each sample in the supplementary information S1.

223

224 **2.3 Stable isotope analysis**

225 Collagen yields from Kastelhöhle-Nord ranged from 2.3 to 16.2%. Collagen
226 preservation at Monruz and Champréveyres was poorer; 12 out of 24 samples failed to
227 produce enough collagen for stable isotope analysis (yields $\leq 0.7\%$), while the other 12
228 samples had collagen yields ranging from 0.8 to 3.6% (supplementary information S1).
229 Samples with adequate collagen were analysed for their nitrogen ($\delta^{15}\text{N}$), carbon ($\delta^{13}\text{C}$), and
230 sulphur ($\delta^{34}\text{S}$) isotopic ratios at the Scottish Universities Environmental Research Centre
231 (SUERC). 1.2–1.5mg aliquots of freeze-dried collagen were weighed into tin capsules and
232 analysed using a Delta V Advantage continuous-flow isotope ratio mass spectrometer
233 coupled via a ConFloIV to an EA IsoLink elemental analyser (Thermo Fisher Scientific,
234 Bremen). For every ten archaeological samples, three in-house standards, calibrated to the

235 International Atomic Energy Agency (IAEA) reference materials, were analysed (Sayle et al.,
236 2019). Results are reported as per mil (‰) relative to the internationally accepted standards
237 VPDB, AIR and VCDT. Measurement uncertainty was determined to be $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$,
238 $\pm 0.2\text{‰}$ for $\delta^{15}\text{N}$, and $\pm 0.3\text{‰}$ for $\delta^{34}\text{S}$, on the basis of repeated measurements of an in-house
239 bone collagen standard and a certified fish gelatin standard (Elemental Microanalysis, UK).
240 Standard quality control criteria were used to assess the $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ data (DeNiro,
241 1985; Ambrose, 1990; Nehlich and Richards, 2009). Each sample was analysed in duplicate
242 and reproducibility was better than $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$, $\pm 0.2\text{‰}$ for $\delta^{15}\text{N}$ and $\pm 0.3\text{‰}$ for $\delta^{34}\text{S}$. All
243 analysed samples had C:N atomic ratios between 3.2–3.6, and %C and %N between 35-
244 46% and 12-16%, respectively, indicating good bone collagen preservation (DeNiro, 1985;
245 Ambrose, 1990). All analysed samples except UPN-240 had C:S and N:S atomic ratios
246 within the recommended ranges of 600 ± 300 and 200 ± 100 , and %S content between 0.14
247 and 0.30% (Nehlich and Richards, 2009)

248

249 **2.4 Radiocarbon analysis and background corrections**

250 Radiocarbon dating was performed at ORAU using their standard procedures, as
251 described by Brock *et al.* (2010). For each sample, approximately 5mg of dry collagen, which
252 had been weighed into tin capsules baked at 500°C for 12 hours, was combusted using an
253 elemental analyser coupled to an isotope ratio mass spectrometer, employing a splitter to
254 allow for collection of the CO_2 (Bronk Ramsey and Humm, 2000; Brock *et al.*, 2010).
255 Samples were graphitised by reduction of collected CO_2 over an iron catalyst in an excess
256 H_2 atmosphere at 560°C (Bronk Ramsey and Hedges, 1997; Dee *et al.*, 2010). ^{14}C dates
257 were measured on the Oxford AMS system using a cesium ion source for ionisation of the
258 solid graphite sample (Bronk Ramsey *et al.*, 2004). To denote the bone pretreatment at UCL
259 rather than at ORAU, all measured dates were given “OxA-V-*www*-pp” numbers, where
260 “*www*” indicates the wheel number, and “pp” is the position of the sample on the wheel
261 (Brock *et al.*, 2010). As collagen extraction was performed at UCL according to the ORAU
262 pretreatment protocol, background corrections were applied to our dates based on repeat
263 AMS measurements at ORAU of known-aged reference samples prepared in the UCL
264 laboratory, following the method outlined by Wood *et al.* (2010). A full description of our
265 correction methodology is detailed in Reade *et al.* (2020). Corrected dates are denoted by
266 adding a “C” to the end of the date code assigned by ORAU. Uncorrected measured date
267 values as well as further details of the correction calculations are provided in the
268 supplemental information S2.

269

270 **3. Results and Discussion**

271

272 **3.1 Chronology of the Lateglacial assemblage at Kastelhöhle-Nord and**
273 **Champréveyres**

274 Six new radiocarbon determinations were made on fauna from the upper horizon at
275 Kastelhöhle-Nord (Figure 2, Table 1). Three of these were undertaken on previously dated
276 specimens for inter-laboratory comparison, and the results reflect those previously obtained
277 (Leesch and Müller, 2012) (Table 1). The new dates for Kastelhöhle-Nord's upper horizon
278 range from $13,550 \pm 60$ ^{14}C BP (OxA-V-2794-25C) to $12,200 \pm 50$ ^{14}C BP (OxA-V-2793-
279 56C), giving a range of calibrated ages between 16,350 – 15,965 cal. BP and 14,260 –
280 13,935 cal. BP, further confirming an extended period of bone accumulation in the horizon.
281 There appears to be a species-based chronological pattern to the results (Figure 2);
282 *Bos/Bison* and horse date to GS-2.1a and reindeer to GI-1. However, this finding is likely
283 coincidental as reindeer dating to GS-2.1a are known at other sites within the same valley
284 system (e.g. Hollenberg-Höhle 3; Müller and Leesch, 2011), as are horse dating to GI-1 (e.g.
285 Kohlerhöhle; Leesch and Müller, 2012). Thus, both species were present within the local
286 landscape at the same time as one another.

287 Archaeologically, the dating of a cut-marked reindeer bone found in association with
288 Magdalenian artefacts to the later, colder part of GI-1ed is problematic when considered
289 against our current understanding of the chronology of Magdalenian/Azilian development
290 and their subsistence systems in the region. While it is recognised that the Kastelhöhle-Nord
291 upper horizon lithic assemblage most probably represents more than one Magdalenian
292 techno-assemblage (Leesch et al., 2012), the reindeer date is significantly later than those at
293 other Magdalenian sites in the region and also later than dates associated with the Early
294 Azilian assemblages at Monruz and Champréveyres. Therefore, it appears reindeer hunting
295 at Kastelhöhle-Nord continued or resumed after the Magdalenian disappeared from the
296 archaeological record in adjacent regions. As the bone was found in the mixed Magdalenian
297 techno-assemblage the question arises whether this lithic tradition survived or was revived
298 with the hunting of reindeer during GI-1ed, or whether there is a yet unrecognised lithic
299 assemblage type admixed in the upper horizon. Comparable late GI-1ed radiocarbon dates
300 on faunal remains (horse, ptarmigans, red deer and dog) have come from the nearby cave of
301 Büttenloch, and from other northern Swiss localities, namely Rislisberghöhle and
302 Kesslerloch (Napierala, 2008; Leesch and Müller, 2012). Chronologically, the dates are
303 compatible with the Azilian phase in Switzerland, although the dated fauna cannot be
304 certainly attributed to the subsistence activities of this culture.

305 One new radiocarbon determination was made on a red deer bone from the Azilian
306 horizon at Champréveyres, which had so far been chronologically constrained by
307 radiocarbon determinations made on charcoal and macrobotanical remains (Leesch, 1997).
308 The date, $12,480 \pm 50$ ^{14}C years BP (OxA-V-2754-49C, Figure 2, Table 1), falls within the

309 range of dates on charcoal from hearth deposits, confirming the contemporaneity of the
310 faunal assemblage with human activity at the site.

311

312 **3.2 Lateglacial ecology and environment at Kastelhöhle-Nord and**

313 **Monruz/Champréveyres**

314 Kastelhöhle-Nord upper horizon $\delta^{13}\text{C}$ values overlap for reindeer and *Bos/Bison*, (–
315 20.3‰ to –19.4‰ and –20.1‰ to –19.7‰, respectively) while horse $\delta^{13}\text{C}$ values differ (–
316 21.3‰ to –20.2‰) (Figure 3, Table 2). A similar offset between reindeer and *Bos/Bison*, and
317 horse is also observed in the nitrogen isotopic data, which ranges from 0.7‰ to 2.3‰ for
318 horse, compared to 2.3‰ to 3.5‰ and 2.6‰ to 4.0‰ for reindeer and *Bos/Bison*
319 respectively (Figure 3, Table 2). The significant species-based differences between $\delta^{13}\text{C}$ and
320 $\delta^{15}\text{N}$ values (Figure 3, supplementary information S3.1 and S3.2) can largely be explained
321 by species ecology and dietary specialisation. The comparable *Bos/Bison* and reindeer $\delta^{13}\text{C}$
322 values indicate ecological overlap. Reindeer typically display higher $\delta^{13}\text{C}$ values than other
323 herbivore species due to lichen consumption; this dietary behaviour has also been observed
324 in some modern bison populations and has previously been suggested for the species in
325 other Late Pleistocene contexts (Larter and Gates, 1991; Julien et al., 2012; Bocherens et
326 al., 2015). The two species also display similar $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values (Figure 3, Table 2),
327 further supporting the interpretation of overlapping habitat preferences. Lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
328 values in horse compared to reindeer is a pattern that is observed across Pleistocene
329 Europe and indicates occupation of a different ecological niche (Stevens and Hedges, 2004;
330 Stevens et al., 2008; Bocherens et al., 2015). The $\delta^{34}\text{S}$ values observed for horse also differ
331 from those of reindeer and *Bos/Bison* (Figure 3, Table 2), further suggesting that the animals
332 were not only occupying different niches, but also possibly different landscapes and/or
333 different topographical features/locations within a given area. However, it should be noted
334 that the species-dependent chronological pattern observed in the radiocarbon dates (Figure
335 2) means that it cannot be certainly demonstrated that any of the individuals analysed here
336 overlap in their chronology, and as such, the differences observed may partly be influenced
337 by temporally changing underlying environmental parameters. Pollen records indicate the
338 vegetation north of the Jura mountains was dominated by a mosaic of *Poaceae*, *Artemisia*,
339 *Juniperus* and *Hippophae* species during GS-2.1a, with *Juniperus* and *Betula* expanding at
340 the start of GI-1e, while climatic proxies suggest both an increase in temperature and
341 precipitation across this time interval (Cupillard et al., 2015). Thus, the observed isotopic
342 data likely represents a combined signal of environmental change and species-specific
343 patterns of habitat utilisation.

344 A similar pattern of variation between horse and reindeer is seen in the Monruz
345 results (Figure 4). At this site average horse $\delta^{15}\text{N}$ values ($1.8 \pm 0.6\text{‰}$) and $\delta^{13}\text{C}$ values (–

346 $21.0 \pm 0.2\text{‰}$) are significantly different to the reindeer values ($2.8 \pm 0.2\text{‰}$ and $-19.8 \pm 0.2\text{‰}$,
347 respectively) (S3.3). Furthermore, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for horse at Monruz and
348 Kastelhöhle-Nord upper horizon are indistinguishable from one another; the same is also
349 observed for reindeer from the two sites (S3.4 and S3.5). By contrast, horse and reindeer
350 $\delta^{34}\text{S}$ values at Monruz are statistically indistinguishable from one another (Figure 4; S3.6),
351 but significantly different to those of the horse and reindeer at Kastelhöhle-Nord (S3.7).
352 Therefore, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values cluster by species, indicating that ecological niche and
353 animal behaviour are the primary factors influencing these values, while $\delta^{34}\text{S}$ values cluster
354 by site, indicating that location-based factors are most strongly represented in the sulphur
355 isotope ratios. Almost twice as much variability is observed in the Monruz $\delta^{34}\text{S}$ values
356 (16.5‰) than in the Kastelhöhle-Nord $\delta^{34}\text{S}$ values (8.8‰), despite the Monruz samples
357 representing a significantly shorter time span (Figure 2) and representing only two, rather
358 than three, different animal species (Table 2). Further, unlike at Kastelhöhle-Nord, the horse
359 and reindeer $\delta^{34}\text{S}$ values from Monruz completely overlap with one another. Thus, while the
360 Monruz $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values suggest that horse and reindeer were occupying different
361 ecological niches, the sulphur isotopic data suggests this was likely taking place within the
362 same geographical region(s), and therefore under the same range of environmental and
363 climatic conditions. The large range in $\delta^{34}\text{S}$ values could indicate both species were
364 displaying a number of different long-distance mobility behaviours, or alternatively, could
365 suggest a high level of environmental variability within a relatively small geographical region.
366 As the Monruz horse produce a significantly greater range of $\delta^{34}\text{S}$ values (16.2‰) than the
367 reindeer (7.0‰), and unlike reindeer, horse generally do not undertake long-distance
368 seasonal migrations, we suggest the second interpretation is more plausible. However, we
369 recognise mobility behaviours may have differed between different environments in Late
370 Pleistocene Europe (e.g. Bignon et al., 2005; Pelligrini et al., 2008; Pryor et al., 2016).

371 The isotopic composition of bioavailable sulphur is spatially variable at a range of
372 scales. At the regional level, soil $\delta^{34}\text{S}$ values are controlled by location-based inputs from
373 underlying bedrock geology, sea spray and the atmosphere (Thode, 1991; Nehlich, 2015).
374 However, Monruz and Kastelhöhle-Nord are situated far from the coast and occupy similar,
375 relatively uniform sedimentary geologies comprised of limestone, sandstone, and clay that
376 are unlikely to account for the range of $\delta^{34}\text{S}$ values that we observe (Asch, 2005; Figure 1).
377 Other potential sources of spatial variation in $\delta^{34}\text{S}$ values relate to more local-scale
378 differences in soil microbial activity, influenced by soil temperature, water content and
379 oxygen availability (Orchard and Cook 1983; Liu et al., 2018; Nitsch et al., 2019). Indeed,
380 paleoenvironmental records from the Swiss Plateau document a highly heterogeneous
381 landscape existed during this period; increasing temperatures led to permafrost thaw,
382 terrestrial landscape instability and the development of localised marshy habitats in some

383 areas, while in other areas it facilitated vegetation development and soil stabilisation (Thew
384 et al., 2009; Rey et al., 2017; 2019). It is these local-scale processes which we suggest are
385 represented in the high level of variation observed in the Monruz $\delta^{34}\text{S}$ values.

386 Only one result is available for the Azilian period from Monruz and Champréveyres.
387 This was the sole sample from an Azilian context at Champréveyres to yield adequate
388 collagen for analysis, and the only red deer sample in our data set. This sample produced
389 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of -20.6‰ and 2.4‰ , respectively, which are comparable to the red
390 deer previously analysed from the site (-20.6‰ and 3.4‰ , Drucker et al., 2009).

391

392 ***Deglaciated versus unglaciated Lateglacial landscape development***

393 In the context of Late Pleistocene Europe, much of the spatial and temporal variation
394 observed in herbivore bone collagen stable isotope values has been linked to soil processes,
395 related to variations in temperature, permafrost extent and proximity to ice sheet margins
396 (Stevens and Hedges, 2004; Stevens et al., 2008; Drucker et al., 2011b; 2012). To explore
397 these possible drivers of the isotopic signatures, and by inference post-LGM environmental
398 change, we compare the temporal patterns observed in fauna from neighbouring regions
399 that had been glaciated at the LGM to those that had remained ice-free during the last
400 glacial cycle. We combine the results of this study with those previously published from
401 regions of Switzerland, the French Jura and Western Alps (Drucker et al., 2003; 2009;
402 2011a; 2011b; 2012; Stevens et al., 2008; Bocherens et al., 2011; Gröcke et al., 2017;
403 Reade et al., 2020; Figure 5; Supplementary Information 5). Sites are assigned to two
404 groups based on reconstructed maximum ice extents; those in locations that remained ice-
405 free through the LGM, and those that were ice-covered at the LGM (Campy, 1992; Bini et al.,
406 2009; Schlüchter et al., 2010). As this analysis combines data from multiple species
407 (*Bos/Bison*, horse, red deer, and reindeer), differences in dietary behaviours mask possible
408 environmental interpretations from the $\delta^{13}\text{C}$ values. Dietary ecology is also likely responsible
409 for some of the scatter in the $\delta^{15}\text{N}$ data, but temporal trends are nonetheless apparent
410 (Figure 5). Herbivore $\delta^{34}\text{S}$ values appear to primarily reflect the underlying environment,
411 irrespective of differences in dietary ecology, and the different temporal patterns in the $\delta^{34}\text{S}$
412 values between the two location-based groups is striking (Figure 5).

413 For $\delta^{15}\text{N}$ values, the temporal pattern of variation appears consistent between the
414 ice-covered and ice-free areas, suggesting that the presence/absence of ice sheets and
415 processes of deglaciation are not the direct primary influences being recorded in the signal.
416 The most notable aspect of the record is the absence of $\delta^{15}\text{N}$ values greater than c. 2.5‰
417 between around 15,200 and 14,800 cal. BP. As this pattern is present in samples that span
418 a large geographical area, which is topographically and environmentally diverse, a regional-
419 scale explanation should be sought. Low herbivore $\delta^{15}\text{N}$ values ($<2.5\text{‰}$) in Lateglacial

420 Europe have previously been linked to environments with nutrient-poor soils, where low
421 temperatures and the presence of permafrost impeded the soil nitrogen cycle, or to
422 increased environmental moisture; conversely, high herbivore $\delta^{15}\text{N}$ values ($>5\text{‰}$) have been
423 considered typical of environments where nitrogen supply is not a limiting factor to plant
424 growth and environmental conditions do not inhibit the soil nutrient cycle (Schulze et al.,
425 1994; Hobbie et al., 1998; Jonasson et al., 1999; Stevens and Hedges 2004; Stark, 2007;
426 Stevens et al., 2008; 2009; Drucker et al., 2011b; 2012; Rabanus-Wallace et al., 2017). Low
427 $\delta^{15}\text{N}$ values occur alongside an absence of high $\delta^{15}\text{N}$ values at various points in the
428 Swiss/French record shown in Figure 5 (at c. 21,000 – 18,200 cal. BP, c. 15,200 – 14,800
429 cal. BP, and c. 12,200 cal. BP). However, we suggest that it is only the 15,200 – 14,800 cal.
430 BP interval that can be discussed with a degree of confidence, as the exclusively low $\delta^{15}\text{N}$
431 values during this time interval are clearly bounded by the presence of higher $\delta^{15}\text{N}$ values
432 both before and after (Figure 5). The timing of this disappearance of $\delta^{15}\text{N}$ values greater
433 than c. 2.5‰ in the Swiss/French record broadly corresponds to the end of Heinrich Event 1
434 (HE1), a period of climatic cooling following the LGM, during which Alpine ice sheets
435 expanded (Hemming, 2004; Ivy-Ochs et al., 2006). Immediately after HE1, a small but
436 significant climatic warming is evident, although lake level data suggests annual precipitation
437 amounts remained relatively low (Magny et al., 2006; Magny, 2013). On the Swiss Plateau
438 localised permafrost degradation and an increase in insect and plant species diversity is
439 evident (Thew et al., 2009; Rey et al., 2017). A similar increase in vegetation density is also
440 evident northwest of the Jura mountains (e.g. Magny et al., 2006). It is possible that if this
441 period corresponds to the first significant regional increase in vegetation after the LGM, such
442 an increase even if relatively small, occurring in an already nutrient-limited environment
443 would initially deplete nutrient availability even further. The effect of this would be a short-
444 term decline in average plant $\delta^{15}\text{N}$ values, followed by a rapid increase, as soils matured and
445 nutrient cycling accelerated (Hobbie et al., 1998; 2005; Ammann et al., 2013).

446 Unlike the nitrogen record, sulphur isotope ratios display a significantly different
447 pattern of change between ice-covered and ice-free areas. Ice-free areas display low $\delta^{34}\text{S}$
448 values ($<-8\text{‰}$) at around 23,000 cal. BP, but then remain consistently high across the
449 deglacial period ($>-8\text{‰}$, except for one outlier). By contrast, in locations that were covered
450 by ice at the LGM, low $\delta^{34}\text{S}$ values ($<-8\text{‰}$) are recorded at around 15,900 to 15,400 cal. BP,
451 increasing to a minimum of -5‰ by 15,000 cal. BP. While some of the scatter in the data
452 can be explained by different patterns of mobility between different species, such influences
453 cannot explain the clear location-specific differences in the temporal sulphur isotopic record.
454 Further, while location-based geological differences may produce different absolute $\delta^{34}\text{S}$
455 values, no relationship is observed between bedrock type, $\delta^{34}\text{S}$, and glaciated/ ice-free
456 location (Figure S4). As such, spatially and temporally variable environmental parameters

457 need to be considered. Temperature-mediated controls on soil mineralisation and
458 volatilisation, and bacterial reduction of sulphur have been suggested to explain temporal
459 changes in herbivore $\delta^{34}\text{S}$ values (Drucker et al., 2011a). However, temperature change
460 alone cannot explain the location-based differences we observe in the data, unless it was
461 acting on a sub-regional scale. Soil maturity has also been linked to differences in herbivore
462 sulphur isotopic ratios (Drucker et al., 2012), but this interpretation is not supported in this
463 instance by the corresponding $\delta^{15}\text{N}$ values.

464 Here, we suggest that the herbivore $\delta^{34}\text{S}$ values reflect local soil conditions that are
465 primarily related to hydrology and microbial activity. Plants acquire sulphur from the soil as
466 sulphate, derived from mineral weathering and atmospheric deposition, and influenced by
467 soil microbial action (Walker, 1957; Krouse, 1980; Robinson and Bottrell, 1997; Newton and
468 Bottrell, 2007). Changing soil hydrological dynamics, particularly the development of water-
469 logged environments that result in anaerobic conditions, can lead to significant differences in
470 plant $\delta^{34}\text{S}$ values brought about by changing bacteria-mediated fractionations (Fry et al.,
471 1982; Trust and Fry, 1992; Groscheová et al., 2000; Nitsch et al., 2019). While the
472 processes that govern soil $\delta^{34}\text{S}$ in relation to changing hydrological conditions are complex
473 and not yet fully understood (Mandernack et al., 2000; Nitsch et al., 2019), we suggest that
474 the different pattern observed between the ice-free and recently-deglaciated regions in post-
475 LGM Switzerland could relate to location specific hydrological dynamics, potentially related
476 ice sheet melt, or more likely, permafrost thaw processes. Indeed, the palaeoenvironmental
477 record from Lake Neuchâtel on the Swiss Plateau identifies a period of permafrost thaw
478 coinciding with considerable instability of the terrestrial landscape and localised marshy
479 conditions, that is largely contemporaneous with the low herbivore $\delta^{34}\text{S}$ values identified in
480 this study at Monruz (Thew et al., 2009). By contrast, while there is greater debate about the
481 distribution and character of permafrost north and west of the Jura, recent studies suggest
482 that if present, it did not persist into the latter part of GS-2.1a (Renssen and Vandenberghe,
483 2003; Bertran et al., 2014; Vandenberghe et al., 2014). This could explain why low $\delta^{34}\text{S}$
484 values during GS-2.1a are not observed in these regions.

485

486 **Conclusion**

487

488 The carbon, nitrogen and sulphur isotopic ratios reported in this study attest to
489 regionally variable environmental development in post-LGM Switzerland. Significant
490 differences between areas that remained ice-free throughout the last glacial cycle and those
491 that were glaciated at the LGM are identified. Deriving such information from archaeological
492 faunal assemblages allows these environmental records to be directly related to human
493 presence in these areas, and to subsistence and settlement strategies in such landscapes,

494 which can more broadly inform on human behavioural ecology in peripheral settings. Our
495 results show the post-LGM period in Switzerland and adjacent regions was characterised by
496 diverse environmental conditions, indicating that a range of habitats and landscapes were
497 available for humans and animals to exploit. Herbivore $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are most
498 strongly influenced by species ecology and dietary behaviours, underpinned by
499 environmental influences. $\delta^{34}\text{S}$ values appear to most strongly correspond to location-
500 specific environmental conditions. Our results suggest that during the period of Magdalenian
501 activity in Switzerland the Swiss Plateau was a dynamic and diverse landscape, while
502 greater environmental stability may have existed north of the Jura Mountains.

503 The absence of high ($>2.5\text{‰}$) $\delta^{15}\text{N}$ values between 15,200 and 14,800 cal. BP, both
504 on the Swiss Plateau and north of the Jura, indicates a regional-scale environmental
505 phenomenon that we suggest is related to the combination of prolonged low temperatures,
506 limited bioavailable soil nutrients, and elevated nutrient demand from increasing vegetation
507 cover. In contrast, low ($<-8\text{‰}$) $\delta^{34}\text{S}$ values occur at different times in different locations, and
508 we suggest that these reflect locally variable hydrological dynamics, either related to
509 changing rates of mineral weathering and soil-bedrock interactions or to changing soil redox
510 conditions, which govern microorganism-mediated isotopic fractionations. We suggest that
511 either interpretation is congruous with the regionally different patterns of ice sheet melt and
512 permafrost thaw.

513

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523 **Author contributions**

524 Conceptualization: RES, HR, SG, TH & IB; Sample collection: HR, SC, DL, WM; Formal
525 analysis: HR, JT, AF, & KLS; Investigation: HR, JT & RES; Supervision: RES; Writing -
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873

874

Project sample code	Species	Element	Collagen yield (%)	$\delta^{13}\text{C}$ (‰)	C/N ratio	AMS Code	^{14}C BP	Calibrated Age BP (2 σ)	Time Period	Ref
Kastelhöhle-Nord, upper horizon										
UPN-232	<i>Bos/Bison</i>	metacarpus	10.4	-19.5	3.3	OxA-V-2794-25C	13,550 \pm 60	16,566–16,107	GS-2.1a	1
			not given	-18.8	not given	ETH-45024	13,435 \pm 50	16,350–15,965	GS-2.1a	2
UPN-214	<i>Equus</i> sp.	phalanx I	2.8	-21.1	3.2	OxA-V-2754-48C	12,880 \pm 50	15,605 – 15,181	GS-2.1a	1
UPN-218	<i>Equus</i> sp.	carpal	8.1	-20.4	3.2	OxA-V-2748-25C	12,560 \pm 50	15,142 – 14,529	GS-2.1a/GI-1e	1
UPN-212	<i>Rangifer tarandus</i>	tibia	5.4	-19.6	3.3	OxA-V-2793-55C	12,380 \pm 50	14,764 – 14,138	GI-1ed	1
			not given	-18.9	not given	ETH-45025	12,395 \pm 45	14,780–14,160	GI-1ed	2
UPN-204	<i>Rangifer tarandus</i>	radius	7.4	-19.5	3.3	OxA-V-2793-54C	12,270 \pm 60	14,740 – 14,129	GI-1ed	1
			not given	-19.8	not given	ETH-45026	12,215 \pm 45	14,265–13,967	GI-1ed	2
UPN-213	<i>Rangifer tarandus</i>	tibia, cut-marked	4.5	-19.6	3.4	OxA-V-2793-56C	12,200 \pm 50	14,260 – 13,935	GI-1ed	1
Monruz and Champréveyres Magdalenian										
n/a	<i>Equus</i> sp.	femur	not given	-20.3	not given	OxA-20699	13,055 \pm 60	15,874–15,349	GS-2.1a	3
n/a	<i>Equus</i> sp.	talus	not given	-20.5	not given	OxA-20700	12,815 \pm 65	15,562–15,092	GS-2.1a	3
n/a	<i>Equus</i> sp.	talus	not given	-20.4	not given	OxA-20701	12,805 \pm 75	15,585–15,053	GS-2.1a	3
Champréveyres Early Azilian										
UPN-240	<i>Cervus elaphus</i>	metatarsal	2.3	-20.9	3.3	OxA-V-2754-49	12,480 \pm 50	15,023 – 14,284	GS-2.1a/GI-1e	1

Table 1. AMS radiocarbon determinations on bone collagen from the sites and levels discussed in the text, and as shown in Figure 2. $\delta^{13}\text{C}$ and C/N ratio measured by IRMS as part of the radiocarbon dating procedure at the Oxford Radiocarbon Accelerator Unit. Calibration of radiocarbon age determinations was performed using OxCal 4.3 (Bronk Ramsey 2017) and the INTCAL13 dataset (Reimer et al. 2013). References (Ref) for dates: ¹this study; ²Leesch and Müller, 2012; and ³Bodu et al., 2009.

Fauna	n	Average $\delta^{13}\text{C}$ (‰)	Max $\delta^{13}\text{C}$ (‰)	Min $\delta^{13}\text{C}$ (‰)	Average $\delta^{15}\text{N}$ (‰)	Max $\delta^{15}\text{N}$ (‰)	Min $\delta^{15}\text{N}$ (‰)	Average $\delta^{34}\text{S}$ (‰)	Max $\delta^{34}\text{S}$ (‰)	Min $\delta^{34}\text{S}$ (‰)
Kastelhöhle Nord, upper horizon										
<i>Bos/Bison</i>	6	-19.9 ± 0.2	-19.7	-20.1	3.2 ± 0.5	4.0	2.6	-6.1 ± 1.9	-4.2	-10.0
<i>Equus sp.</i>	5	-20.8 ± 0.4	-20.2	-21.3	1.6 ± 0.5	2.3	0.7	-2.3 ± 0.9	-1.2	-3.8
<i>Rangifer tarandus</i>	10	-19.7 ± 0.3	-19.4	-20.3	2.8 ± 0.4	3.5	2.3	-5.5 ± 1.5	-1.3	-7.1
Monruz										
<i>Equus sp.</i>	7	-21.0 ± 0.2	-20.8	-21.4	1.8 ± 0.6	2.9	1.1	-12.3 ± 5.2	-3.6	-19.8
<i>Rangifer tarandus</i>	4	-19.8 ± 0.2	-19.6	-20.1	2.8 ± 0.2	3.2	2.6	-13.8 ± 2.9	-10.3	-17.3
Champréveyres										
<i>Cervus elaphus</i>	1	-20.7	-	-	2.4	-	-	(-7.2)	-	-

Table 2. Summary statistics for carbon, nitrogen and sulphur isotopic ratios for each species and archaeological site. Each sample was analysed in duplicated by IRMS at the Scottish Universities Environmental Research Centre. Data in () was deemed unreliable based on standard quality control criteria. Full results are presented in the Supplementary Information 1.

875 **Figure Captions**

876

877 Figure 1: Map showing the location of Monruz, Champréveyres and Kastelhöhle-Nord.
878 Bedrock geology is from the International Geological Map of Europe (IGME 5000; Asch
879 2005). Black line indicates present day country borders. White hatching indicates
880 reconstructed limits of Last Glacial Maximum (LGM) ice sheet extent from Becker et al.
881 (2015). Symbols indicate archaeological sites from which isotopic data used in our
882 discussion comes (full data in Supplementary Information 5), from areas that were covered
883 by ice at the LGM (pink circles) and those in areas that remained ice free throughout the
884 LGM (black squares). Inset: location of Switzerland in Europe indicated by red box.

885

886 Figure 2. Calibrated AMS radiocarbon determinations on faunal bone collagen from sites
887 discussed in the text. Calibration was performed using OxCal 4.3 (Bronk Ramsey 2017) and
888 the INTCAL13 dataset (Reimer et al. 2013) and plotted with the Last Glacial period
889 INTIMATE event stratigraphy and NGRIP ice core $\delta^{18}\text{O}$ values values (top; North Greenland
890 Ice Core Project members. 2004; Rasmussen et al., 2014). Purple = *Bos/Bison*, blue =
891 horse, red = reindeer, green = red deer. Kastelhöhle-Nord dates from this study (OxA codes)
892 and Leesch and Müller (2012; ETH codes); Monruz and Champréveyres Magdalenian dates
893 from Bodu (2009); Champréveyres Azilian dates from this study. Symbols *, †, and
894 ◀ indicate date is on same bone specimen.

895

896 Figure 3. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ values of Kastelhöhle-Nord upper horizon samples. Overlap
897 in values can be seen between *Bos/Bison* (green triangles) and reindeer (*Rangifer tarandus*,
898 orange circles), while horse (*Equus* sp., blue squares) are dissimilar in their isotopic values.
899 Enlarged symbols represent directly dated samples reported in Figure 2.

900

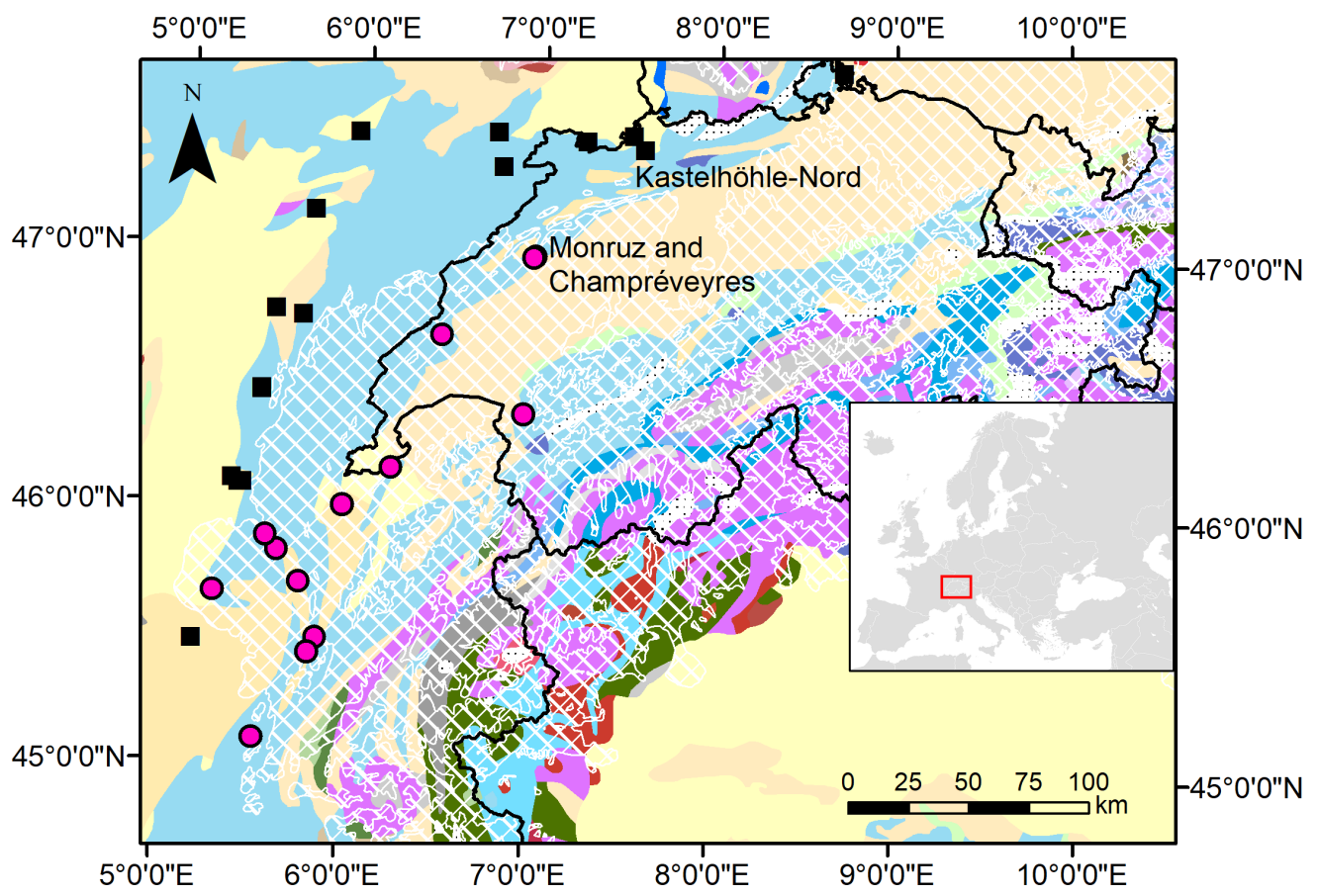
901 Figure 4. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ values from reindeer (*Rangifer tarandus*, circles) and horse
902 (*Equus* sp, triangles) from Kastelhöhle-Nord upper horizon (yellow) and Monruz (green).
903 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values cluster by species, while $\delta^{34}\text{S}$ values cluster by location.

904

905 Figure 5. $\delta^{15}\text{N}$ (middle) and $\delta^{34}\text{S}$ (bottom) isotope values from LGM and Lateglacial fauna
906 (*Bos/Bison*, horse, red deer, reindeer) from the French and Swiss Jura, western Alps and
907 Swiss Plateau (full data in Supplementary Information 5). INTIMATE event stratigraphy and
908 NGRIP ice core $\delta^{18}\text{O}$ values (top; North Greenland Ice Core Project members. 2004;
909 Rasmussen et al., 2014). Black symbols indicate samples from locations that remained ice-
910 free throughout the LGM, pink symbols indicate samples from locations that were ice-

911 covered at the LGM, as displayed in Figure 1. Circles indicate directly dated specimens (by
912 radiocarbon), triangles indicate context dated specimens, where age has been inferred from
913 dates on other faunal specimens from the same site/stratigraphic context.
914

Figure 1



Bedrock geology

amphibolite	granite	meta-sediment group	sand
basalt	granulite	mica schist	sandstone
carbonates, consolidated	gravel	migmatite/anatexite	shale/slate
clay	greenschist	mudstone	siltstone
claystone	limestone	phyllite	syenite
conglomerate	marlstone	plutonic ultramafic group	tholeiitic basalt
diorite	meta-rhyolite group	quartzite	tonalite
dolomite/dolostone	meta-sandstone	rhyodacite	undifferentiated
gneiss		rhyolite	

Figure 2

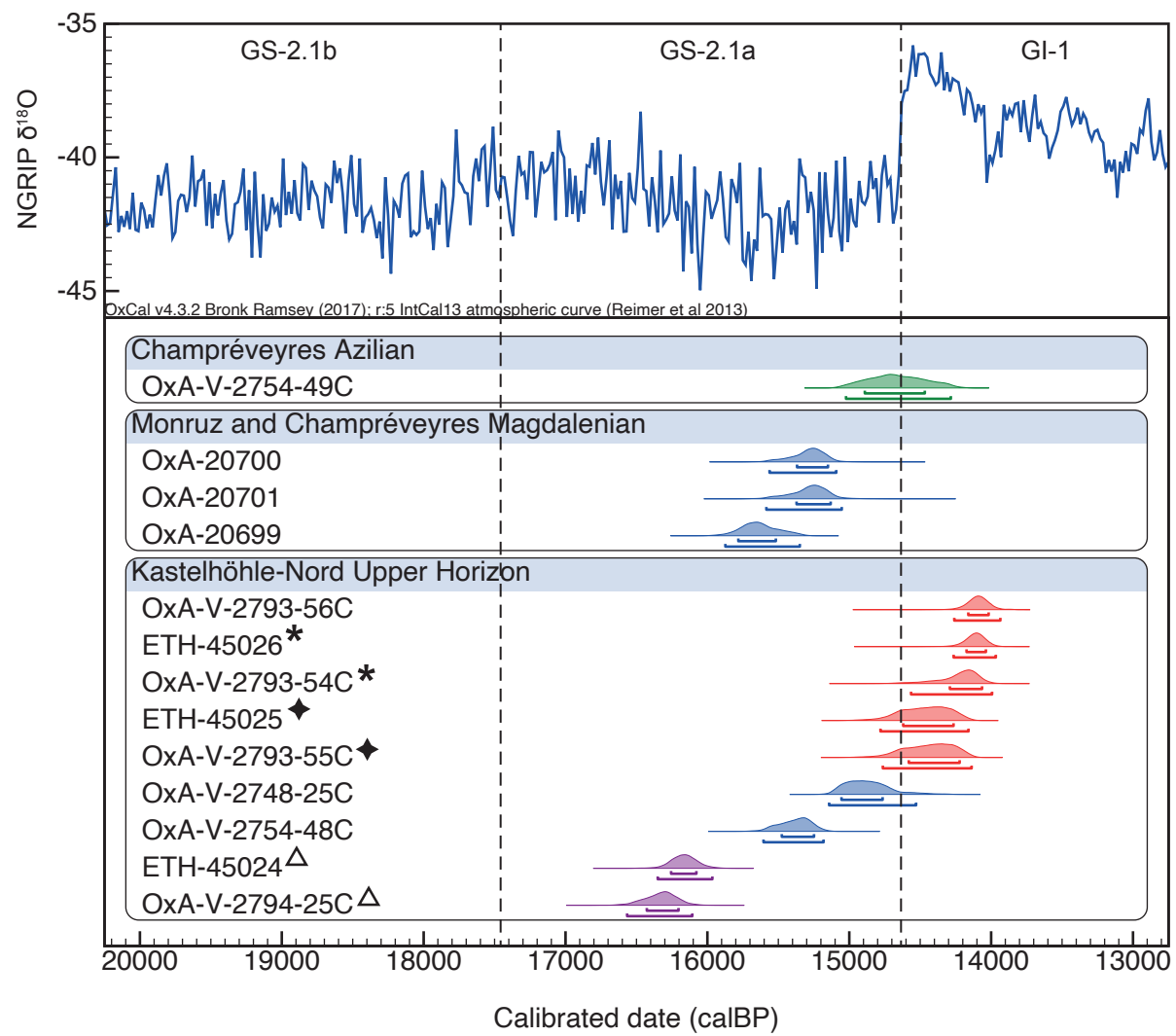


Figure 3

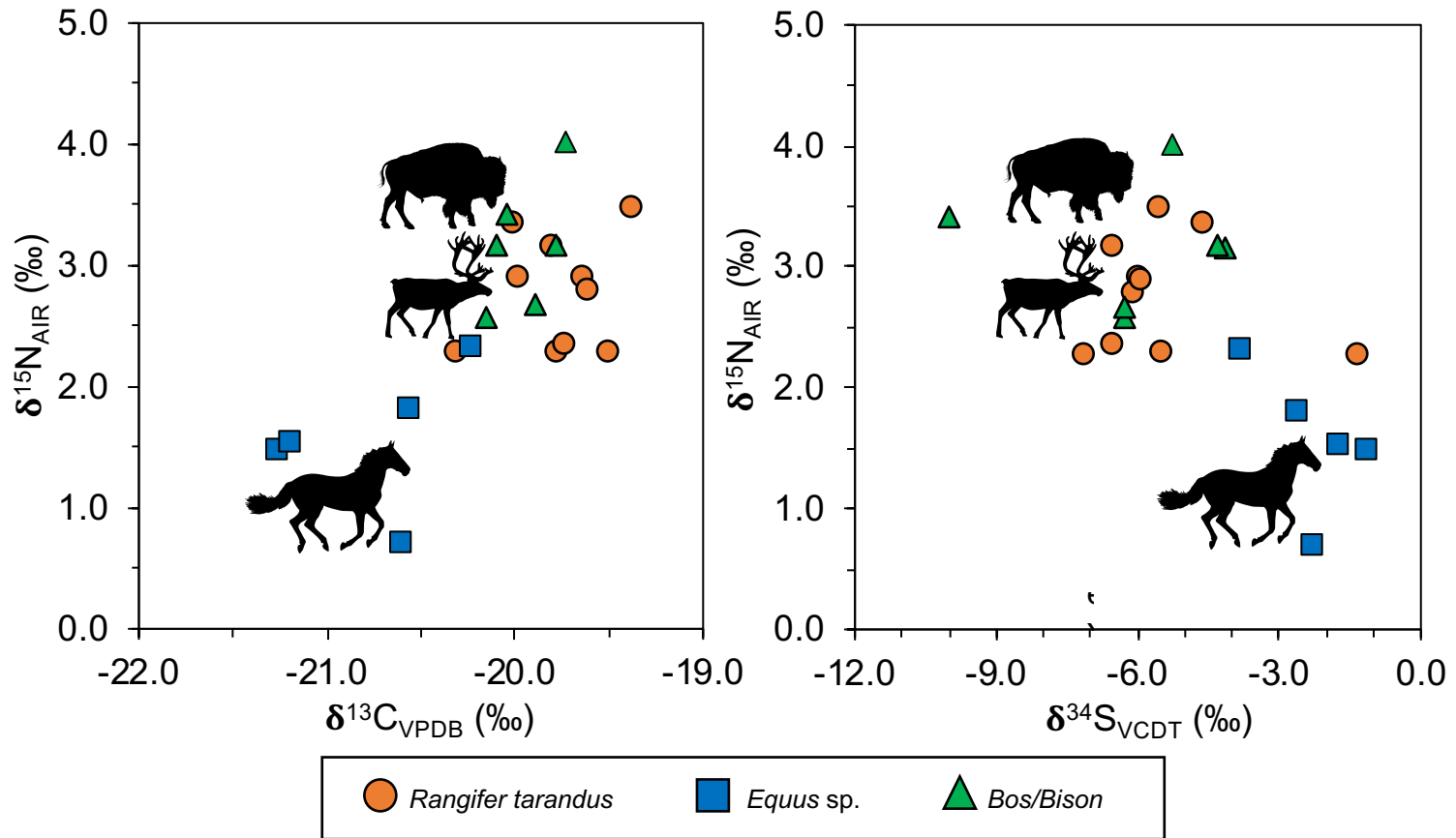


Figure 4

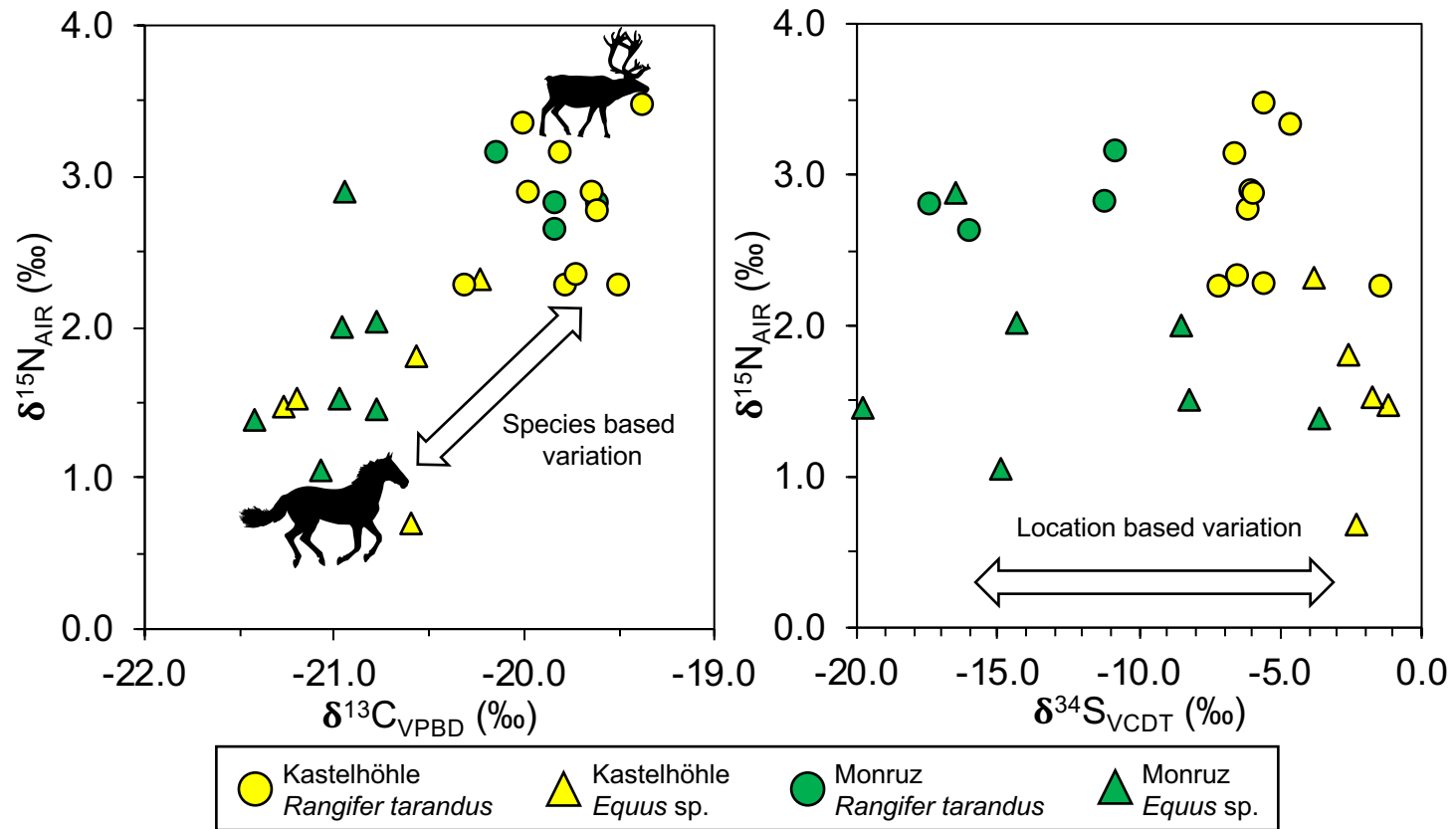


Figure 5

