

1 Mountain agroecosystems long-term trajectories in the North-Western Alps

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19 Abstract

20 Past trajectories of alpine agroecosystems are legacies that we should consider to improve
21 our understanding of current responses to global environmental changes. By integrating
22 archaeology, history and lake sediment-derived ancient DNA records, we reconstructed the
23 nature and intensity of agropastoral activities in the Northwestern French Alps. We
24 investigated their spatiotemporal trajectories and interactions with the erosion dynamic and
25 vegetation cover between 880 and 2440 m a.s.l. Climatic conditions in the upper altitude case
26 study site predominantly controlled plant community composition and erosion. In contrast,
27 the other sites were influenced mainly by (agro-)pastoral activities. There, the first significant
28 human-driven changes in plant community composition occurred earlier (Mid-Late Bronze
29 Age or Iron Age) above ca. 2000 m a.s.l. than below (Early to High Middle Ages). This pattern
30 mirrors the altitudinal temporal trajectory of (agro-)pastoral activities development.

31 Regarding erosion trajectories, all sites show stable non-degraded and degraded states
32 separated by a transition phase caused by (agro-)pastoral activities. However, this does not
33 necessarily occur when the first significant or the most intense activities develop due to the
34 different sensitivities of the systems. From the High Middle Ages or Late Middle Age/Modern
35 Period, resistance or resilience phases relative to erosion are evidenced for all agroecosystems
36 (other than the upper site). These patterns highlight adaptations of agrarian socio-
37 ecosystems, possibly thanks to soil management strategies with soil protection and/or just
38 being the consequence of changes in practice for other purposes. Whether in terms of plant
39 community composition or erosion, our trajectories evidence the vulnerability of systems
40 above ca. 2000 m a.s.l. to changes in human activities and variations in climate.

41 Keywords

42 Alpine agro-ecosystems, soil erosion, landscape, trajectories, lake sediment ancient DNA
43 (*sedaDNA*), inter-disciplinarity

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47 1 Introduction

48 Since prehistoric times, mountain environments such as the Alps, have attracted
49 human populations; hunting, gathering, pastoralism, arable agriculture and mining
50 constituting key activities (Walsh and Giguet-Covex 2019). People have been attracted to
51 these *a priori* “hostile territories”. While complex topography and harsh climates render
52 access and mobility difficult, these physical characteristics also result in a significant diversity
53 of ecological niches across short horizontal distances, primarily due to the altitudinal gradient
54 (Archipiélago vertical in the Andes, Murra 1976; Guillet et al. 1983; Lomolino 2001). This
55 diversity within mountain ecosystems facilitates the production of a wide range of goods and
56 services (Grêt-Regamey et al. 2012). These physical characteristics also render landscapes
57 highly susceptible to slope processes (i.e. rockfalls, avalanches, erosion) and other natural
58 risks such as torrential floods (Giguet-Covex et al. 2012; Wilhelm et al. 2013). Furthermore,
59 climate changes are often exacerbated in mountain areas, as we see in the context of current
60 global warming (Beniston 2006; Hock et al. 2019). Consequently, mountain ecosystems are
61 susceptible to natural or human-driven environmental and climatic changes. Environmental
62 and climate conditions can influence lifeways, land use, and landscape management (Guillet
63 et al. 1983; Balée 2006). We might consider how these conditions influence the choices made
64 by alpine farmers and societies: Such choices might comprise adaptation by developing new
65 subsistence strategies (activities/practices) and/or migration to establish settlements
66 elsewhere. In a worst-case scenario, a society might “disappear”, not a choice but a
67 consequence. Characteristic forms of adaptation to erosion include the construction of
68 terraces for crops, which also increase water storage in soils. Another form of adaptation that
69 overcomes seasonal grass/fodder shortages is transhumance (as defined in Gilck and Poschlod
70 2019), where herds and flocks pasture at high-altitude during the summer and stay in the
71 valleys or more remote lowlands during winter.

72 The concept of “trajectories” is an interesting framework that facilitates the analysis
73 of these complex systems (Dearing 2008). By definition, in physics, a trajectory is a pathway
74 that is influenced by several multiscalar factors. The path of the considered entity is defined
75 as a function of position in the reference system and momentum. By analogy, we assume that
76 the trajectory of any socio-environmental system is in part conditioned by initial physical
77 properties (geology, topography, climate, soils, hydrology) and that its subsequent pathway
78 and speed of change are also influenced by multiscalar factors that are likely to change over
79 time (Toulouse et al. 2017). The representation of such trajectories can then be used to
80 evidence shifts in system functioning, such as degradation, resilience and resistance phases or
81 adaptation processes and the legacy of past human activities on the current ecosystem state
82 (Dearing 2008; Scheffer et al. 2012).

83 Historical archives, archaeological research, and lake-sediment analyses provide
84 complementary data for investigating complex human-climate-environment interactions

85 (Dearing et al. 2008; Gilck and Poshold 2019). Despite the large number of multi-proxy and
86 interdisciplinary studies focused on alpine societies and their environmental impacts (Wick
87 and Tinner 1997; Schmidt et al. 2002; Koinig et al. 2003; Giguët-Covex et al. 2011; Vanni re et
88 al. 2013; Roepke and Krause 2013; Brisset et al. 2013; Dietre et al. 2014; Walsh et al. 2014),
89 questions about the precise nature of agropastoral activities, their spatiotemporal trajectories
90 and their interactions with environmental/climatic changes have not yet been fully resolved.
91 This is primarily due to the lack of suitable proxies for the precise documentation of human
92 activities at local scales and over long periods. However, in the current context of
93 unprecedented global changes (climate, land-use, pollution, decline of biodiversity), detailed
94 studies with long-term perspectives of these agrarian socio-ecosystems are of primary
95 importance.

96 Here we present an interdisciplinary synthesis that documents the altitudinal
97 variability in the history of agro-(sylvo)-pastoral activities and the trajectories of mountain
98 agroecosystems. The synthesis encompasses five sites covering the altitudinal range between
99 874 to 2447 m a.s.l. in the North-Western Alps. The dataset is derived from lake sediment
100 ancient DNA (sedaDNA) analyses focused on plants and mammals and sedimentological or
101 geochemical analyses for local-scale reconstruction of the precise nature of agropastoral
102 activities and their impacts on plant community composition and erosion dynamics. Analyses
103 of coprophilous fungi spores and selected pollen taxa are also included where available to
104 help constrain the history of agricultural and pastoral activities. By integrating all indicators of
105 agropastoral activities, we propose a synthetic index of the (agro-)pastoral intensity to
106 facilitate the analysis of the agroecosystem trajectories. Moreover, some study sites have
107 benefited from archaeological and historical research.

108 2 Study sites

109

110 Mountain societies have developed specific activities across the different vegetation
111 belts (Guillet et al. 1983). The valley bottoms and sub-montane to montane belts can be
112 exploited for cultivation, hay/fodder production, livestock farming and forestry, whereas
113 subalpine areas are dedicated to pastoralism and, on occasion, haymaking. This specificity of
114 mountain landscapes has led to the development of seasonal vertical mobility from the
115 valleys, or other regions, such as lowland Provence, to the high-altitude pastures, i.e. the
116 "Alpages". Our study sites are distributed across these vegetation belts, from the montane to
117 the alpine/nival belts (Fig. 1; Table 1). They cover different massifs and valleys from the
118 external to the internal Alpine zones, i.e. with different accessibility, geological and thus
119 topographical features and climatic conditions (internal massifs are drier and warmer than
120 external massifs; Theurillat and Guisan 2001). The external subalpine massifs comprise the
121 Bauges massif with Lake La Thuile (874 to 1209 m a.s.l.) and the Haut-Giffre massif with lakes
122 Gers (1540 to 2385 m a.s.l.) and Anterne (2063 to 2494 m a.s.l.), the Vallon de Sales (1600 m
123 to 2733 m a.s.l.) and Anterne-Pormenaz massifs (1700 to 2700 m a.s.l.). Lakes Verney (2088
124 to 2930 m a.s.l.) and Savine (2447 to 3312 m a.s.l.) are in the inner massifs of Grand Paradis in
125 the Aoste Valley (Italie) and Mont-Cenis in the Maurienne Valley (France), respectively. More
126 details on geology, current vegetation cover and human activities are provided in
127 Supplementary material 1. The period covered by the records varies between 4600 years at
128 Verney and Gers, and 6000 to 6500 years at La Thuile, Anterne and Savine.

129

3 Material and methods

3.1. (agro-)pastoral activities and activity intensity

The *sed*aDNA data from the five lakes were produced following similar laboratory protocols. There are, however, some differences in the extraction procedure and the number of PCR replicates across certain lakes (Supplementary table 1). The same treatment procedure (bioinformatic and subsequent filtering) was applied to high-throughput sequencing data (Giguët-Covex et al. 2019). Taxa used for the reconstruction of (agro-)pastoral history for each lake are shown in Fig. 2. Taxonomic, taphonomic or methodological gaps from the DNA record were compensated via reference to selected pollen taxa from La Thuile and coprophilous fungi spore analyses from Gers and Verney (Supplementary table 1, Supplementary figure 3). Details regarding the strengths and weaknesses associated with each method are provided in Supplementary material 2.

To analyse agroecosystem trajectories, we also developed a synthetic index reflecting the intensity of (agro-)pastoral activities. The proposed index is the aggregation of all (agro-)pastoral activity proxies (Supplementary table 1). The selected markers are standardised via Z-scores. Then, the synthetic index is obtained by calculating the mean of the standardised proxies. The hypotheses underpinning this index are 1) the different sensitivities of the proxies due to taphonomic/methodological issues (*Sporormiella* more sensitive to low-intensity activities than animal DNA; Giguët-Covex et al. 2019) and 2) ecological preferences related to the intensity of activities (*Plantago sp.* for extensive and intensive activities and *Rumex sp.* for intensive activities and/or the presence of resting places). Moreover, this index considers that the more diversified the activities, the greater the intensity of the activities. One criticism of this index, when it comes to assessing human impact on plant community composition and soil stability, is that it does not consider deforestation due to difficulties in discriminating human- and climatic-induced forest cover loss on sites around the tree line. Therefore, we note that the intensity of human activity reflected in our index is underestimated for some periods.

3.2. Plant community composition

To assess the overall trajectories of plant communities, we performed nonmetric multidimensional scaling (NMDS) using the Bray-Curtis dissimilarity indices with the function *metaMDS* from the VEGAN package v2.5.6 in R (Oksanen et al., 2013; Kruskal 1964; Legendre and Legendre 2012). The dataset is based on the number of DNA copies (i.e. the number of DNA reads) for each taxon (N.B. cultivated plants at La Thuile were not included in the NMDS as we analyse the impact of agropastoral activities on plant communities). PCR replicates were grouped with two replicates by sample, i.e., by age. This treatment reduces “noise” in the dataset due to PCR stochasticity and yields a more robust analysis. A colour code was used to discriminate the different cultural periods, and a spatial median for each phase was determined using the function *ordispider* from the VEGAN package. The position of this median was then used to draw the trajectory of plant communities. This NMDS analysis and representation facilitate the identification of similarity or dissimilarity in plant community composition between the samples of different ages: the closer two points are, the more similar the composition and vice versa.

3.3. Erosion proxies

177 For the reconstruction of erosive processes, we selected different erosion indicators
178 (Supplementary table 1); these depend on each study area's geomorphologic and sedimentary
179 contexts. Other than Lake La Thuile, the lakes presented in this study are dominated by detrital
180 clastic and organic matter. In lakes Savine, Anterne and Gers, many of these detrital inputs
181 are transferred to the lake during flood events. These events result in specific sedimentary
182 deposits characterised by fining-upward facies from well-sorted coarse particles at the bottom
183 to a clayey cap (Arnaud et al. 2002). Consequently, in these contexts, the flood deposit
184 frequency and the total sedimentary accumulation, i.e., the continuous sedimentation rate
185 and the flood deposit thickness, are pertinent erosion proxies. Their signal will depend on the
186 precipitation frequency and intensity and sediment availability, which is greatly influenced by
187 human land use (Giguet-Covex et al. 2012). To integrate the entire erosion dynamic and assess
188 the complexity of the underlying mechanisms, mean values for the different cultural periods
189 of each of these proxies were assessed (detailed discussion in Supplementary material 6). In
190 lake Verney, where flood deposits are absent, the sedimentation rate represents a reliable
191 proxy of the erosion dynamic (Bajard et al. 2017a). However, in Lake La Thuile, where bio-
192 precipitation of carbonates and aquatic organic matter were also significant during certain
193 periods of low erosion (Bajard et al. 2017b), titanium is preferred because it is a purely detrital
194 element not affected by weathering processes. To analyse the erosion trajectories in response
195 to the intensity of (agro-)pastoral activities, these site-specific erosion proxies were
196 standardised (Z-scores), and mean and standard deviation values for each cultural period were
197 calculated.

198
199

200 **3.4. Archaeological and historical research**

201

202 Archaeological surveys and excavations have been carried out in or close to three of the
203 lake catchments (Fig. 1; 4). Between lakes Gers and Anterne in the Vallon de Sales, a research
204 program has documented human occupation from the Late Middle Ages to the contemporary
205 period (Guffond and Mélo 2018), including zooarchaeological analyses (Fig. 4; Supplementary
206 table 2). This research is supplemented by interpreting historical documents (land registries,
207 old photographs, texts), which facilitate understanding human occupation and land-use.
208 Adjacent to this area, in the massifs of Anterne and Pormenaz, archaeological investigations
209 identified several phases of activity from the Neolithic to the Modern Period (Rey et al., 2022;
210 Fig. 4). Around Lake Verney, on both sides of the Petit Saint-Bernard pass (Fig. 1), from 700 to
211 2500 m a.s.l., the archaeological fieldwork discovered sites dating from the Neolithic to the
212 Middle Ages (Crogiez-Pétréquin 2016; Rey and Moulin 2019; Rey and Collombet 2020).

213

214 **4 Results and interpretations**

215

216 **4.1. Detailed history of agropastoral activities: an altitudinal evolution**

217

218 The synthetic index of (agro-)pastoral activities, represented by box plots for each
219 cultural phase and lake, outlines an altitudinal trajectory over time with different activity
220 intensities across the different vegetation belts (Fig. 3). This evolution is discussed in the light
221 of proxies indicating the nature of activities inferred from, lake sediments (Fig. 2,

222 Supplementary figure 3) along with archaeological (Fig. 1, 4) and historical research carried out
223 in the vicinity of the lakes or from neighbouring Alpine landscapes.
224

225 **Late Neolithic Period.** In mid to high-altitude areas, evidence for pastoral activities is
226 negligible or uncertain, leaving the debate open regarding the existence of high-altitude
227 pastoralism during this period (Schwörer et al. 2015; Dietre et al. 2017, 2020; Hafner and
228 Schwörer 2018). Indeed, the low level of *Bos* DNA (genus of wild and domestic cattle) detected
229 at Savine and Anterne at 3300 and 2900 BC, respectively, might be attributed to; the actual
230 presence of cattle, sporadic contamination, or the presence of Aurochs (Fig. 2). Moreover, at
231 Anterne, the decrease in tree cover (*Pinus sp.* DNA) and increase in erosion during this period
232 could be due to pastoral developments and the transition toward the Neoglacial Period. At
233 Gers, the low concentration of *Sporormiella sp.* spores could also reflect low levels of pastoral
234 activity or the presence of wild herds, as *Sporormiella sp.* develops on herbivores' faeces
235 (Davis and Shafer 2006). The absence of archaeological evidence, whether in the subalpine
236 Bauges and Haut-Giffre massifs or around the Petit Saint-Bernard Pass (Fig. 4; Rey 2016; Rey
237 et al. 2022; Rey and Moulin 2019), supports the absence or low intensity of pastoral activities
238 in the high altitudinal zones during the late Neolithic. In these areas, as in other subalpine
239 massifs (e.g. Chartreuse, Martin et al. 2012), artefacts are often instead associated with
240 hunting and gathering activities or the collection of mineral resources.

241 In the montane belt at La Thuile (Bauges massif), the landscape was dominated by fir and
242 alder forest, probably comprising some forest clearings as suggested by the decrease in *Abies sp*
243 DNA (Supplementary figure 3). In this context, the detection in several samples, but few
244 replicates, of *Bos* and *Ovis* DNA might suggest the development of a sylvo-pastoral system. This
245 extensive practice (a system with relatively few animals spread across a relatively large area) is
246 expected to have a low impact on erosion (titanium, Supplementary figure 3), which, in turn, is
247 not conducive to DNA transfer to the lake. Moreover, such a practice reduces animal DNA
248 production. These conditions can explain the low animal DNA detection and low intensity of
249 pastoral activity (Fig. 2, 3). In another subalpine massif (Vercors, Fig.1 star 1), archaeobotanical
250 and zooarchaeological analyses from a sheepfold cave at 580 m a.s.l. also evidence cattle and
251 caprine fodder derived from trees and shrubs from the pastures and/or within the shelter
252 (Delhon et al. 2008). Sheepfold caves also exist in the Bornes subalpine massif (La Balme de Thuy,
253 620 m a.s.l.; Fig. 1 star 2; Ginestet et al. 1984; Remicourt 2009) and in the Haute Maurienne (Les
254 Balmes à Sollières-Sardières, 1350 m a.s.l.; Fig. 1 star 3; Vital and Benamour 2012; Martin and
255 Lundström 2012). In the Tarentaise area, pastoral activities are also evidenced by
256 zooarchaeological remains of sheep, goat and cattle as early as the mid-Neolithic (4300-3300 BC,
257 Le Chenet des Pierres at Bozel, 940m a.s.l.; Fig. 1 star 4; Chiquet 2019).

258
259 **Mid to Late Bronze Age.** At all high-altitude sites (Savine, Verney and Anterne), 1600-1000
260 BC corresponds to the start of significant pastoral activities (Figs. 2, 3). This is mainly evidenced
261 by the high and regular detection of DNA from the ruderal *Plantago sp.* (Fig. 2). At Anterne, this
262 hypothesis is strengthened by the presence of *Ovis* DNA, albeit in low quantities, probably due
263 to taphonomic issues (Supplementary material 2.1.) and a tipping point recognised in the erosion
264 dynamic, characterised by a permanent increase in flood deposit frequency and thickness
265 (Supplementary Fig. 3; Giguet-Covex et al. 2011). At Verney, the concentration of *Sporormiella*
266 *sp.* spores suggests extensive pastoral activities as early as 2250 BC, but more intensive activities

267 from 1100 BC. Similarly, in a Swiss lake located in the upper subalpine belt (Sulsseewli at 1922 m
268 a.s.l.; Fig. 1), the first occurrence of sheep DNA is dated to 1850 BC, while significant sheep DNA
269 detections appear from 1450 BC (Garcés-Pastor et al. 2022).

270
271 Unlike the Southern French Alps, where several high-altitude enclosures have been
272 discovered (Walsh and Mocci 2011), the equivalent archaeological evidence is limited in the
273 North. The remains of a wooden structure dated to the mid (1630-1450 BC) and late Bronze Age
274 (1410-1220 BC) have been excavated close to Anterne at Le Laouchet (1950 m a.s.l., Fig. 3; Rey
275 et al. 2022). An ethnoarchaeological study in the Italian Alps showed that non-dairying
276 pastoralists are less visible in the landscape than dairying pastoralists (Carrer 2016). This
277 ethnoarchaeological analogy might help explain the relative dearth of archaeological evidence
278 for pastoralism in some areas.

279
280 At lower altitudes, at Gers and La Thuile, low-intensity pastoral activities are apparent
281 (Fig. 3). They are evidenced at Gers by low numbers of *Sporormiella sp.* spores and low detection
282 of *Plantago sp.* DNA. A similar pattern in the pollen record of *Plantago sp.* is observed at La Thuile
283 (Supplementary figure 3; Bajard et al. 2016). However, no specific pastoral indicators are
284 available for this period (no *seda*DNA was detected for taphonomic reasons, and no *Sporormiella*
285 *sp.* analyses were undertaken). Combined, these results from the low-to-mid altitudes suggest
286 small-scale pastoral activities or practices that differ from those seen at higher altitudes (Fig. 2,
287 3).

288
289 **Iron Age and Roman Period.** During the Iron Age, (agro-)pastoral activities reemerge at high
290 altitude (Savine, Verney, Anterne), while they remain low at lower altitude (Gers and La Thuile)
291 (Fig. 3). At Anterne and Verney, sheep and/or cattle DNA is detected along with *Plantago sp.* (Fig.
292 2). At Verney, there are also high levels of *Sporormiella sp.* spores and DNA from *Rumex sp.*, a
293 nitrophilous plant which may indicate the presence of significant herds/flocks and/or stalling
294 areas. In the Eastern Swiss Alps, high-altitude dairy practices have been inferred from the
295 analyses of lipids in Iron Age pots (Carrer et al. 2016). Together, these results support the notion
296 of the increasing value of “Alpages” and may reflect the economic development of alpine
297 societies.

298 The Roman Period is characterised by an intensification of pastoral activities from the
299 subalpine to the alpine/nival belts (Savine, Verney, Anterne and Gers), i.e. over a wider altitudinal
300 range (Fig. 3). Both sheep and cow are present in the records from Anterne and Savines (Fig. 2).
301 However, only cow DNA is recorded at Verney, Gers, and La Thuile, which might reflect the
302 increased economic importance of this domesticate (Fig. 2). Such a pattern is also observed at
303 Sulsseewli (Garcés-Pastor et al. 2022). The synthetic index may underestimate the intensity of
304 pastoral activities at Gers and Anterne due to taphonomic issues affecting the DNA records
305 (Supplementary material 2.1.).

306 Archaeological data from some of our study areas attest to significant levels of human
307 activity and movements into the “Alpages” during the Iron Age. A trend that increased during the
308 Roman Period. Around Anterne, several archaeological structures were dated to the Iron Age and
309 Roman Period (Fig. 4; Rey et al. 2022). At Verney, ruins of Roman buildings, a possible road station
310 of the “Via Romana” (Crogiez-Pétréquin 2016), indicate the movement of people across the Petit
311 Saint-Bernard pass, perhaps engaged in trade activities. Indeed, the integration of our study area
312 into the Roman Empire triggered the growth of commercial activities and networks due to the

313 significant requirement of the Roman Empire for wool and meat and its appetite for alpine cheese
314 (Frayn 1984; Segard 2009; Pliny the Elder, “Natural History” 77-79 AD, book XI, XCVII.).

315
316 The low levels of cattle DNA, *Plantago* and *Rumex sp.* at La Thuile (montane belt) reflect
317 lower pastoral pressure than that seen in the higher altitudes during the Iron Age and Roman
318 Period (Fig. 2). However, other activities, i.e. the cultivation of fruit trees (*Prunus sp.*) and some
319 cereals, are recorded, revealing the development of an agropastoral system (Fig. 2). The
320 disappearance of fir DNA is also notable.

321
322 **End of the Roman Period and Early Middle Ages.** During this period, in the alpine/nival
323 and upper subalpine areas, pastoral activities decline (Fig. 2, 3). A trend characterised by the
324 absence or low detection of animal DNA (*Bos* or *Ovis*) (Fig. 2). Short phase(s) of pastoral revival
325 are suggested at all sites, but they are not always contemporary. Around Anterne,
326 archaeological excavations have revealed new cabins, some with enclosures, but only below
327 1950 m a.s.l., i.e. lower than Lake Anterne (Fig. 4; Rey al. 2022). Below, at Gers, coprophilous
328 fungi spores, *Plantago sp.* and *Rumex sp.* DNA suggest significant activity during the Early
329 Middle Ages (500 to 900 AD; Fig. 2). In the same vegetation belt, around Lake Bénit (Fig. 1), the
330 coprophilous fungal spore record also suggests a high level of pastoral activity (Bajard et al.
331 2018). In the montane belt at La Thuile, this period corresponds to a significant development
332 in agricultural activity (Fig. 3). We see cereal cultivation, broad beans, and hemp, which may
333 reflect retting activities and a decline of forest cover affecting fir, alder and beech (Fig. 2; Bajard
334 et al. 2017b).

335 Interestingly, the apparent post-Iron Age/Roman period movement of economic
336 activity towards the lower altitudes, i.e. in the montane and lower subalpine belts, is also
337 reflected in the medieval toponymy of farms and pastures and terms associated with alpine
338 farming in the Austrian Alps (Gilck and Poschlod 2019). The first half of the Early Middle Ages
339 corresponds to the so-called “Dark Ages Cold Period” (Helama et al. 2017). These climatic
340 conditions may have partly explained the focus of more intense activities toward lower
341 altitudes. The probable shorter summer season might explain the apparent decrease in
342 activities in the highest mountain pastures.

343
344 **High Middle Ages to the Early Modern Period.** This period corresponds to a new
345 intensification of human activity across the montane to the alpine belts (Fig. 2, 3). At La Thuile
346 (montane zone), activities diversified with the cultivation of fruit trees, such as pears, walnuts,
347 plum or cherries, and grapes, along with the intensification of livestock farming (Fig. 2). During
348 the coldest phase of the Little Ice Age (LIA), from 1500 AD, grapes disappeared from the DNA
349 record but not the pollen signal, which indicates that these cultures still existed regionally
350 (Supplementary figure 3). As the *sedDNA* represents a local signal, this result can be
351 interpreted as reflecting the impact of climate cooling on the choice of suitable crops and on
352 the development of the wine-growing “terroirs”. At this time, the cultivation of other fruit
353 trees also decreased.

354 Higher up, in the upper subalpine/alpine areas, the lake *sedDNA* signals from *Bos*, *Ovis*
355 and *Capra hircus*, evidence a new phase of intensive grazing activity (Fig. 2). The presence of
356 cattle, sheep and goats, the latter only detected in the sediments from Gers, is also attested
357 by archaeozoological evidence from excavations in the Vallon de Sales (Fig. 4, Supplementary
358 table 2). Bones from pigs and equids were also identified. Interestingly, DNA from all lake
359 sediment records indicate the predominance of cattle over sheep from the High/Late Middle

360 Ages; the moment at which the proportion of cattle/sheep change varies across each lake
361 catchment, but the dates have to be considered with caution due to uncertainties in the age-
362 depth models and non-continuous sampling (Fig. 2). Other than at Verney, this change seems
363 to be progressive, with a transition phase characterised by a decrease of sheep DNA and an
364 increase of cattle DNA between the 11th and 13th (La Thuile, Anterne) or 13th and 15th centuries
365 (Gers). The total disappearance of sheep in the DNA records follows this. This pattern of change
366 in the composition of domesticates is reflected in fifteenth-century historical documents in the
367 Northern French Alps (Carrier, 2013; Dodgson, 2019). In the Swiss Alps, this change in
368 composition is also recorded in historical archives dating to the end of the 13th century (Aerni
369 1991) and lake sediments between the 11th and 13th centuries, with a total disappearance of
370 sheep DNA from the 17th century (Sulsseewli, Garcés-Pastor et al. 2022). Socioeconomic
371 demands can explain this change in animal composition. Indeed, from the 11th to the
372 12th centuries, monks, lay landlords, and wealthier peasants developed commercial sheep
373 farming, primarily due to the expanding market for wool (Dodgson, 2019). Then, from the 13th-
374 15th centuries, the predominance of cattle herds is explained by the increasing lowland-urban
375 demand for alpine cheeses, butter, and milk (Aerni, 1991; Dodgson, 2019). Around Anterne,
376 this change in animal composition coincides with the appearance of complex structures
377 composed of cabins with several rooms and contiguous enclosures of different sizes (Fig. 4;
378 Rey et al. 2022). These structures may reflect the development of mountain pasture farms,
379 where the milk is processed to make cheese and other secondary products. In the Vallon de
380 Sales, there was a change from large pastoral cabins to smaller, contiguous cabins between
381 the 14th and 16th centuries (Fig. 4), which also suggests a change in the pastoral organisation
382 of this small valley (Guffond and Mélo 2018). This correlated with the faunal remains that show
383 lower numbers and reduced diversity in the post-medieval period (15th-16th centuries) (Fig. 4;
384 Supplementary table 2). Here, we see heterogeneity in the development and evolution of
385 mountain pastoral systems at small spatial scales (Vallon de Sales vs Anterne/Pormenaz).

386
387 From the 10th century, we can distinguish three peaks of enhanced pastoral activity
388 across all palaeo-records based on the synthetic index and/or animal DNA detection (Fig. 2,
389 grey areas a, b, c). They are not all synchronous, possibly due to dating uncertainties and the
390 different sampling resolutions, but overall, the first peak runs from the 10th to 13th centuries,
391 the second from the 13th to 16th centuries, and the last from the 17th to 19th centuries. This last
392 peak is associated with an increase in the number of contiguous cabins and zooarchaeological
393 remains at Sales, along with hamlets of chalets around Anterne (Fig. 4, Supplementary table
394 2). All these data mirror the increase in communities constituted by families and their livestock,
395 attested to in the historical documents associated with the commune (Sixt-Fer-à-Cheval) (Mélo
396 pers. Com.; Supplementary figure 4). This demographic increase is not an isolated event, with
397 population increases apparent across the Northern French Alps (Crook et al. 2004; Elleaume
398 et al. this issue). While all data types suggest increases in settlement and economic activities
399 during this period, activity intensity is not very high, especially when compared with previous
400 peaks. Different practices or a period of summering reduced by the colder conditions of the
401 LIA (Büntgen et al. 2006) might explain this apparent contradiction.

402
403 **Late Modern to Contemporary Periods.** From the 19th/20th centuries, all sites
404 show a decline in pastoral activity intensity (Fig. 2, 3). The decline is seen in the records of cattle
405 DNA and *Sporormiella sp.* spores (Fig. 2). Furthermore, in the montane belt, arable activities
406 decrease. These reduced levels of agropastoral activity correspond to a demographic decline

407 (Supplementary figure 4) due to industrialisation, technological developments, improvements in
408 modes of transport, world wars, and urbanisation. These trends were seen across the entire
409 Alpine arc (Carrer 2016; Andres 2016). Global climate warming and agropastoral decline allowed
410 forest recovery across low to mid-altitude areas (Supplementary figure 3; Bajard et al. 2016;
411 Tasser et al. 2017; Elleaume et al. this issue).

412
413

414 **4.2. Relationships between agropastoral activities and landscape trajectories**

415 In order to assess the impact of human activity on changes in plant community
416 composition trajectories, the NMDS analysis and mean values of the synthetic index of (agro-
417)pastoral activities were combined (Fig. 5; Supplementary figure 5). The spatial median for
418 each cultural phase in the NMDS is used to position a circle of proportional size relative to the
419 mean intensity of (agro-)pastoral activities. We also compare erosion proxies with the intensity
420 of agropastoral activities to assess the impacts of the agropastoral activities and practices on
421 the erosion trajectory (Fig. 6; Supplementary figures 7, 8). This approach facilitates the
422 assessment of similarities and differences in the evolution and functioning of the different
423 landscape systems through time and allows the proposition of a testable general model for
424 future research.

425

426 **Plant composition trajectories.** At Savine, i.e. in the alpine/nival belt, no clear temporal
427 trajectory appears in the NMDS analysis (Fig. 5). However, the samples corresponding to the
428 “pre-anthropogenic” period on the one hand, and those corresponding to the Modern Period, on the
429 other, form two obvious different sample groups. These periods match the two climatic extremes
430 of the Holocene, i.e. the Holocene Climatic Optimum (HCO, 8000 to 5400 cal. BP) and the LIA
431 (1300-1850 AD). Moreover, the points corresponding to the Late Neolithic represent a transition
432 between the HCO and the Neoglacial period. These results suggest that climate played an
433 important role in shaping plant community changes in these alpine/nival areas (see more details
434 in Supplementary material 5.2.), which agrees with our understanding of high mountain
435 ecosystems (Theurillat and Guisan, 2001; Körner 2003; Lamprecht et al. 2018). The scattered
436 distribution corresponding to the other periods, mainly from the mid-Bronze Age, suggests the
437 presence of a mosaic landscape, possibly promoted by the development of pastoral activities.
438 For the other study sites, the plant community composition trajectories follow the cultural
439 phases characterised by changes in the intensities of (agro-)pastoral activities (Fig. 5,
440 Supplementary figure 5). As a general trend, we observe that the dissimilarity between the initial
441 plant communities, and those communities in later periods, usually increases with time. The
442 primary shifts in plant composition in the upper part of the subalpine and alpine belts occurred
443 during the Middle Bronze Age at Verney and the Late Iron Age at Anterne. Other significant shifts
444 in the plant composition trajectory are recorded later, i.e. during the Roman Period, Early Middle
445 Ages, High Middle Ages and Late Middle Ages or the Modern Period (Fig. 5, Supplementary figure
446 5). At lower altitudes, in the montane to the lower subalpine belts, the principal shifts in plant
447 composition trajectories occurred later, from the Early or Late Middle Ages. More subtle changes
448 are also seen in the Iron Age and Roman Period as well as the Early Middle Ages at Gers (Fig. 5,
449 Supplementary figure 5). As with the evolution of human occupation and land use, the principal
450 vegetation composition changes are first recorded in the upper mountain areas and then in the
451 mid to low altitudes. A more detailed assessment of plant community composition trajectories
452 reveals rare and minor “resilience” phases. They are characterised by return paths toward
453 previous plant community composition after a decline in human disturbance (Fig. 5). A resilience

454 phase is recorded from the Contemporary Period in the montane and lower subalpine belts (i.e.
455 at La Thuile and Gers). They are attributed to forest recovery, which had not (yet) reached the
456 highest vegetation belts (Supplementary figure 6). At Verney in the upper subalpine/alpine belt,
457 minor resilience phases are observed at the end of the Roman Period/beginning of the Early
458 Medieval Period and from the Contemporary Period.

459
460
461 **Erosion trajectories.** Our records show a diversity of erosion trajectories, despite some
462 similar trends in human land use (Fig. 6A; Supplementary figure 7). This may be explained by
463 variations in the sensitivity of landscapes to climate and human-triggered erosion due to initial
464 physical and related biological (vegetation cover) characteristics. Lakes, where flood deposits are
465 recorded, are naturally sensitive to climate-triggered-flood deposits due to the steep slopes, bare
466 soils or glacial deposits that produce easily erodible materials. When the catchment has always
467 been above the treeline (with no possible soil destabilisation due to deforestation) and does not
468 comprise extensive good quality pasture attractive to grazers but does comprise steep slopes,
469 bare soils, or glacial deposits, we expect climatic changes to act as the primary drivers of erosion
470 dynamics throughout the record. This scenario is illustrated at Savine, where the development of
471 significant grazing activities during the Roman Period did not strongly influence flood deposit
472 frequency. Only the total sediment accumulation, i.e. flood deposit thickness and continuous
473 detrital sedimentation, record substantial increases, largely due to continuous sedimentation
474 (Supplementary figure 8 and comments; Sabatier et al. 2017). However, the LIA strongly
475 impacted this site, pushing the system toward a new and degraded steady-state (Fig. 6A; Dearing
476 2008). At Anterne and Gers, the catchments also present steep slopes and bare soils, making
477 these systems naturally susceptible to erosion processes as at Savine (Giguët-Covex et al. 2012;
478 Bajard et al. 2020). However, because these systems comprise good-quality pastures, the
479 pastoral activities pushed them toward new and degraded steady-states (Fig. 6A, Supplementary
480 figure 7). Conversely, the slopes around Lake Verney are mostly gentle with highly developed
481 vegetation cover (also due to the more internal massif location). This type of system is expected
482 to be very resistant to climate and human-triggered erosion, which is what we observe here
483 (Supplementary figure 7). However, possibly due to long-term human disturbance combined with
484 climatic degradation, this system was finally pushed toward a degraded steady-state. Indeed, the
485 first human disturbances may have started to degrade and destabilise the soils, but the
486 potentially mobilised sediments must have been temporarily trapped in intermediate sinks. La
487 Thuile, which was in a densely forested area with moderate slopes, is not naturally sensitive to
488 erosion processes and does not, therefore, constitute a useful record for climate-driven erosion.
489 Significant human disturbance via deforestation and agricultural activities was crucial in
490 rendering the system sensitive to erosion, thereby pushing it toward a degraded steady-state
491 (Fig. 6A).

492
493 Although the erosion trajectories differ across the sites, we can identify four trajectory
494 patterns. The most “classical” patterns correspond to the expected increase in erosion due to
495 human (agricultural activities, deforestation, cutting or burning of shrubs) or climatic
496 disturbances, followed by a tendency to return to the initial state after the disturbance has
497 ceased. Alternating “degradation” and “resilience” phases are represented by oblique and
498 vertical feedback loops for human and climatic disturbances, respectively (Fig. 6B). Two other
499 less frequent trajectory types, termed “unusual patterns”, are also observed. They correspond
500 to 1) an increase of agropastoral activities with no erosion response (rightward horizontal

501 arrow), i.e. to a “resistance” phase, and 2) a decrease in erosion while human activities remain
502 steady or see a slight increase (vertical/oblique downward arrow), i.e. to an “adaption” phase.
503 A “resistance” phase is recorded between the Neolithic and Iron Age at Verney, probably due
504 to the site’s initial physical and biological conditions considered above (Supplementary figure
505 7). Another “resistance” phase appeared at Anterne during the Iron Age, but it is only visible
506 in the total sediment accumulation (Supplementary figure 8) and not in the flood frequency.
507 This apparent discrepancy reflects the complexity of erosion mechanisms, probably due to
508 interactions between climatic conditions, human activities and practices, and initial
509 environmental conditions (see Supplementary material 6 for more details). Otherwise, the
510 other “resistance” and “adaptation” phases occurred from the High Middle Ages at Anterne
511 and La Thuile, the Late Middle Ages at Gers, as well as Bénit (Bajard et al., 2018), and from the
512 Late Middle Ages and the Early Modern Period at Verney (Fig. 6A; Supplementary figures 3,
513 7). Also, all these resistance and adaptation phases developed after an anthropic erosive
514 “crisis”. At La Thuile, Gers and Anterne, the erosive crises are characterised by the progressive
515 disappearance of soil surface horizons and then the deeper horizons (Bajard et al. 2017b;
516 2020; Giguet-Covex et al. 2011; Pansu et al. 2015). Moreover, at La Thuile, Bajard et al. (2017b)
517 show that the agricultural system reached a point where soil loss exceeded soil formation, i.e.
518 when the system became unsustainable. Then, the system returned to a sustainable situation.
519 This shift occurred during the phase of activity diversification, with the development of fruit
520 tree cultivation (Fig. 2). Also, fir, alder, beech and oak increased in the DNA and pollen records
521 (Bajard et al. 2016; Supplementary figure 3). The combination of these results leads us to
522 consider the role of land use management, such as tree plantations, forest management, and
523 possibly terrace construction (observed in soil profiles but undated), in reducing erosion.
524 Some have suggested that terracing in the Alps was initiated by monasteries (see Scaramellini
525 and Varoto 2008). Furthermore, this period corresponds to the start of land division based on
526 inheritance from one generation to another (Mouthon 2009). The associated development of
527 parcel limits possibly led to a topography modification and reduced erosion. Moreover, this
528 observed “adaption” pattern raises the question of farmers’ awareness of erosion problems
529 linked to their activities. This “awareness” appears in historical archives from Cistercian monks
530 installed in 1132 AD in the Abbey of Tamié (Bauges Massif), which avoided cutting trees on
531 steep slopes and mountain tops to limit erosion (Crook et al. 2004). At higher altitudes, the
532 unusual erosion patterns correspond to the increased size of cowherds relative to sheep
533 flocks. This evolution was also probably associated with changes in pastoral practices, perhaps
534 in herd management. For example, such herds might have been concentrated near farms for
535 milking, i.e. for our study sites in areas downstream from the lakes or outside the lake
536 catchments.

537
538 Lakes in the lower part of the subalpine belt and the montane belt show higher resilience
539 than lakes in the upper part of the subalpine belt. Indeed, in the Contemporary period, when we
540 see a decrease in pastoral/agropastoral pressure at all altitudes, only lower sites (Gers and La
541 Thuile) show significant reductions in erosion (Fig. 6A, Supplementary figure 7). This pattern may
542 be explained by the permanent presence of trees in lower altitude catchments combined with
543 warmer conditions facilitating forest regeneration and expansion after disturbance, quite
544 different to the sparse woodland or treeless landscapes in the upper and colder altitudes. As for
545 the plant community composition, these belts are more resilient due to their altitudinal position
546 and, thus to the initial conditions of the systems.

547

549 Conclusion and perspectives

550

551 The combined palaeoenvironmental, archaeological and historical evidence facilitated
 552 the characterisation of broad-scale and long-term trajectories of human activities, including
 553 their intensities, across our altitudinal gradient. Significant pastoral activities first developed in
 554 the high-altitude zones during the Mid-Late Bronze Age. During the Roman Period, they saw
 555 significant developments across the lower subalpine to the alpine/nival belts. In the montane
 556 belt, while the first arable cultures appeared during the Late Iron Age/Roman periods,
 557 intensification of these activities was recorded in the Early Middle Ages. During the High and
 558 Late Middle Ages, all the vegetation belts were used for pastoral activities, while in the montane
 559 belt, we see the diversification of crops.

560

561 This altitudinal evolution of human activities is mirrored in the trajectory of the plant
 562 community composition, with earlier impact recorded in the upper subalpine and alpine areas
 563 than in the lower subalpine and montane belts. Rare and minor resilience phases were observed,
 564 demonstrating how modern mountain landscapes are a legacy of human land use and
 565 management cumulated over millennia. When we look at erosion histories, trajectories differ
 566 from one site to another due to variations in their sensitivity to erosion processes. However, we
 567 can recognise similar response patterns to disturbances. Interestingly, “unusual patterns”,
 568 characterised by the absence or a reduced impact of agropastoral activities on erosion, are
 569 observed everywhere after 1000 AD. Finally, whether in terms of plant community composition
 570 or erosion, our trajectories evidence the vulnerability of systems above ca. 2000 m a.s.l. to
 571 changes in human activities and practices, as well as variations in climate. This vulnerability must
 572 be considered in the capacity of these environments to support the current changes.

573

574 The altitudinal model of agropastoral developments and their interactions with
 575 landscapes should now be tested across more sites. In particular, our study sites are
 576 concentrated on the north-facing slopes; it would also be interesting to investigate sites with
 577 the greatest exposure to the sun, where cultivated land could develop at higher altitude
 578 (Elleau et al. this issue). The model could also integrate perialpine areas to elucidate the
 579 organisation of land use across an entire territory, thus highlighting interactions between the
 580 lower and upper zones. Moreover, developing our approach in other parts of the Alps, or other
 581 mountains in the world, would allow the assessment of locally specific or shared characteristics
 582 of mountain agroecosystems.

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598 Author's contribution

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900 *Figure 1. Location of the main sites (lakes and archaeological sites) discussed in the manuscript. The Neolithic*
901 *sites indicated by the stars are located in the Vercors subalpine massif (1: La Grande Rivoire 580 m a.s.l.), the*
902 *Bornes-Aravis subalpine massif (2: La Balme de Thuy 620 m a.s.l.), the Haute-Maurienne Valley (3: Les Balmes à*
903 *Sollières-Sardières, 1350 m a.s.l.) and the Tarentaise Valley (4: Le Chenet des Pierres à Bozel, 940 m a.s.l.). The*
904 *altitudinal positions in the different vegetation belts of all the sites are also presented on the right side of the*
905 *figure.*

906
907 *Figure 2. Synthesis of (agro-)pastoral activity histories in the Northwestern Alps from the montane to the*
908 *alpine/nival belts. For each site, ruderal taxa are presented in order to compare these with mammal DNA data*
909 *(herbivorous domestic animals) and, when available, with coprophilous fungi. At La Thuile, cultivated taxa*
910 *recorded by DNA and pollen for cereals are also presented. In addition to these data indicating the nature of the*
911 *activities and practices, a synthetic index representing the intensity of (agro-)pastoral activities has been*
912 *calculated for each site. The grey areas show the phases of intense pastoral activities discussed in the text during*
913 *the High/Late Middle Ages, and the black dotted lines the medieval transition in animal composition.*

914
915 *Figure 3. Box plot by cultural periods evidencing the temporal and altitudinal trajectory of the intensity of (agro-)*
916 *pastoral activities in the Northwestern Alps.*

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919 *Figure 4. Synthesis of archaeological sites and composition of zooarchaeological remains for the different periods*
920 *in The Vallon de Sales and around Anterne. Positions of the palaeoenvironmental records available close to these*
921 *sites.*

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924 *Figure 5. Temporal trajectories in plant composition evidenced through NMDS analyses from lake sedDNA data*
925 *in different vegetation belts. The stress values for the ordinations are relatively high (0,17 at Gers and 0,19 at*
926 *Savine, Anterne).*

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928 *Figure 6. Erosion trajectories in response to agropastoral and pastoral activities in the northwestern Alps. A) Specific*
929 *trajectories for the different studied sites. B) Representation of generic patterns of the erosion trajectory in response*
930 *to human activities.*

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