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

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Abstract

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

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

Keywords

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

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1 Introduction

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

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

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

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

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

2 Study sites

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

3 Material and methods

3.1. (agro-)pastoral activities and activity intensity

The *seda*DNA 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 (Giguet-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 Fig. 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; Giguet-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

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

3.4. Archaeological and historical research

Archaeological surveys and excavations have been carried out in or close to three of the lake catchments (Fig. 1; 4). Between lakes Gers and Anterne in the Vallon de Sales, a research program has documented human occupation from the Late Middle Ages to the contemporary period (Guffond and Mélo 2018). Zooarchaeological remains were found and analysed as part of this research (Fig. 4; Supplementary table 2). This research is supplemented by interpretating historical documents (land registries, old photographs, texts), which facilitate understanding human occupation and land-use. Adjacent to this area, in the massifs of Anterne and Pormenaz, archaeological investigations identified several phases of activity from the Neolithic to the Modern Period (Rey et al., 2022; Fig. 4). Zooarchaeological remains were only found and analysed at Anterne. At Pormenaz this was not possible due to the acidic conditions of this crystalline massif. Around Lake Verney, on both sides of the Petit Saint-Bernard pass (Fig. 1), from 700 to 2500 m a.s.l., the archaeological fieldwork discovered sites dating from the Neolithic to the Middle Ages (Crogiez-Pétrequin 2016; Rey and Moulin 2019; Rey and Collombet 2020).

4 Results and interpretations

4.1. Detailed history of agropastoral activities: an altitudinal evolution

The synthetic index of (agro-)pastoral activities, represented by box plots for each cultural phase and lake, outlines an altitudinal trajectory over time with different activity intensities across the different vegetation belts (Fig. 3). This evolution is discussed in the light of proxies indicating the nature of activities inferred from, lake sediments (Fig. 2, Supplementary Fig. 3) along with archaeological (Fig. 1, 4) and historical research carried out in the vicinity of the lakes or from neighbouring Alpine landscapes.

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

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

Mid to Late Bronze Age. At all high-altitude sites (Savine, Verney and Anterne), 1600-1000 BC corresponds to the start of significant pastoral activities (Fig. 2, 3). This is mainly evidenced by the high and regular detection of DNA from the ruderal *Plantago sp.* (Fig. 2). At Anterne, this hypothesis is strengthened by the presence of *Ovis* DNA, albeit in low quantities, probably due to taphonomic issues (Supplementary material 2.1.) and a tipping point recognised in the erosion dynamic, characterised by a permanent increase in flood deposit frequency and thickness (Supplementary Fig. 3; Giguet-Covex et al. 2011). At Verney, the concentration of *Sporormiella* *sp.* spores suggests extensive pastoral activities as early as 2250 BC, but more intensive activities from 1100 BC. Similarly, in a Swiss lake located in the upper subalpine belt (Sulsseewli at 1922 m a.s.l.; Fig. 1), the first occurrence of sheep DNA is dated to 1850 BC, while significant sheep DNA detections appear from 1450 BC (Garcés-Pastor et al. 2022).

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

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

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

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

Archaeological data from some of our study areas attest to significant levels of human activity and movements into the “Alpages” during the Iron Age. A trend that increased during the Roman Period. Around Anterne, several archaeological structures were dated to the Iron Age and Roman Period (Fig. 4; Rey et al. 2022). At Verney, ruins of Roman buildings, a possible road station of the “Via Romana” (Crogiez-Pétrequin 2016), indicate the movement of people across the Petit Saint-Bernard pass, perhaps engaged in trade activities. Indeed, the integration of our study area into the Roman Empire triggered the growth of commercial activities and networks due to the significant requirement of the Roman Empire for wool and meat and its appetite for alpine cheese (Frayn 1984; Segard 2009; Pliny the Elder, "Natural History" 77-79 AD, book XI, XCVII.).

The low levels of cattle DNA, *Plantago* and *Rumex sp*. at La Thuile (montane belt) reflect lower pastoral pressure than that seen in the higher altitudes during the Iron Age and Roman Period (Fig. 2). However, other activities, i.e. the cultivation of fruit trees (*Prunus sp.*) and some cereals, are recorded, revealing the development of an agropastoral system (Fig. 2). The disappearance of fir DNA is also notable (Supplementary Fig. 3).

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

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

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

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

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

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

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

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

4.2. Relationships between agropastoral activities and landscape trajectories

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

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

at La Thuile and Gers). They are attributed to forest recovery, which had not (yet) reached the highest vegetation belts (Supplementary Fig. 6). At Verney in the upper subalpine/alpine belt, minor resilience phases are observed at the end of the Roman Period/beginning of the Early Medieval Period and from the Contemporary Period.

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

Although the erosion trajectories differ across the sites, we can identify four trajectory patterns. The most “classical” patterns correspond to the expected increase in erosion due to human (agricultural activities, deforestation, cutting or burning of shrubs) or climatic disturbances, followed by a tendency to return to the initial state after the disturbance has ceased. Alternating “degradation” and “resilience” phases are represented by oblique and vertical feedback loops for human and climatic disturbances, respectively (Fig. 6B). Two other less frequent trajectory types, termed “unusual patterns”, are also observed. They correspond to 1) an increase of agropastoral activities with no erosion response (rightward horizontal arrow), i.e. to a “resistance” phase, and 2) a decrease in erosion while human activities remain steady or see a slight increase (vertical/oblique downward arrow), i.e. to an “adaption” phase. A “resistance” phase is recorded between the Neolithic and Iron Age at Verney, probably due to the site’s initial physical and biological conditions considered above (Supplementary Fig. 7). Another “resistance” phase appeared at Anterne during the Iron Age, but it is only visible in the total sediment accumulation (Supplementary Fig. 8) and not in the flood frequency. This apparent discrepancy reflects the complexity of erosion mechanisms, probably due to interactions between climatic conditions, human activities and practices, and initial environmental conditions (see Supplementary material 6 for more details). Otherwise, the other “resistance” and “adaptation” phases occurred from the High Middle Ages at Anterne and La Thuile, the Late Middle Ages at Gers, as well as Bénit (Bajard et al., 2018), and from the Late Middle Ages and the Early Modern Period at Verney (Fig. 6A; Supplementary Fig. 3, 7). Also, all these resistance and adaptation phases developed after an anthropic erosive “crisis”. At La Thuile, Gers and Anterne, the erosive crises are characterised by the progressive disappearance of soil surface horizons and then the deeper horizons (Bajard et al. 2017b; 2020; Giguet-Covex et al. 2011; Pansu et al. 2015). Moreover, at La Thuile, Bajard et al. (2017b) show that the agricultural system reached a point where soil loss exceeded soil formation, i.e. when the system became unsustainable. Then, the system returned to a sustainable situation. This shift occurred during the phase of activity diversification, with the development of fruit tree cultivation (Fig. 2). Also, fir, alder, beech and oak increased in the DNA and pollen records (Bajard et al. 2016; Supplementary Fig. 3). The combination of these results leads us to consider the role of land use management, such as tree plantations, forest management, and possibly terrace construction (observed in soil profiles but undated), in reducing erosion. Some have suggested that terracing in the Alps was initiated by monasteries (see Scaramellini and Varoto 2008). Furthermore, this period corresponds to the start of land division based on inheritance from one generation to another (Mouthon 2009). The associated development of parcel limits possibly led to a topography modification and reduced erosion. Moreover, this observed “adaption” pattern raises the question of farmers’ awareness of erosion problems linked to their activities. This “awareness” appears in historical archives from Cistercian monks installed in 1132 AD in the Abbey of Tamié (Bauges Massif), which avoided cutting trees on steep slopes and mountain tops to limit erosion (Crook et al. 2004). At higher altitudes, the unusual erosion patterns correspond to the increased size of cowherds relative to sheep flocks. This evolution was also probably associated with changes in pastoral practices, perhaps in herd management. For example, such herds might have been concentrated near farms for milking, i.e. for our study sites in areas downstream from the lakes or outside the lake catchments.

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

Conclusion and perspectives

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

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

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

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Author’s contribution

CGC, MB, WC, DE, FGF, LG, PS, PC, CG, FA, EM, PJR and CB contributed to the sampling and/or data production. CGC, JP, KJW, contributed to the design of the study. All authors contributed to the writing of the manuscript.

Data availability

The datasets presented in this study can be found on Neotoma database at XXX.

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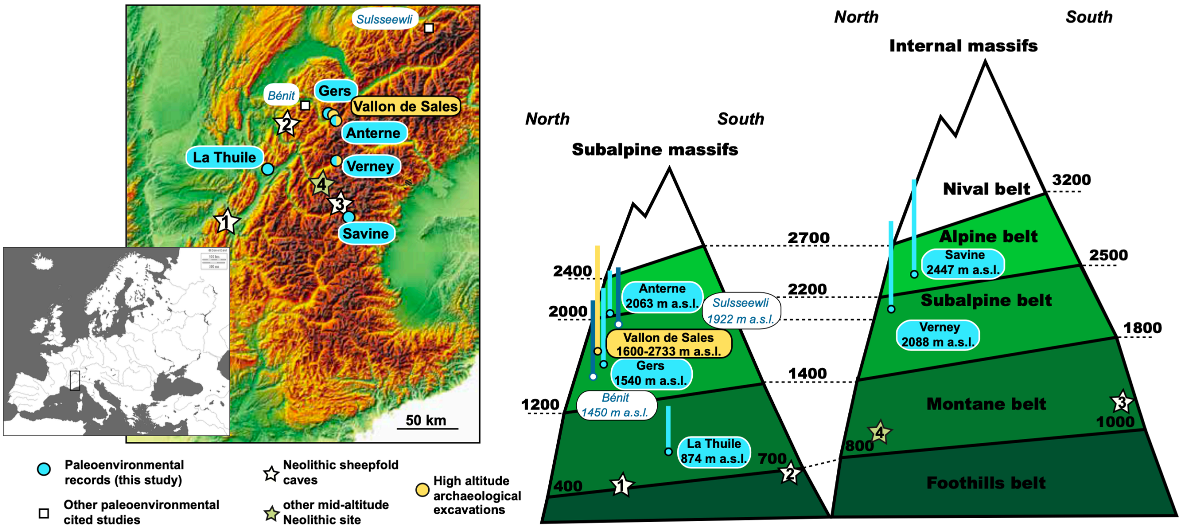

Figure 1. Location of the main sites (lakes and archaeological sites) discussed in the manuscript. The Neolithic sites indicated by the stars are located in the Vercors subalpine massif (1: La Grande Rivoire 580 m a.s.l.), the Bornes-Aravis subalpine massif (2: La Balme de Thuy 620 m a.s.l.), the Haute-Maurienne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

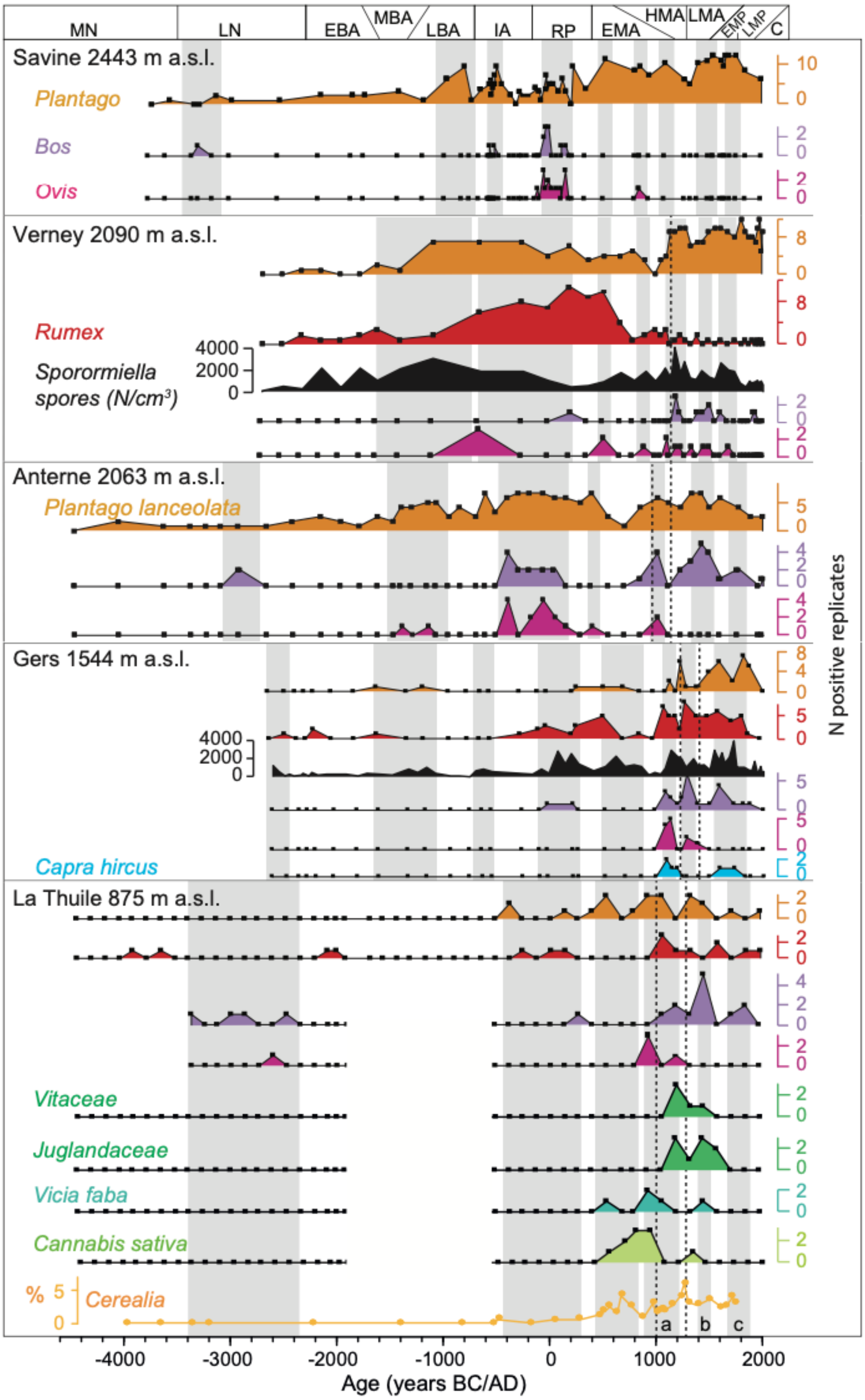

Figure 2. Synthesis of (agro-)pastoral activity histories in the Northwestern Alps from the montane to the alpine/nival belts. For each site, ruderal taxa are presented in order to compare these with mammal DNA data (herbivorous domestic animals) and when available, with coprophilous fungi. At La Thuile, cultivated taxa recorded by DNA and pollen for cereals are also presented. The names of the cultural periods are abbreviated as follows: MN as Middle Neolithic, LN as Late Neolithic, EBA, MBA and LBA as Early, Middle and Late Bronze Age, IA as Iron Age, RP as Roman Period, EMA, HMA and LMA as Early, High and Late Middle Ages, EMP and LMP as Early and Late Modern Period and C as Contemporary Period. The grey areas show the phases of pastoral activities discussed in the text. The last grey areas are named a, b, c, for more clarity in the text. The black dotted lines show the medieval transition in animal composition.

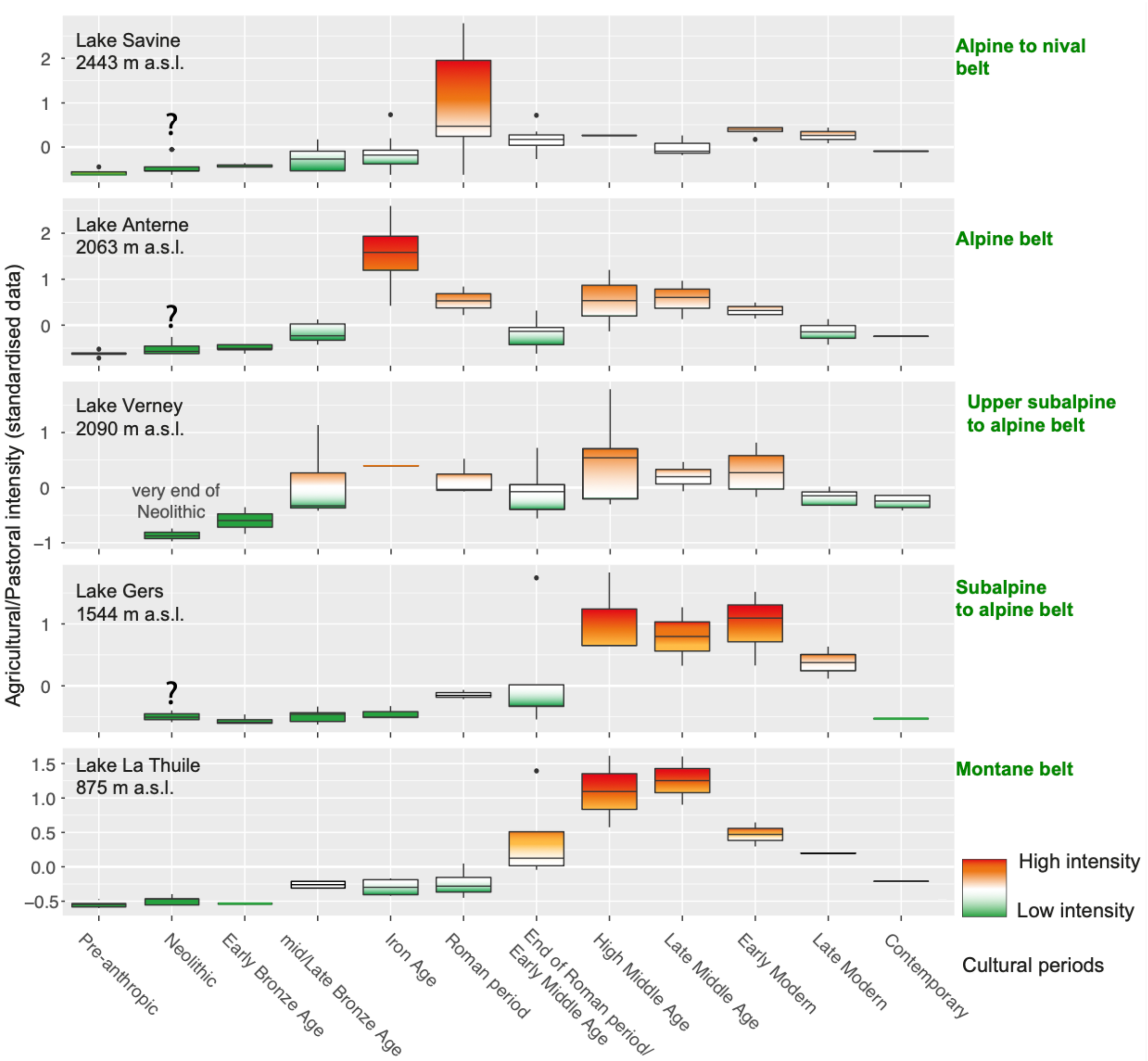

Figure 3. Box plot by cultural periods evidencing the temporal and altitudinal trajectory of the intensity of (agro-)pastoral activities in the Northwestern Alps.

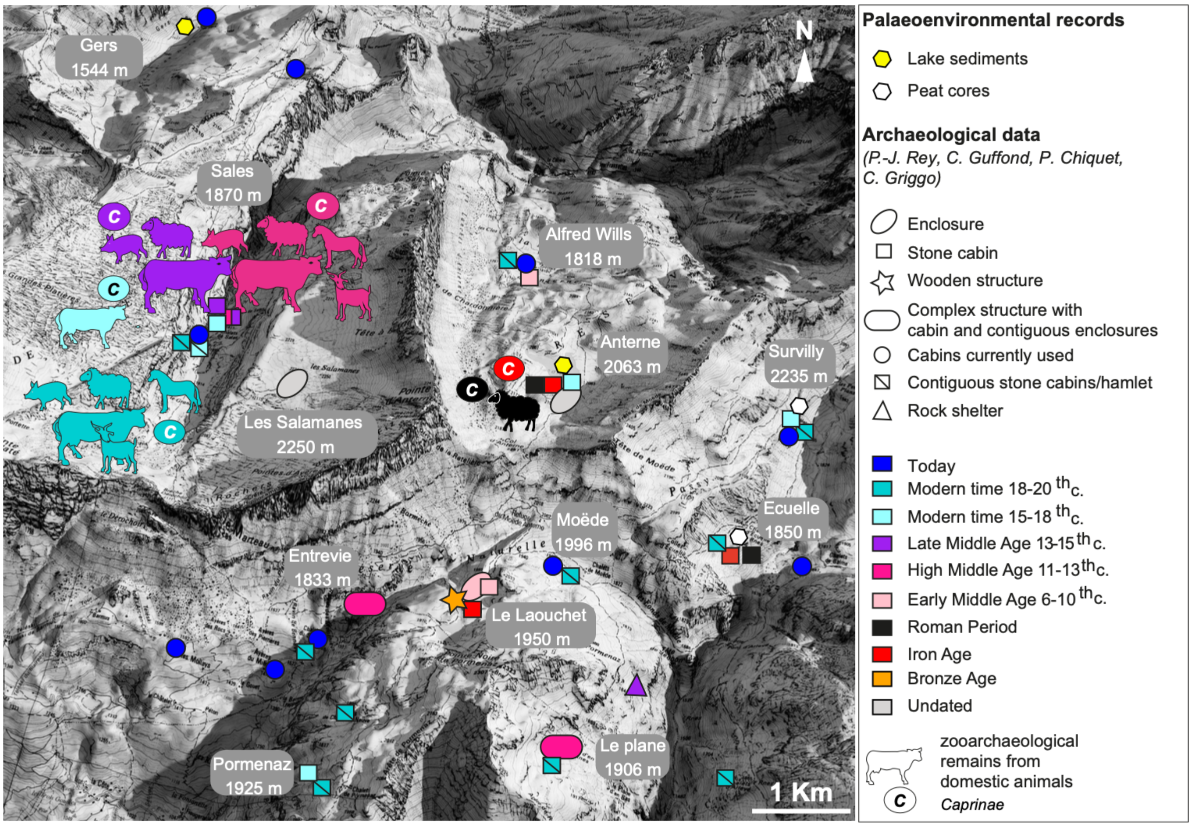

Figure 4. Synthesis of archaeological sites and composition of zooarchaeological remains for the different periods in The Vallon de Sales and around Anterne. Positions of the palaeoenvironmental records available close to these sites.

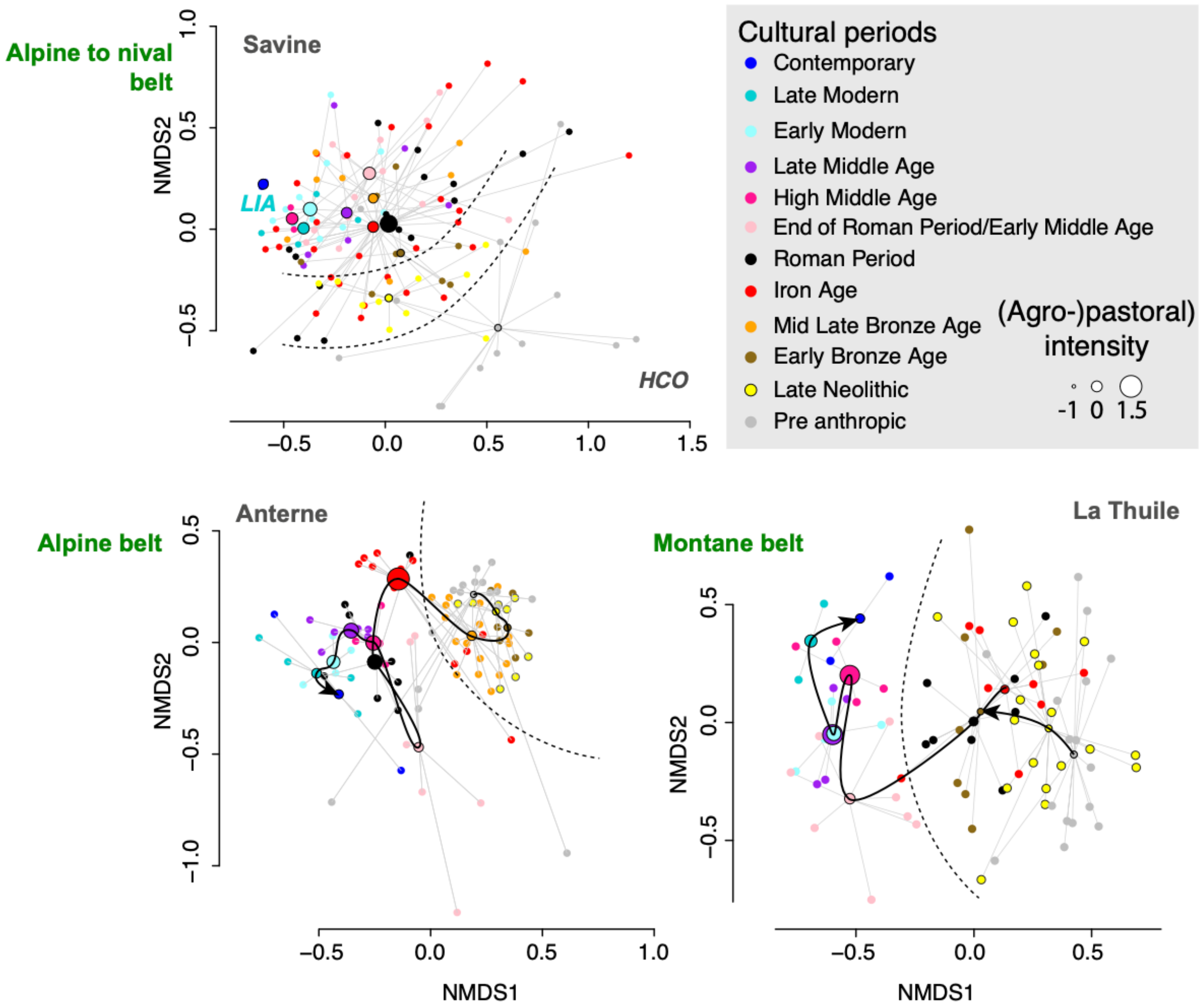

Figure 5. Temporal trajectories in plant composition evidenced through NMDS analyses from lake sedDNA data in different vegetation belts. The stress values for the ordinations are relatively high (0,17 at Gers and 0,19 at Savine, Anterne). HCO means Holocene Climatic Optimum and LIA Little Ice Age.

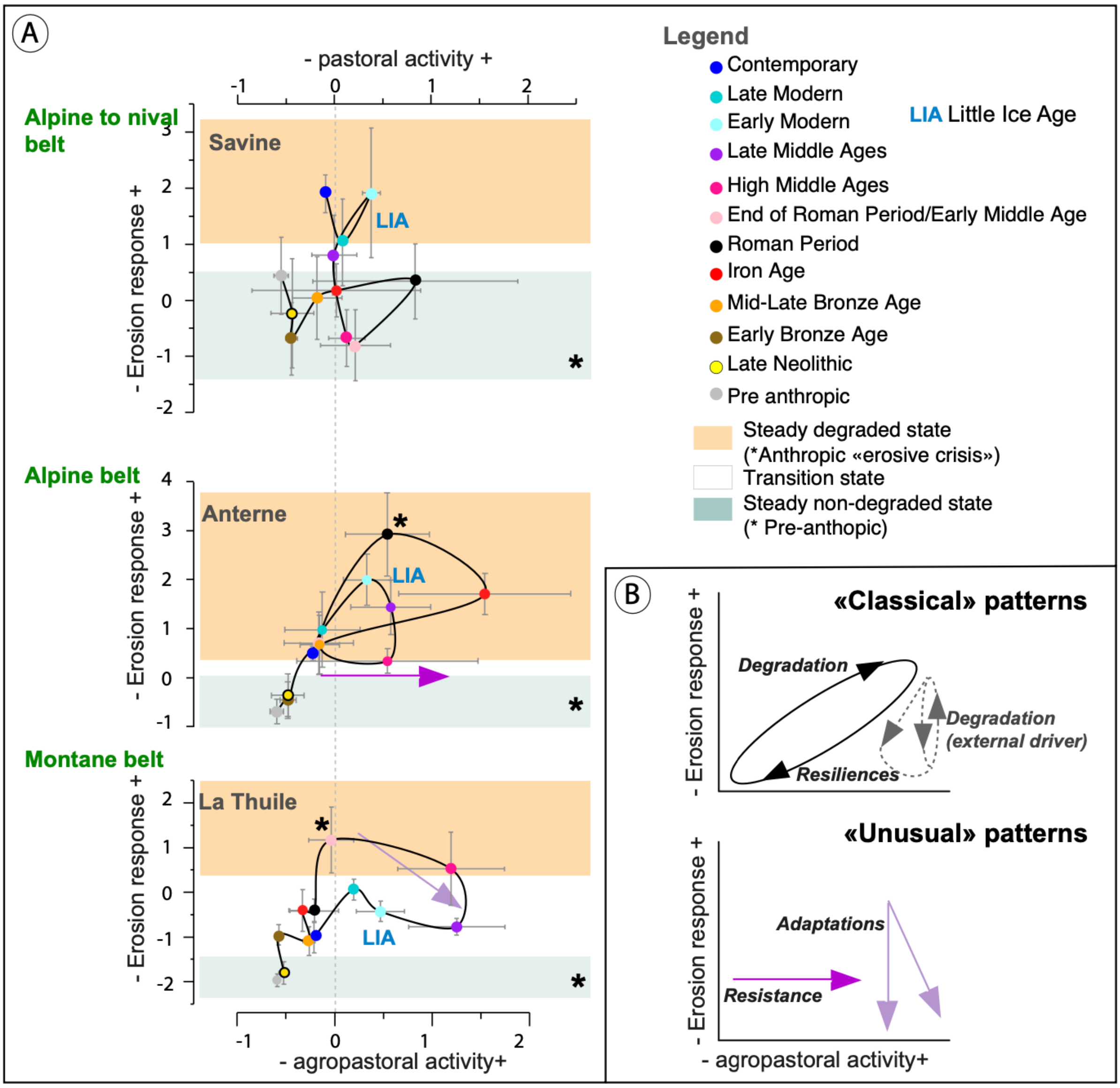

Figure 6. Erosion trajectories in response to agropastoral and pastoral activities in the northwestern Alps. A) Specific trajectories for the different studied sites. B) Representation of generic patterns of the erosion trajectory in response to human activities.