

**Ecosystem elementomes across the Anthropocene:
Palaeoecological trajectories of the onset of human activities
and environmental biogeochemical shifts**

Javier de la Casa Sánchez

ADVERTIMENT. L'accés als continguts d'aquesta tesi queda condicionat a l'acceptació de les condicions d'ús establertes per la següent llicència Creative Commons:  <https://creativecommons.org/licenses/?lang=ca>

ADVERTENCIA. El acceso a los contenidos de esta tesis queda condicionado a la aceptación de las condiciones de uso establecidas por la siguiente licencia Creative Commons:  <https://creativecommons.org/licenses/?lang=es>

WARNING. The access to the contents of this doctoral thesis it is limited to the acceptance of the use conditions set by the following Creative Commons license:  <https://creativecommons.org/licenses/?lang=en>

Ecosystem Elementomes across the Anthropocene

UAB
Universitat Autònoma
de Barcelona



Palaeoecological trajectories of the onset
of human activities and environmental
biogeochemical shifts



Javier de la Casa (2025)

Under the supervision of Josep Peñuelas, Jordi Sardans & Sandra Nogué

Ecosystem elementomes across the Anthropocene:

Palaeoecological trajectories of the onset of human activities and environmental biogeochemical shifts.

Javier de la Casa

Under the supervision of:

Josep Peñuelas, Jordi Sardans & Sandra Nogué

**To Julen, for the world you will discover,
where beauty always finds its way. May the harmony be with you.**

**To Jane and Wangari (rest in peace), for inspiring the kid
that believed that anything could be healed.**

Table of contents

Author statement.....	7
Abstract.....	8
General Introduction.....	11
Ecosystem elementomes. What and why.....	12
The Anthropocene debate.....	12
The elementome framework.....	13
Towards assessing past ecosystem elementomes (palaeoelementomes): palaeoecology meets elementomes.....	16
How is the elementome measured from palaeoenvironmental records?.....	17
Objectives.....	18
Thesis outline.....	20
First Chapter: Challenges and opportunities for addressing past ecosystem elementomes from natural archives.....	23
Abstract.....	24
Introduction.....	25
Sedimentary records: lakes.....	27
Sedimentary records: soils.....	29
Biospheric records: peat.....	30
Biospheric record: Tree-rings.....	31
Final remarks.....	32
Second Chapter: Unveiling two millennia of ecosystem changes in the Azores through Elementome Trajectory Analysis.....	35
Abstract.....	36
Introduction.....	37
Materials and Methods.....	39
Results.....	44
Discussion.....	47
Conclusion.....	53
Third Chapter: Erosion and geochemical legacies of the human colonisation of Atlantic islands.....	54
Abstract.....	56
Introduction.....	57
Results.....	59
Discussion.....	65

Methods.....	70
Fourth Chapter: Biogeochemical and vegetation coupling in the Alps: climate change and livestock effects on alpine ecosystems across the Holocene.....	75
Biogeochemical and vegetation coupling in the Alps: climate change and livestock effects on alpine ecosystems across the Holocene.....	76
Abstract.....	76
Introduction.....	76
Results & Discussion.....	78
Methods.....	86
Fifth Chapter: soundtraj: Ecological trajectories through sonification and animation of multivariate environmental data.....	91
Abstract.....	92
Introduction.....	93
Sonification workflow.....	94
Final remarks.....	96
General Discussion.....	97
Elementomes shifting across peaks and islands.....	98
Q1: Can palaeoenvironmental records (e.g. lake sediments) be a good source describing ecosystem elementomes using elementome trajectory analysis?.....	100
Q2: How can we represent and quantify ecosystem elementomes?.....	101
Q3: How does the onset of human activities affect ecosystem elementomes?.....	103
Q4: Are ecosystem elementomes shifting more dramatically in post-industrial times or with the onset of human activities?.....	105
Q5: Can human impact on ecosystem elementomes be discriminated against other factors like climate or vulcanism?.....	106
Q6: How shifting ecosystem elementomes interact with biodiversity patterns?.....	107
Steps towards “palaeoelementomics”.....	108
General conclusions.....	111
Appendix I. Other contributions beyond the thesis.....	116
Appendix II. Supplementary Material for the Second Chapter.....	118
Appendix III. Supplementary Material for the Third Chapter.....	134
Appendix IV. Supplementary Material for the Fourth Chapter.....	145
References.....	177
Refereces for aesthetics and illustrations.....	226

Author statement

This research was supported by the FPU grant (Formación de Profesorado Universitario) from the Spanish Ministry of Science and Innovation (MCINN), and the participation in from my PhD supervisors: European Research Council (ERC) under the European Union's Horizon Europe research and innovation programme (ERC_CoG-101045309-TIME-LINES) and by the Spanish Government through grants TED2021-132627B-I00 (NUTRIARID) PID2022-140808NB-I00 (SOILDEEPCHANGE) and PID2023-153125NB-I00 (ATOM-ECOLOGY). CREAM (Centre for Ecological Research and Forestry Applications) provided substantial help and support, specially from resources derived from the Severo Ochoa Centres of Excellence programme (CEX2023-001340-S).

I personally have a strong background in climate activism, which motivated me to start the PhD journey about the concerning human-driven shifts in biogeochemical cycles. Although science is not an apolitical body, my aim in this research is to pursue objectivity and avoid allowing personal biases to influence the interpretation of data.

I use “I” when statements belong to my own perspective. I use “we” when the action comes from the collective effort of my supervisors and me in the introduction, discussion and conclusion; and to all the mentioned coauthors in each of the chapters of the thesis

It matters what matters we use to think other matters with; it matters what stories we tell to tell other stories with; it matters what knots knot knots, what thoughts think thoughts, what descriptions describe descriptions, what ties tie ties. It matters what stories make worlds, what worlds make stories.

Marilyn Strathern told by Donna Haraway

Abstract

The function and structure of ecosystems are strongly modulated by their elemental composition, referred to as the ecosystem elementome. The disruption of biogeochemical cycles over the last century has drawn increasing attention to the study of the elemental composition of organisms and ecosystems under anthropogenic pressures, with particular focus on carbon, nitrogen, and phosphorus. To understand long-term shifts in ecosystem elementomes, assessments must extend beyond the past few centuries. However, this is challenged by the absence of direct measurements of elemental composition. Natural archives, including palaeoenvironmental records such as lake sediments, soil profiles, peat records, and tree rings, preserve valuable information on past ecosystems events that can be dated chronologically. These records provide a powerful opportunity to reconstruct historical changes in ecosystem structure and functioning as well as the imprint of human activities, including agriculture, pastoralism, forest management, and settlement.

Through Elementome Trajectory Analysis, developed within this thesis, we examined the temporal trajectories of samples within a multivariate space defined by their elemental composition across the record. We first applied this approach to five records from the Azores archipelago, spanning the last two millennia, in order to test the insights provided by Elementome Trajectory Analysis against relevant ecological milestones identified in previous palaeoecological studies. We then upscaled the study to 21 records from Atlantic islands, covering regions from Svalbard to the Falklands and extending across three millennia of ecosystem change. Our analyses focused on ecosystem elementomes before and after human arrival, as well as across different historical periods and colonisation histories. Extending our analysis from island to mountain ecosystems, we examined 12 lakes in the European Alps spanning the last eight millennia, integrating sediment elemental composition with plant community reconstructions from sedimentary ancient DNA to explore feedbacks between elementomes and vegetation dynamics.

We found that Elementome Trajectory Analysis provided robust characterisations of ecosystems, consistent with previous palaeoecological assessments. In addition, it allowed the quantification of trajectories in terms of magnitude, speed, and direction of change, thereby indicating the stability of ecosystem elementomes. The analysis of Atlantic islands revealed a strong and persistent trend of increased erosion after human arrival, reflected in the dominance of terrigenous elements within the ecosystem elementome and with higher accumulation rates. Our results from the European Alps showed that the introduction of livestock during the Bronze Age reduced the coupling between plant communities and ecosystem elementomes. While greater livestock abundance was associated with increased plant diversity, it also decreased carbon and nitrogen stocks. Finally, we present an alternative approach to interpreting Elementome Trajectory Analysis through sonification. We developed soundtraj: an open-source tool that translates graphical outputs of Principal Coordinate Analysis (PCoA) into auditory reconstructions, enabling the audition of elementome trajectories and the sensory perception of speed, an aspect that generally remains blind in PCoA plots.

Overall, this work highlights the power of palaeoelementomes (i.e. the elemental composition from palaeoenvironmental records) to reveal the long-term legacies of human activities and their enduring influence on ecosystem dynamics and structure. Future steps are needed toward a better understanding of elements and ecosystems across time scales; this work aims to contribute to that ongoing effort.



General Introduction:

Ecosystem elementomes. What and why

The elemental composition of ecosystems (ecosystem elementome) is a key environmental trait defining ecosystem structure and function (Peñuelas et al., 2020; Welty et al., 2017). Living organisms and ecosystem elementomes are intrinsically linked. The availability of macronutrients (e.g. carbon, nitrogen, phosphorus...), micronutrients (e.g. calcium, iron...) and other elements needed at trace concentrations (e.g. manganese, zinc...), or with toxic effects (e.g. cadmium, lead, arsenic, mercury...), represent essential resources for the growth and metabolic activity of autotrophic and heterotrophic producers, including bacteria, fungi, and plants (Peñuelas et al., 2019). Element availability, as well as stoichiometric ratios, exert strong control over community composition, productivity, and functional traits (Fernández-Martínez, 2022; Sterner & Elser, 2002). For instance, the N:P ratio can determine which phytoplankton species dominate in a lake, affecting overall productivity and nutrient cycling rates (Glibert, 2016; Margalef, 1978). In turn, community assemblages modulate biogeochemical cycling through processes such as organic matter deposition, nutrient assimilation, nutrient resorption, litter and exudates production, elemental sequestration, and the vertical and horizontal redistribution of nutrients (Hooper & Vitousek, 1998; Jobbágy & Jackson, 2004). At the same time, ecosystem elementomes respond to environmental perturbations such as climate change, land-use, or pollution offering valuable insights into the impacts of global change. Shifts in ecosystem elementomes can induce profound alterations in ecosystem structure and functioning. Hence, understanding long-term dynamics of ecosystem elementome shifts is crucial to face the environmental challenges of this century.

The Anthropocene debate

Human activities have completely shaped ecosystems on a global scale, including ecosystem elementomes (Richardson et al., 2023). The term Anthropocene is controversial within the scientific community, as it emphasises the profound impact of human activities on ecosystems at a global scale. Human societies have reshaped global ecosystems with growing intensity and complexity, leading to rapid ecological changes that frequently exceed natural variability (Nogué et al., 2025). The Anthropocene refers to a proposed epoch in Earth's history in which humans have become a dominant force shaping geological and ecological processes. Beyond the debate over whether the Anthropocene should be formally recognised as a geological epoch, questions remain regarding when and where its onset began. Simplistically, there are two main lines of thought. One states that the Anthropocene started after the Industrial Revolution (1850 CE) with the unprecedented increases in carbon dioxide (Crutzen & Stoermer, 2017), or later with the Great Acceleration (Kuwae et al., 2024; Steffen, Broadgate, et al., 2015), arguing that the globalisation and intensification of human activities has left a clear geological and biological signature distinct from the rest of the Holocene: high extinction rates (Barnosky et al., 2011), biota homogenisation (Williams et al., 2024), the accumulation of materials and radionuclides, as well as human-caused modification of sedimentary processes (Waters et al., 2016; Zalasiewicz et al., 2011). Following this line of a contemporary shift in the epoch, the Anthropocene is often renamed

as Capitalocene (Parenti & Moore, 2016) to highlight that the accumulation of capital and global consumerism is responsible for all drivers of change.

The other line of thought states that the Anthropocene started much earlier (Foley et al., 2013). In fact, before the Great Acceleration and contemporary to the Industrial Revolution, Antonio Stoppani coined the term “Anthropozoic” era (Stoppani, 1873). This era is suggested as a novel geological era starting at the beginning of the Stone Age and characterised by the first appearances of carved stone. Other research considers the Neolithic (eight to four millennia ago) as the onset of the Anthropocene. The Neolithic Revolution brought agriculture and domestication of animals driving important changes to ecosystems. Sedentarism increased the human pressure on settled ecosystems, specially of forest, which began to be cut and burnt and replaced by crop fields (Ruddiman, 2018). Forest burning and rice cultivation increased methane carbon dioxide and methane levels much earlier than the Industrial Revolution (Ruddiman, 2003). Resource overconsumption and changes in climatic conditions even led to the collapse of ancient societies across the globe (Peñuelas & Nogué, 2023). Finally, another proposal for the start of the Anthropocene associates it with the European arrival to the American continent in the fifteenth century, which is considered the first major event of global biotic exchanges (Mann, 2012).

Out of the lines of this thesis, I would like to highlight alternative perspectives on the Anthropocene, such as those proposed by Donna Haraway, that emphasise the entanglement of humans with other species and technologies, challenging traditional narratives that centre solely on human dominance over nature. Haraway advocates for Anthropocene not as an epoch but as a transition phase towards the “Chthulucene” (Haraway, 2016), a period where humans actively engage in multispecies co-existence, and sympoietic relationships emphasising care, responsibility, and interdependence with other life forms rather than domination over them.

The elementome framework

The importance of acknowledging elements to describe ecosystem dynamics motivated the development of “atomic ecology” (Sardans & Peñuelas, 2024), which studies ecosystems and organisms based on their atomic (elemental) composition and use. The first steps towards the atomic ecology approach focused on the elemental composition of plants, which led to proposing the term “elementome” to define the content and proportion of all or most of the elements that characterises an organism (Peñuelas et al., 2019). This concept reflects the idea that each organism has a distinct elemental profile that is fundamental to its biological function, and ecological niche. The biogeochemical niche theory states that species elementomes are linked to their elemental requirements to carry out its functions, and therefore, species elementome can explain niche differentiation, resource partitioning, and how species coexist in communities. This has been demonstrated for forest trees (Sardans et al., 2021), linking also plant elementomes with further ecosystem functions (Diniz et al., 2025; Li et al., 2025), and extending the species elementome framework beyond plant species (Camp et al., 2022; Pacheco et al., 2020). Moving from organisms, the elemental composition

of the ecosystem (ecosystem elementome) defines which elements are available for the organisms to sustain their biogeochemical niche. Therefore, studying elementomes at an ecosystem level is fundamental for the development of an atom-based ecology.

Shifting the focus from organisms to ecosystems, research has begun to explore changes in elementomes at the ecosystem level, including the interactions and relationships between elements (Ochoa-Hueso et al., 2021). However, research has predominantly focused on the dynamics of three key elements: carbon (C), nitrogen (N), and phosphorus (P), whose disrupted biogeochemical cycles since the Industrial Revolution are now central to the Planetary Boundaries framework (Rockström et al., 2009). The increased availability of C, due to fossil fuel combustion (Sundquist, 1993), and N (Fowler et al., 2013; Galloway et al., 2013) and phosphorus (M. Chen & Graedel, 2016), due to excessive fertilisation has completely changed the nutrient paradigm. Increments in the three elements after the Industrial Revolution have been globally identified in lake systems (Bao et al., 2021; Ji et al., 2024; M. Wang et al., 2021). N fertilisation resulted in increased C storing in soils (Janes-Bassett et al., 2021; Ling et al., 2025; Tipping et al., 2017) and decoupling of N and P cycles (Hong et al., 2025), as well as carbon dioxide fertilisation effects has contributed to N stocks (Zaehle, 2013). Global N enrichment has led to P limitation and alterations of the C cycling in terrestrial ecosystems (Luo et al., 2022). A comparable pattern was detected in seawater and planktonic samples, where C:N and C:P ratios rose substantially during the late twentieth century, indicating P limitation, before subsequently declining most likely associated with enhanced anthropogenic P inputs (J. Liu et al., 2025). All these shifts in ecosystems elementomes, at least for C, N and P holds potential and measured risks on biodiversity, ecosystem productivity, food security, and human health (Peñuelas et al., 2020). Management solutions and further understanding of ecosystem elementome dynamics is urgently needed.

While the literature on increases in C, N, and P and their consequences continues to expand, the fate and role of many other elements remain understudied (Sardans & Peñuelas, 2015). In that sense, applying an elementome approach (i.e. considering all, or most of all, elements at the same time) can reveal relevant insights into ecosystem dynamics and element imbalances beyond C, N and P, with elements that play relevant roles in ecosystems (Li et al., 2021; Rengel, 2007; Turner et al., 2016). In addition to addressing which elements are becoming limited or accumulating on ecosystems, studying ecosystem elementomes can start to tackle questions related to how fast the elementome changes, in which magnitude and if there is a clear pattern of change.

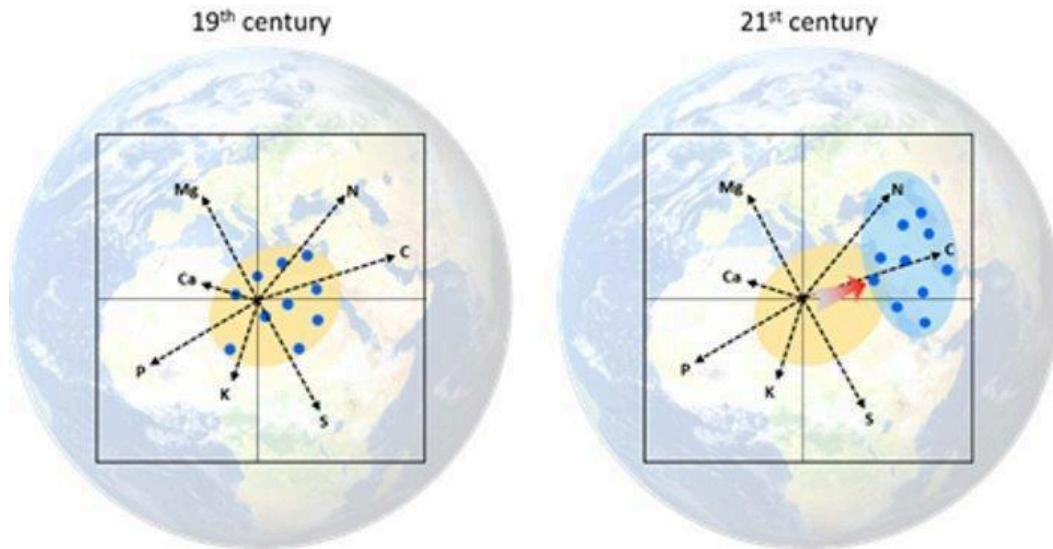


Figure 1: Hypothesised elementome shift before (left) and after (right) the Industrial Revolution and the Great Acceleration. The increase in C and N availability, due to fossil fuel combustion and overfertilisation, is expected to shape post-industrial elementomes. Figure from (Peñuelas, 2021).

Depicting elementomes in plants and other organisms does not convey big difficulties for simpler organisms, which elementome can be assessed from all the individuals (Bidwell et al., 2019; Fernández-Martínez, 2022). However, more complex organisms such as trees can be analysed considering different functional parts such as leaves (He et al., 2025; Sardans et al., 2021) or roots (Guo et al., 2025; M. Hu et al., 2025). In all cases, the limits of what is the organism, and what is not, is clear. However, assessing the elementome of an ecosystem can be an intimidating task. For terrestrial ecosystems, soil, air, water bodies, and living organisms can be considered parts integrated in an ecosystem. However, the soil and the water bodies could be considered different but connected ecosystems, reflecting a meta-ecosystem rather than a single ecosystem (Loreau et al., 2003). This epistemological dilemma is crucial to our understanding of ecology but should not hamper our aim to push our knowledge of ecosystem elementomes forward. Assessing ecosystem elementomes holds the challenge of conceptualising an ecosystem (i.e. what do we measure to measure ecosystem elementomes); but also, the conceptualisation of the elementome (i.e. how do we integrate the elemental data). The analysis of single elements and stoichiometrical ratios is the most common approach in biogeochemical studies (Peñuelas et al., 2019; Sterner & Elser, 2002) but limits the ability to integrate a complete elementome.

Finally, to understand ecosystem elementome dynamics across the Anthropocene, it is essential to investigate human impacts on ecosystems before the Industrial Revolution. Important questions include: How did different civilisations manage fire, forest, agriculture, livestock, and materials (e.g. metallurgy, stones)? How did different environments respond to

the onset of those human activities (Dubois et al., 2018) and other natural factors such as climate and vulcanism? These are the questions that the PhD project will address.

Towards assessing past ecosystem elementomes (palaeoelementomes): palaeoecology meets elementomes

The study of the ecosystem elementome across studying the elemental composition of palaeoenvironmental records (palaeoelementome) hold potential for detecting long-term trends of ecosystem elementome shifts. Palaeoecology can be understood as the study of interactions between ancient organisms and their environment, using fossil and sedimentary evidence to reconstruct past ecosystems and ecological processes (Birks, 2008).

The palaeoecological framework works well for reconstructing past ecosystem elementomes. Depositional archives such as lake sediments, soil and peat accumulate material, preserving often a continuous record of elemental composition over time. The remains of past ecosystems are for example, fossil pollen from past vegetation (Castilla-Beltrán, Nascimento, et al., 2021; Nogué et al., 2022; Zargar et al., 2025), diatoms indicating lake trophic stages (Pla-Rabés & Catalan, 2018), or even sedimentary ancient DNA (*sedaDNA*) from past organisms (both plants and animals) (Alsos et al., 2024; Brown et al., 2025). The palaeoecological records covering the past several thousand years can also be dated using radiocarbon (^{14}C) and lead-210 (^{210}Pb) dating methods. These techniques provide precise age estimates that allow reconstruction of ecosystem changes and elemental composition over time. In the case of lake sediments, their biogeochemical composition results from multiple factors: the catchment bedrock, biological inputs from terrestrial and aquatic organisms, materials transported by runoff, and chemical reactions occurring at the lake bottom (Lacourse & Gajewski, 2020). Therefore, the elemental composition of lake sediments can reflect past ecosystem elementomes considering both terrestrial and lacustrine inputs. Similar techniques are applied to other palaeoenvironmental records such as peat and soils. However, the depositional nature of lakes usually allows for resolution at higher resolution than peat and soils, especially o varved lakes, which provide yearly evidence of change (McCarthy et al., 2025)

Palaeoenvironmental records are also excellent archives of human activities. For instance, fire activity can be revealed from charcoal analysis (Power et al., 2008) or biomarkers like polycyclic aromatic hydrocarbons (PAHs) (Chirakkal et al., 2025). Livestock can be tracked from specific fungal spores (Davies, 2019), biomarkers that indicate both human and livestock presence such as coprostanol (Bethell et al., 1994) and *sedaDNA* of the domesticated animals (Garcés-Pastor et al., 2025), which can accurately depict different domesticated species. Although research on human legacies on ecosystems has advanced considerably, critical uncertainties remain. These include limited understanding of emerging and hybrid cultural–natural ecosystems, difficulties in forecasting rates of ecological change, and challenges in establishing precise timelines for the drivers behind these changes (Nogué et al., 2025)

Sedimentary sequences from oceanic islands are important for studying human impacts, since the system can be studied before and after the arrival of humans. Island ecosystems drastically changed with human arrival (Nogué et al., 2021). This suggests that whether the Anthropocene began earlier or later in different islands, and whether its onset occurred more rapidly on oceanic islands (Whittaker et al., 2017). Similarly, high-elevation mountain ecosystems are isolated enough to provide clear signals of the onset of human activities (Flantua et al., 2020). Records from these isolated ecosystems, such as oceanic islands and mountain environments, offer an ideal foundation for describing long-term trends in ecosystem elementomes under human pressure and enable the discussion of earlier manifestations of the Anthropocene.

How is the elementome measured from palaeoenvironmental records?

The elemental composition of palaeoenvironmental records can be assessed by diverse methods. The most popular instruments are X-Ray fluorescence (XRF) core scanners and field portable scanners (pXRF) (Schillereff et al., 2016). They allow non-destructive and fast analysis of the content of most rock-forming elements. However, light elements such as C, N, and oxygen are not measurable with these instruments, and other light elements such as sodium, magnesium, aluminium, silicon or phosphorus can be measured, but obtaining robust results is often complicated (Bertrand et al., 2024).

XRF core scanners offer high resolution continuous sampling of the cores, while pXRF is suitable for discrete samples, for example, soil samples from profiles in archaeological excavations (Hunt & Speakman, 2015). Both approaches offer an outline of the geochemical changes across the palaeoenvironmental record. Inductively coupled Plasma Optical Emission Spectrometry (ICP-OES) or Inductively coupled Plasma Mass Spectrometry (ICP-MS) are also common in palaeoenvironmental records, especially when more precise concentrations of elements are pursued (Provete et al., 2024). C and N, together with their stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) can be measured accurately with an elemental analyser (Brodie et al., 2011). The C content is measured from samples that have been decarbonised, to estimate only the organic carbon. Across the thesis, the C values correspond to total organic carbon (TOC). In contrast to the continuous measurements of XRF core scanners, C and N data are discrete. Thus, combining inorganic elements (XRF) with C and N measurements force a discrete assessment of the elementome.

Solved the challenge of finding a measurable proxy for past ecosystem elementomes and human activities, the next step is to decide on the best statistical approach to describe the changes in the elementome. Trajectory analysis has recently gained attention in community ecology (De Cáceres et al., 2019; Sánchez-Pinillos et al., 2023; Sturbois, Cáceres, Bifolchi, et al., 2023; Sturbois, Cáceres, Sánchez-Pinillos, et al., 2023). This approach consists of generating a multivariate space with a set of variables and then drawing the temporal trajectories of consecutive samples within the multivariate space. The trajectories can then be

used to describe temporal shifts between variables, but also can be quantified in terms of variability, speed and direction. With elementome trajectory analysis we can integrate all available elemental data into single metrics. In this PhD thesis we use an Elementome Trajectory Analysis that is defined as the trajectory within a multivariate space by the elemental composition of samples in a palaeoenvironmental record (palaeoelementome). Different human activities would impact on the elementome trajectories (Figure 2).

Objectives

This PhD thesis aims to describe and quantify long-term shifts in ecosystem elementomes, associated with the onset of different human activities. The research is guided by the following research questions:

Q1: Can palaeoenvironmental records (*e.g. lake sediments*) be a good source describing ecosystem elementomes using elementome trajectory analysis?

First and Second Chapters

Q2: How can we represent and quantify ecosystem elementomes?

Second and Fifth Chapters

Q3: How does the onset of human activities affect ecosystem elementomes?

Second, Third and Fourth Chapters

Q4: Are ecosystem elementomes shifting more dramatically in post-industrial times or with the onset of human activities?

Second and Third Chapters

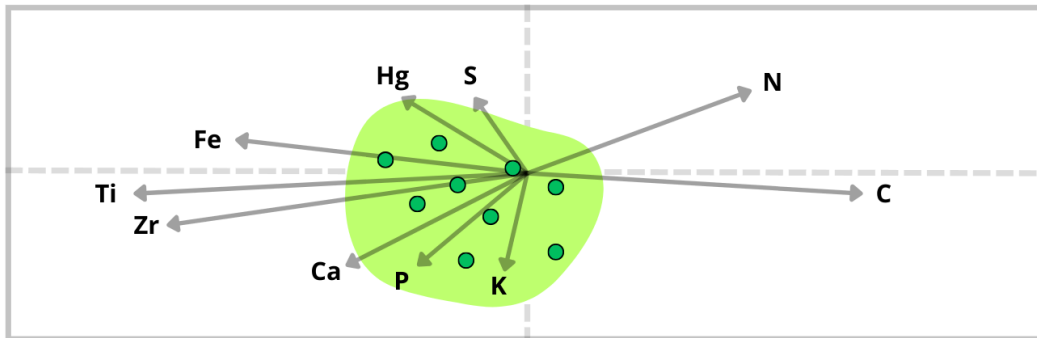
Q5: Can human impact on ecosystem elementomes be discriminated against other factors like climate or vulcanism?

Second, Third and Fourth Chapters

Q6: How shifting ecosystem elementomes interact with biodiversity patterns?

Fourth Chapter

Hypothetical Ecosystem Elementome previous to human activity

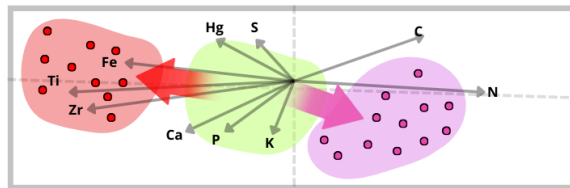


After settlement



Terraforming and resource extraction leads to increased erosion in the catchment

Settlement derived sewage and organic waste fuel algal production and deposits plant-derived material

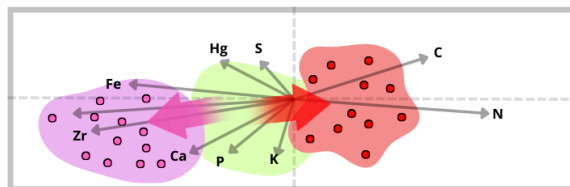


After deforestation



Fires and logging increase the erosion of the catchment, increasing the lithogenic inputs into the lake

At the same time, if carbon-rich soils and calcinated material erodes and arrives with the runoff, the organic composition may increase

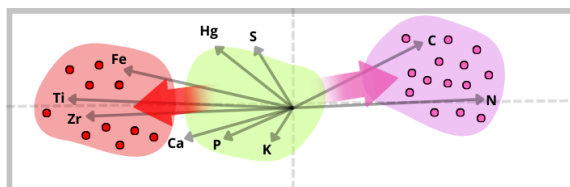


After livestock introduction



Livestock can increase organic matter in lake sediments by adding manure, enhance nutrient deposition.

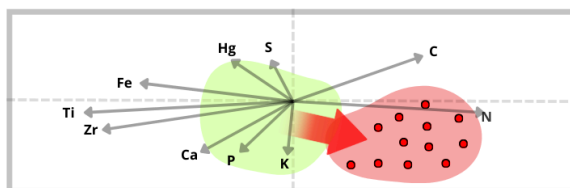
At the same time, the decomposition of organic matter can accelerate and be liberated to the atmosphere before is washed into the lake. Moreover, grazing induces erosion.



After agriculture



Agriculture increases organic matter in lake sediments by supplying nutrient-rich runoff that fuels algal production and deposits plant-derived material



After mining/industrial activities



Mining and other industrial activities increase the content of trace elements, and are sometimes associated with a decrease in plant productivity

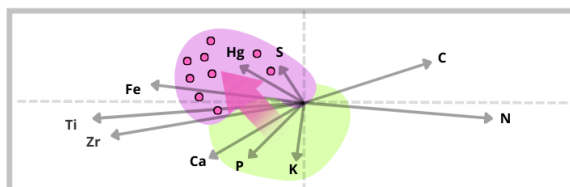


Figure 2. Hypothetical elementome shifts associated to different anthropogenic disturbances.

Thesis outline

In the **First Chapter** (*Challenges and opportunities for addressing past ecosystem elementomes from natural archives*), we discuss the potentials and limitations of four natural archives that can inform about past ecosystem elementomes: lake sediments, soil profiles, peat records and tree-rings. The concept of this work was developed during a research stay with the DendrOlavide group in Pablo de Olavide University, in Sevilla. The aim of the visit was to build bridges between XRF assessments of sedimentary records and dendrochemistry. The laboratory of Raúl Sánchez-Salguero and Andrea Hevia counts with an XRF tree-core scanner, enabling the test of Elementome Trajectory Analysis in tree-rings. In this chapter, we discuss the caveats of tree-ring dendrochemistry to reconstruct ecosystem elementomes, proposing future directions for the use of tree-rings in palaeoelementome studies.

The **Second Chapter** (*Unveiling two millennia of ecosystem changes in the Azores through Elementome Trajectory Analysis*) of the thesis aims to evaluate both lake sediments and elementome trajectory analysis as reliable tracers of past ecosystem elementomes. The study was done in collaboration with a network of researchers working on the Azores archipelago: Pedro Raposeiro, Santiago Giralt, Sergi-Pla, Armand Hernandez, and Mario Benavente, which previously published a paper (Raposeiro et al., 2021) that inspired this initial work. In collaboration with Miquel de Cáceres, who introduced trajectory analysis to community ecology and developed the useful *ecotraj* package (De Cáceres & Djeghri, 2025), we developed the Elementome Trajectory Analysis approach. We applied this method to five lakes in the Azores Archipelago, each with a detailed reconstruction of human activities and ecosystem disturbances. We tested five metrics derived from Elementome Trajectory Analysis: elemental turnover, directionality, speed, explored area and three-centroid length. Moreover, we compared the metrics from elementomes that included C and N, and elementomes that only integrated XRF data. The slight differences between “complete” elementomes (i.e. including C and N) and XRF-driven elementomes to the next chapter. This chapter is published in *Ecological Indicators*.

In the **Third Chapter** (*Erosion and geochemical legacies of human colonisation on Atlantic islands*) we upscaled the elementome analysis to 21 palaeoenvironmental records from islands across the Atlantic. We looked for collaborations with researchers that carried out XRF analyses on sedimentary sequences from islands. Three of the records were analysed during a research visit to the University of La Laguna (with Lea de Nascimento and Álvaro Castilla-Beltrán), where I subsampled sediment cores from Cabo Verde and the Canary Islands. The XRF analyses were later conducted at our laboratories at the Autonomous University of Barcelona (UAB) and in the Centre for Ecological Research and Forestry Applications (CREAF). Five of the records had not been previously published, while the remaining datasets were open access, at least for some of the elemental data. Our aim is to depict the impact of human arrival to island ecosystems, focusing on in which direction the elementomes may shift, and in changes in the dynamism of the trajectories. Moreover, our interest is to detect different signals in the distinct waves of anthropisation of the islands: from the first settlers to the European colonisations during their overseas expansion, to the

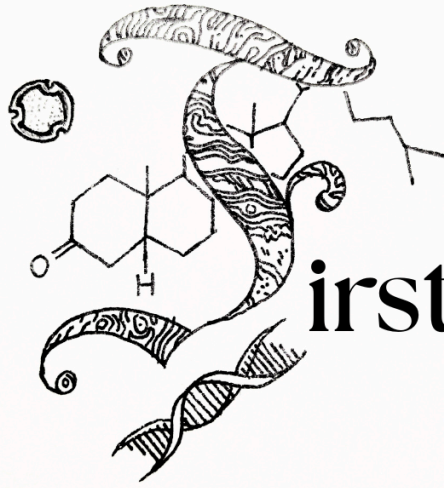
onset of industrial societies. The complete dataset is also part of a data stewardship pilot, which aims to foster data-sharing in the XRF community and harmonisation of the data. This is part of the PalaeOpen COST Action, in collaboration with Neotoma.

For the **Fourth Chapter** (*Biogeochemical and vegetation coupling in the Alps: climate change and livestock effects on alpine ecosystems across the Holocene*), the aim is to assess long-term feedback between ecosystem elementomes, and plant communities. This research was possible thanks to a research stay in The Tromsø Arctic University Museum, under the supervision of Inger Greve Alsos and Anthony Brown. After learning from the *sedaDNA* laboratory protocols and DNA interpretation together with Sandra Garcés-Pastor and Scarlett Zetter we used a network of 12 alpine lakes previously dated and analysed for *sedaDNA* to answer the main question. The *sedaDNA* analysis shows robust data for plant communities and the relative abundances of wild and domesticated mammals. XRF core scanning was also previously performed to the cores at the same levels as the *sedaDNA*. All together provide a robust foundation to study the parallel long-term dynamics of plant communities and ecosystem elementomes, looking at their coupling across time and different climatic and anthropogenic disturbances.

The **Fifth Chapter** (*soundtraj: Ecological trajectories through sonification and animation of multivariate environmental data*) explores sonification of elementome trajectories. Together with Lina Bautista and Julia Múgica (Axolot collective) we generated data-driven sound, which transforms the values of the principal components into tones that shift with elementome changes. The tool extends to all kind of temporal progression of multivariate data (e.g. species abundance) and is now open to everyone that want to use it with their own datasets (de la Casa et al., 2025b). In this chapter, our aim is to translate the classic two-dimensional PCoA plots that visually represent the elementome into sound. But it is undeniable that this works open the doors for future explorations of outreach strategies and alternative discussions in the art-science interface.

The **General Discussion** aims to gather all the results and answer the research questions raised here in the general Introduction.

Finally, the **Appendices** and the **References**. The **First Appendix** consists of a list of works that are not chapters of the thesis but are related with the topic: research papers, conference participations and outreach and community activities. **Second, Third and Fourth Appendix** contains the supplementary information of the **Second, Third and Fourth Chapter**, respectively.



irst Chapter:

Challenges and opportunities
for addressing past ecosystem
elementomes from natural
archives



Challenges and opportunities for addressing past ecosystem elementomes from natural archives

Javier de la Casa, Josep Peñuelas, Jordi Sardans, Andrea Hevia, Raúl Sánchez-Salguero & Sandra Nogué.

Abstract

Anthropogenic disruption of global nutrient cycles and pollution has brought attention to reconstructions of the elemental composition of ecosystems. Natural archives (i.e. lake sediments, soil profiles, peat records, and tree-rings) are good sources of reconstructing past environments, and the advances in methods facilitate their use. Here we discuss the potential and limitations of each archive to assess the ecosystem elementome. For this we take into consideration which compartment of ecosystems (i.e. atmosphere, biosphere, hydrosphere, pedosphere or lithosphere) is dominating the biogeochemical signals in each archive. Lake sediments and soil profiles offer elementome assessments from all ecosystem compartments at a catchment scale. Lake sediment offers fine and robust chronologies, but unlike soil, are affected by in-lake processes. Peat reflects biospheric changes, which are at the same time atmospheric changes, in the case of bogs, and hydrological/pedological in fens. Tree-rings offer a challenging interpretation of biogeochemical data because of nutrient translocation (vertically and horizontally) for physiological needs. However, they can offer valuable insights of changes in the element accumulation at a biospheric level. With this work, we aim to give the readers an overview of the different possibilities of natural archives to answer important questions about long-term biogeochemical trends; considering as well as the caveats of each record to define palaeoelementomes.

Introduction

Global change is consistently affecting the Earth system biogeochemical cycles, especially the C, N and P cycles (de la Casa et al., 2025; Peñuelas et al., 2020; Rockström et al., 2009). However, fewer studies address changes in the elemental composition of ecosystems in previous episodes of the story of human and life (palaeoelementome), which have also been affected by climate change, geological disturbances or anthropogenic pressures. Natural archives, or palaeoenvironmental records (e.g. lake sediments, soil profiles, peat records, and tree-rings), are excellent tools for unveiling information about past ecosystems.

Advancements in instruments for measuring inorganic and organic elemental composition have enhanced our understanding of past biogeochemical legacies in ecosystems. X-ray fluorescence (XRF) provides a rapid, non-destructive method for analysing the inorganic geochemistry (Rothwell, 2006). While XRF is efficient for relative elemental variations, Inductively Coupled Plasma–Optical Emission Spectrometry (ICP-OES) and Inductively Coupled Plasma–Mass Spectrometry (ICP-MS) offer far more precise and accurate quantification of elemental concentrations, with higher cost and requiring destructive sample preparation (Gill, 2014). In contrast, for key biogeochemical elements such as carbon (C), nitrogen (N), and oxygen (O), which cannot be directly measured with XRF or ICP techniques, dedicated elemental analysers are employed, providing robust measurements of total organic and inorganic fractions.

Distinct natural archives have demonstrated to be essential in the study of terrestrial ecology at longer temporal scales. Depositional records encapsulate information about the fossil remains that are being sedimented, in the case of lake sediments or soil profiles; or accumulated in the case of peats (Bottjer, 2016). The dating of depositional records consists of different techniques. Radiocarbon dating is the most common and implies the sampling of organic remains across the record to determine their ^{14}C contents (Lacourse & Gajewski, 2020). Other techniques based on natural and artificial radionuclides, ^{210}Pb or ^{137}Cs (Benoit & Rozan, 2001), offer alternatives for dating recent sediments. This allows us to reconstruct past environments through the analysis of several proxies that get trapped in the record. Remains of pollen, spores and phytoliths help to reconstruct past vegetation (Castilla-Beltrán, De Nascimento, et al., 2021; Nogué et al., 2021; Rashid et al., 2019; Zargar et al., 2025), which is also doable through the analysis of sedimentary ancient DNA (Alsos et al., 2024; Garcés-Pastor et al., 2025). Charcoal remains or biomarkers are also widely used to depict natural and anthropogenic perturbation in the ecosystems (Dubois & Jacob, 2016; Power et al., 2008). Dendrochronology on the other hand uses wood to infer the past. Each tree-ring is considered as a yearly metric, and their anatomy and chemical composition is used to infer past environments. While dendrochronology is the most commonly applied palaeoclimatic study (Sheppard, 2010), tree-rings also provide valuable information into fire regimes (Parks et al., 2025), pollution (Kirdyanov et al., 2020), and flooding events (Ballesteros-Cánovas

et al., 2015). Although all the natural archives mentioned have strong potential for reconstructing past ecosystem elementomes, interpreting biogeochemical data from each comes with its own peculiarities and limitations. For example, each archive is more sensitive to changes in different compartments of the terrestrial ecosystems, such as the atmosphere, biosphere, hydrosphere, pedosphere, and lithosphere (Figure 1). Here, we aim to discuss the potential and limitations of lake sediments, soil profiles, peat records and tree-rings in assessing the elemental composition of past environments, as these archives are among the most suitable for inferring the elementome of terrestrial ecosystems. While not considered in this study, ice cores are relevant sources of information about past ecosystems from aerosols and gases trapped in the ice, revealing the biogeochemical composition of the cryosphere and the atmosphere, but less information (Hörhold et al., 2023; Vimeux et al., 2009). Although speleothems can retain palaeoecological information (Campbell et al., 2023; Columbu et al., 2020) they are excluded here because this study focuses on archives with a stronger direct ecological signal rather than primarily palaeoclimatic reconstructions (McDermott, 2004). Other natural archives such as marine sediments, corals were not considered, as they provide less information about terrestrial ecosystems. Our aim is to highlight the insights that each archive provides, alongside their constraints, to evaluate which record, or combination of records, is best suited for addressing different research questions about the ecosystem palaeoelementome.

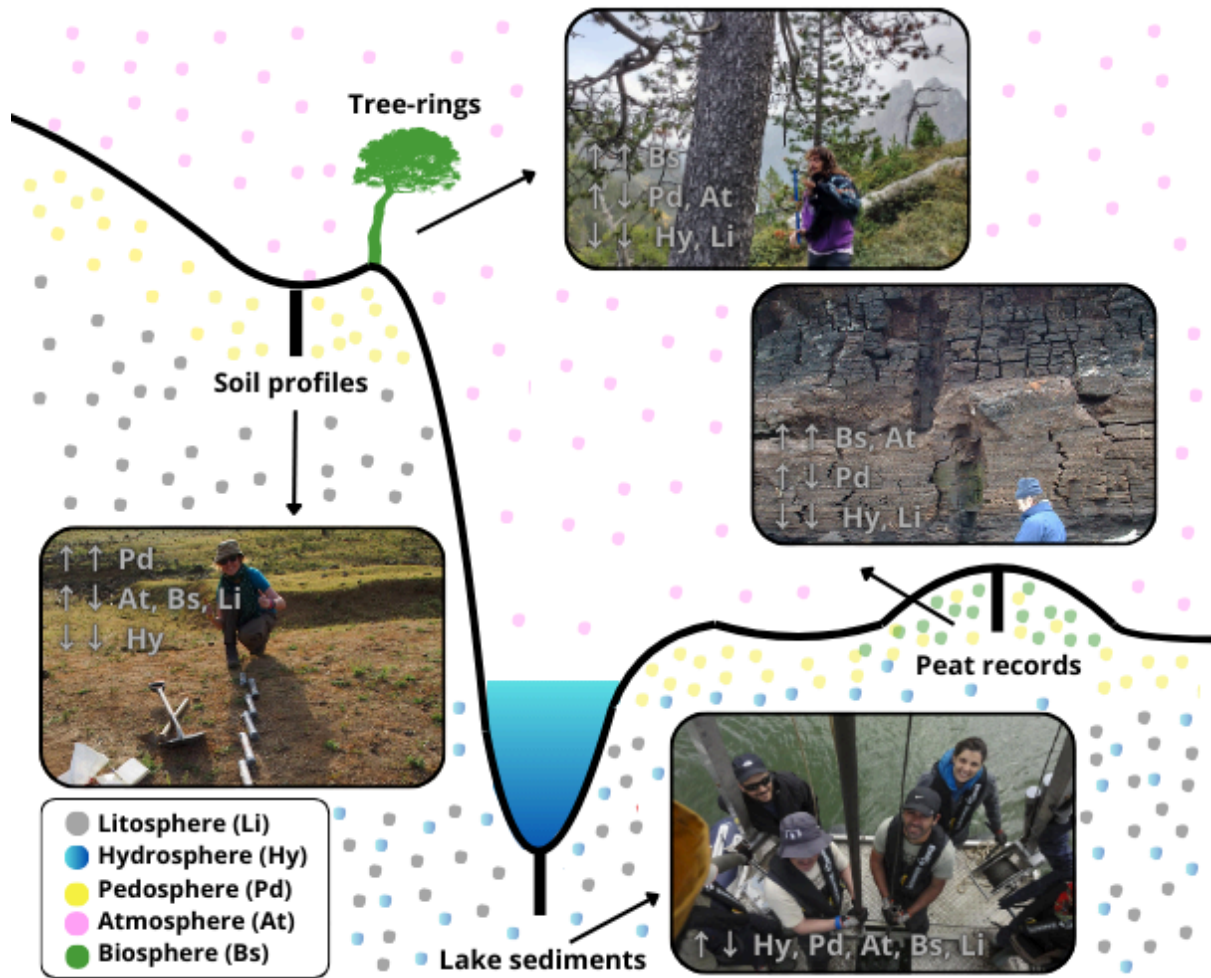


Figure 1. Representation of the different compartments of terrestrial ecosystems, and the potential of natural archives to detect changes in the composition of each compartment. The pictures represent different sampling campaigns. Tree-rings: Aigüestortes Natural Park, Spain. Soil profile: Santo Antao, Cabo Verde (Castilla-Beltrán et al., 2019). Peat record: Hooker’s Point, Falkland Islands/Malvinas (Scaife et al., 2019). Lake sediments: Lake Funda, Flores, Azores (Ritter et al., 2022)

Sedimentary records: lakes

Lake sediments are one of the most popular archives, due to the preservation of different proxies, the possibility to capture long timescales and the consistent depth age models. The biogeochemical content of lake sediments responds to changes in the chemistry of the air, water, inputs of watershed material, and to the biological activity within the lake waters (Dubois et al., 2018). This makes lake sediments good reservoirs of changes across all the ecosystem "spheres", but not as good at depicting clear signals from a specific compartment. For instance, the organic content of the sediment can have multiple sources: atmospheric deposition, increased lake productivity or material from the watershed (Mittelbach et al., 2025; Tipping et al., 2016). Multiproxy analysis enables tracing the origin of the organic

matter to its corresponding source. Stable isotopes $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in lake sediments help distinguish organic matter sources (Douglas et al., 2022; Gu et al., 1996; Herczeg et al., 2001; Martinez et al., 2024; Torres et al., 2012). $\delta^{13}\text{C}$ separates terrestrial inputs (e.g., C3 plants with low $\delta^{13}\text{C}$) from aquatic production (higher $\delta^{13}\text{C}$), while $\delta^{15}\text{N}$ differentiates atmospheric deposition or nitrogen fixation (low $\delta^{15}\text{N}$) from in-lake productivity or anthropogenic inputs (high $\delta^{15}\text{N}$). These markers together clarify the balance of watershed, in-lake, and atmospheric contributions. Interpretation of recent $\delta^{13}\text{C}$ values must account for the Suess effect, which lowers atmospheric $\delta^{13}\text{C}$ due to fossil fuel emissions (Graven et al., 2020; Verburg, 2007). Biomarkers or the analyses of organic compounds and pollen remains are also a good tool, revealing the origin of organic inputs (De Jonge et al., 2025). Besides organic matter, biogenic silica and carbonates from shell organisms are also relevant sources of biospheric biogeochemical signals (S. Liu et al., 2021). Lithogenic particles arrive at the lake from watershed runoff and can shed light to erosion dynamics in the catchment. Thus, bedrock mineralogy (e.g. karstic materials in sinkholes, lakes on siliceous and bedrocks) and the landscape dynamics (e.g. landslides, vegetation cover) are the main controls of the lithogenic signal (Bertrand et al., 2024). However, they can also be sourced from the atmosphere, especially from volcanic eruptions (Jiang et al., 2024), dust transportation and deposition (Ballantyne et al., 2011; Bullard et al., 2016; Pérez-Martínez et al., 2020) or anthropogenic loadings (Sarkar et al., 2015). Elements like titanium and zirconium are good proxies for erosion, as their main route to the sediments is runoff (Milnes & Fitzpatrick, 2018)

Historical reconstructions of lake sediment biogeochemistry can be skewed by in-lake processes. Bioturbation alters sedimentary dynamics and can complicate dating and biogeochemical interpretations, specially at shallow waters (Martin et al., 2005). Moreover, the redox environment in the lake sediments affects the accumulation of some elements. Phosphorus is a great example, oxic conditions promoting P binding to iron oxides, while anoxic conditions lead to the reduction of iron and subsequent release of P into the water (Li et al., 2018; Tu et al., 2023). It is important to note that the surface samples of the record may be in the active, oxic zone, and thus the biogeochemical content will not be similar from what will eventually be preserved deeper down. Removing the top samples or unconsolidated material is a common practice as it does not represent the long-term preserved signal (Gregory-Eaves & Smol, 2024). Shallow waters, ponds, and reservoirs are typically more sensitive to biogeochemical changes due to stronger sediment–water interactions, limited stratification, and greater influence from external inputs (Pilla et al., 2020; Qin et al., 2020). Changes in lake acidity (Boyle, 1991) and water level (Fischer et al., 2020), and catchment alterations (McGowan et al., 2025; Moyle et al., 2024) across timescales should be considered, as will influence biogeochemical dynamics.

Sedimentary records: soils

Before discussing soil profiles, it is important to distinguish between soil profiles from depositional records and palaeosols. A soil profile in a depositional environment, such as a volcanic caldera (de Nascimento et al., 2020) or an alluvial plain (Castilla-Beltrán et al., 2018), develops while new material is continually added through processes like ash fall, sedimentation, or colluviation. In those settings, soil horizons may form but are often weakly developed or repeatedly reset by burial, creating a more continuous though mixed record of inputs and surface conditions. In contrast, palaeosols represent a former land surface that developed under stable conditions and was later buried by younger deposits, preserving the soil features as a “fossilised” horizon (Orr & Roberts, 2024). Unlike depositional soil profiles, palaeosols provide a discrete snapshot of environmental and ecological conditions at a particular time, rather than an ongoing sequence (Stein et al., 2021), which holds potential for reconstructing biogeochemical cycling at discrete periods of time (Dzombak, 2021). Similarly, archeological soils (e.g. abandoned settlements, middens) provide snapshots from anthropogenic depositional environments that are also worth studying (Bintliff & Degryse, 2022), especially to understand human influence of ecosystems. In this section, however, we will discuss soil profiles from natural depositional environments, as they provide continuous reconstructions of terrestrial ecosystems.

Lake sediments and soil profiles from depositional environments share several similarities in how their stratigraphy is shaped by external processes and landscape dynamics. However, lake sediments generally provide more continuous and fine-resolution archives due to the relatively stable depositional environment of the lake, where sediments settle under water and are quickly buried in anoxic conditions that enhance preservation. In contrast, soil profiles are exposed to ongoing biological and human activity, root growth, pedogenesis, and leaching, which can mix or alter chemical signals over time (Li et al., 2021; Lin, 2011) and complicate dating of and the resolution of the records (Chichagova & Cherkinsky, 1993). Thus, while both archives reflect similar catchment processes, lake sediments often yield more coherent and temporally precise records. Unlike lake sediments, soil profiles are not influenced by in-lake processes, making them more suitable for reconstruction of soil dynamics. Soil records are essential for building trajectories of soil organic carbon, assessing timelines of sequestration and losses (Li et al., 2025; Wang et al., 2010). Similar to lake sediments, $\delta^{13}\text{C}$ is an excellent tracer of carbon sources, capturing shifts between C3/C4 vegetation, or the decline of $\delta^{13}\text{C}$ in vegetation and the atmosphere due to fossil carbon signals (Suess effect) (Krüger et al., 2024). Together with $\delta^{15}\text{N}$ can enlarge our understanding of soil organic matter (Park et al., 2023). The strong influence of carbon by depth (Balesdent et al., 2018), as well for other elements like phosphorus (Owens et al., 2008) should be taken into account when reconstructing elemental dynamics across time, as it is not only time influencing the composition, but depth. Top samples should be analysed separately, corrected or removed, to avoid skewed reconstructions

Biospheric records: peat

From a pedological perspective, peat records should be considered soil records (Lourenco et al., 2023). However, peats are constituted mainly by plant organic matter, thus providing an excellent library to reconstruct elementome changes at a biospheric level. Unlike the previously discussed soil profiles, peat waterlogged and anoxic environments allow better conservation than soils, facilitating the preservation of biological proxies and even natural mummification of dead bodies (Painter, 1991). Peat has two sections: the acrotelm, which is the upper part, with less compacted biological material and fluctuating water content, and thus oxic and anoxic conditions. The catotelm is the deeper part of the peat, is permanently waterlogged and this anoxic. There are two types of peat depending on their reliability to groundwater. Fens are peats that are fed with soil and groundwater. They are nutrient rich, have neutral pH and are usually grass-dominated. Fens are more sensitive to changes in the groundwater (hydrosphere) levels and composition. Increases in nutrient rich waters may reduce carbon sequestration in fens (Ehnavall et al., 2025; Larsson et al., 2017). Also, reductions of the water table can dry the acrotelm and induce aerobic respiration of the organic material, liberating carbon from the peat. The other type of peat is the bog. Bogs are ombrotrophic, meaning that they rely only on precipitation and the water retention capacity of the plants, especially *Sphagnum* sp (Joosten & Clarke, 2002). This leads to bogs being limited in nutrients and acidic. Ombrotrophic bogs form high lumps of moss (hummocks or peat mounds) which accumulate material with strong potential for stratigraphical studies. However, this deposited material should not be considered a sedimentary record like soil profiles and lake sediments. Bog records are thus sensitive to atmospheric elementome change, making them excellent sources for biospheric elementome shifts. Because bogs are less affected from geochemical imprints of runoff, as they grow from plant accumulation rather than sediment accumulation. This makes them especially useful archives in studies where runoff-related alterations of geochemical composition are not the primary concern

Over time, fens (minerotrophic peats) may accumulate enough material to raise above the watertable, and transition to bogs (ombrotrophic peats) (Hughes et al., 2000). Pollen, geochemistry and stable isotopes can help to identify the transition (Da Silva et al., 2022; Hobbie et al., 2017). Although rare, opposite bog-fen transitions have been recorded (Blaus et al., 2020). Bogs have been used for studying past climate (Booth & Jackson, 2003), studying long-term macronutrient dynamics (Schillereff et al., 2016), anthropogenic signals after the Industrial Revolution (Garcés-Pastor et al., 2023; Sellers et al., 2025) or ancient societies (Yeloff et al., 2007; Yu et al., 2010). As major carbon sinks, peatlands have been extensively studied for carbon accumulation. However, direct elemental comparison of recently formed surface peat with deeper, older layers can be misleading, since surface peat is still undergoing decomposition (Young et al., 2019). This is known as the acrotelm effect, and is applicable to other elements (Astolfi et al., 2023). Net carbon balances should not be calculated from carbon accumulation rates from recent samples. Acrotelm samples should be removed, or integrated within empirical models that consider autogenic long-term peat decomposition (Young et al., 2021).

Biospheric record: Tree-rings

Moving from depositional records, tree-rings are one of the most used archives to reconstruct past environments. Each ring determines a yearly chronology, which makes them easier to date in comparison with the previous archives. Not all tree species form rings, and in the species that do, harsh conditions can lead to missing rings, or the creation of false rings as response to stress (De Micco et al., 2016; Esper et al., 2013). The range of time is limited by the long survival of the trees. However, combined chronologies can be constructed beyond single trees. Using wood relics (e.g wood preserved in ancient buildings, fossil woods) alone or combined with living trees is feasible, providing longer timelines (Büntgen et al., 2021; Friedrich et al., 2004; Nicolussi et al., 2005; Pilcher et al., 1984; Roig et al., 2001). The elemental composition of the trees can be calculated with ICP techniques, or with specific XRF analysers (Sánchez-Salguero et al., 2019). Some elements and isotopes are used to infer tree productivity or reconstruct climate (Arosio et al., 2025; Hevia et al., 2018; Levesque et al., 2019), or even help as indicators of tree chronology, when tree-rings are not apparent (C. V. Wood, 2014). Contrary to geochemical assessments in depositional records, dendrochemistry is a less popular field, and its interpretations are full of challenges.

The atmospheric contributions to dendrochemical signals are better defined than ones derived from the soil (Binda et al., 2021). Proxies derived from direct stomatal uptake of atmospheric compounds are generally the most reliable. This reliability stems from their direct, non-mediated assimilation and their restricted movement within the tree, as these chemicals circulate primarily in the phloem sap, confined to narrow pathways. Thus, $\delta^{13}\text{C}$ can provide robust insights into increases in the uptake of fossil fuel-derived carbon dioxide (Cernusak & Ubierna, 2022). Water stable isotopes ($\delta^2\text{H}$ and $\delta^{18}\text{O}$) can track hydrological patterns (Cintra et al., 2025); and atmospheric mercury pollution can be reconstructed robustly (Clackett et al., 2018). Contrary, elements sourced from the soils as macronutrients (e.g. nitrogen, phosphorus, potassium), micronutrients (e.g. iron, manganese, zinc) and even toxic trace elements (e.g. cadmium, chromium) produce less reliable temporal trends. However, they have been widely used to track pollution (S. Chen et al., 2021; Monticelli et al., 2009; Schneider et al., 2019) or volcanic eruptions (Hevia et al., 2018; Pearson et al., 2005). Although the accumulation of pollutants is evidenced, the time may not match the pollution episode. Tree-rings have been also used to reconstruct nitrogen (Oulehle et al., 2022) and phosphorus (Kohler et al., 2019) availability and acquisition. Elements are actively translocated within plant tissues for their metabolic needs, complicating the reconstruction of palaeoelementomes. This is apparent when looking at hardwood (i.e. inner dead xylem) and sapwood (outer xylem that conducts sap and stores nutrients). Mobile elements like potassium radically increase its content in sapwood compared to hardwood, while may decrease like calcium in *Pinus uncinata* (Binda et al., 2021; Hevia et al., 2018). Increases in elements in the recent year (outer rings), thus, may not represent an accumulation of the element towards the present, but a physiological pattern of radial transport of nutrients. This transport may also be vertical (Inagawa et al., 2023).

Since element uptake takes place principally from the soil, dendrochemistry primarily reflects nutrient uptake from the pedosphere, which makes tree rings a complex and sometimes ambiguous archive for palaeoelementome reconstructions for the reasons explained above. Nevertheless, they hold considerable potential. To fully unravel the value of dendrochemistry, several steps are required. First, comparing dendrochemical records with parallel archives such as soils, peat, or lake sediments (Kuosmanen et al., 2020) can help validate interpretations and further understand element flow in three-rings (Binda et al., 2021). Second, improving our understanding of nutrient mobility at a species level is essential for developing robust models and calibrations. This has been tested with artificial enrichment of elements in controlled experiments (Durand et al., 2020; Hagemeyer & Weinand, 1996; Kohler et al., 2019; Tomlinson et al., 2014), but further mechanistic studies are also needed. Finally, separating analyses of sapwood and heartwood can aid to distinguish temporal vs physiological patterns, as heartwood acts as a long-term nutrient sink. This distinction could be particularly useful when combining dendrochemical values from different trees, relict or alive

Final remarks

Now that the potential and limitations of each natural archive has been pointed out (Table 1) we can think on the use of each archive to respond to different research questions about palaeoelementomes. If the aim is to know about how much the biosphere has changed, tree-rings offer the advantage of tracing at an individual level, while peats do at a community level. However, for tree-rings to be used, complementary soil records should be taken to validate dendrochemical reconstructions, and at the same time, reconstruct nutrient availability from soils. The main challenge here is the different time resolution: yearly in tree-rings while centennial in soil records. For this reason, lake sediments (decadal and annual resolutions) could be used instead of soil profiles. Lake sediments and soil profiles would be the most suitable to track elemental changes derived from the whole catchment. This includes erosion episodes, livestock introduction, vegetation shifts or polluting activities. Lithospheric changes, sourced from the leaching bedrock, should not be neglected in sedimentary records (Boyle et al., 2013; Boyle, 2007). To track changes in the atmospheric element content and transportation, ombrotrophic bogs would be the best choice.

While XRF measurements offer valuable opportunities for reconstructing elemental trends at palaeo scales, some elements may not be reliably quantified through this method, even if detected. Phosphorus is a good example. Although XRF can register its presence, it often underrepresents its true concentration due to matrix effects or low sensitivity. In contrast, spectrophotometry techniques provide more robust and accurate quantification of P (Boyle et al., 2023; Moyle et al., 2024; Oxmann et al., 2008), making them preferable when precise elemental data are required. Therefore, studies focusing on long-term elemental trends should be mindful of such methodological caveats. Further research aimed at evaluating potential misinterpretations, particularly from surface samples, will be crucial for developing models

and methodologies that can integrate elemental data more effectively, without discarding valuable records.

Table 1. Differences across the four selected natural archives

	Lake sediments	Soil profiles	Peat records	Tree-rings
Chronology	Radiocarbon and other radionuclides	Radiocarbon and other radionuclides	Radiocarbon and other radionuclides	Tree-ring count (when rings are apparent). Radionuclides can date relict wood
Temporal span	Hundreds to hundreds of thousands of years	Hundreds to hundreds of thousands of years	Over 10.000 years (peat formed at the end of last ice age)	From a single tree between 100 to 1000 years (with exceptions). Combining living trees with relict wood can expand the timeline
Temporal resolution	Decadal. Annual in varved sediments (McCarthy et al., 2025)	Centennial to millennial scale	Decadal to centennial	Annual
Spatial scale	Although widespread, arid areas lack lake formations	Worldwide	Although peat can be found in all continents, heights and climate zones, they are unequally distributed, mainly in the Northern Hemisphere	Widespread but limited by tree distribution. Moreover, in areas like the tropics tree-ring forming species are scarce
Challenges: Surface effects	Oxic lake bottom show more surface disturbance and altered recent signals, while anoxic conditions generally preserve a clearer and more intact recent elemental record.	The active top layer(s) accumulate more carbon, which will eventually be decomposed	The acrotelm effect (oxic active layer)	Physiology driven differences between sapwood and hardwood
Ecosystem compartment driving the shifts	Mixed	Mainly pedosphere, with effect of the rest	Biosphere and atmosphere	Biosphere, atmosphere and pedosphere



H — 1
 B — 5
 C — 12
 N — 7
 O — 8
 F — 9
 Na — 11

Ti — 22
 V — 23
 Cr — 24
 Mn — 25
 Fe — 26
 Co — 27
 Ni — 28
 Cu — 29
 Zn — 30
 Ga — 31
 Ge — 32
 As — 33
 Se — 34
 Br — 35
 Kr — 36
 Rb — 37
 Sr — 38
 Y — 39
 Zr — 40
 Nb — 41
 Mo — 42
 Tc — 43
 Ru — 44
 Rh — 45
 Pd — 46
 Ag — 47
 Cd — 48
 In — 49
 Sn — 50
 Sb — 51
 Te — 52
 I — 53
 Xe — 54
 Ba — 56
 La — 57
 Ce — 58
 Pr — 59
 Nd — 60
 Pm — 61
 Sm — 62
 Eu — 63
 Gd — 64
 Tb — 65
 Dy — 66
 Ho — 67
 Er — 68
 Yb — 70
 Lu — 71
 Hf — 72
 Ta — 73
 W — 74
 Re — 75
 Os — 76
 Ir — 77
 Pt — 78
 Au — 79
 Hg — 80
 Tl — 81
 Pb — 82
 Bi — 83
 Po — 84
 At — 85
 Rn — 86
 Fr — 87
 Ra — 88
 Ac — 89
 Th — 90
 Pa — 91
 U — 92
 Np — 93
 Pu — 94
 Am — 95
 Cm — 96
 Bk — 97
 Cf — 98
 Es — 99
 Fm — 100
 Md — 101
 No — 102
 Lr — 103

Zr — 90
 Nb — 94
 Mo — 96
 Ru — 104,4
 Rh — 104,4
 Pd — 106,6
 Ag — 108
 Cd — 112
 Ur — 116
 Sn — 118
 Sb — 122
 Te — 128?
 J — 127
 Cs — 133
 Ba — 137

? — 180
 Ta — 182
 W — 186
 Pt — 197,1
 Ir — 198
 Os — 199
 Hg — 200
 Au — 197?
 Bi — 210?
 Tl — 204
 Pb — 207

Unveiling two millennia of ecosystem changes in the Azores through Elementome Trajectory Analysis

Javier de la Casa, Sandra Nogué, Miquel de Cáceres, Sergi Pla-Rabés, Jordi Sardans, Mario Benavente, Santiago Giralt, Armand Hernández, Pedro M. Raposeiro & Josep Peñuelas

Abstract

The elemental composition of ecosystems responds to environmental perturbations such as land-use change, offering valuable insights into the impacts of global change. This study applies trajectory analysis to two millennia of elemental composition (elementome), including carbon (C), nitrogen (N), and other geochemical elements recorded from five lakes in the Azores archipelago. By integrating multivariate elemental data, we aim to reconstruct past environmental shifts and understand long-term ecosystem dynamics in response to anthropogenic and non-anthropogenic impacts.

We quantified elementome trajectory analysis metrics, such as elemental turnover, trajectory directionality, and trajectory speed, as ecological indicators to quantify the magnitude and graduality of island ecosystem disturbances. We also tracked elemental shifts over time using CONISS analysis and compared these shifts with previously published environmental reconstructions from the same lakes. Additionally, we analysed and compared trajectory shapes across the lakes to identify patterns and differences.

Our results indicate that the elementome trajectories primarily reflected changes in erosion rates, in-lake biological activity, and catchment dynamics, characterised by distinct patterns of climate variability, wildfires, and agropastoral activities. Trajectory shapes revealed different patterns across shallow and deeper lakes. Our findings demonstrate the utility of Elementome Trajectory Analysis for disentangling the complex interplay between natural and anthropogenic drivers of ecosystem change in island environments, providing a powerful new tool for palaeoecological reconstructions and for monitoring changes at a catchment level.

Introduction

Ecological studies often rely on individual elements (e.g. N)(Cui et al., 2021) or elemental ratios (e.g. C:N:P ratios) (Sardans et al., 2012) to assess resource limitations (Li et al., 2018) or potential stoichiometric imbalances that might cascade through the ecosystem (Cui et al., 2021; Peñuelas et al., 2020). While elemental ratios are undoubtedly relevant for ecosystem analysis, the elementome approach (Peñuelas et al., 2019; Sardans & Peñuelas, 2024) aims to provide a holistic representation of the relative proportion of elements in an ecosystem. The concept of elementome has been used to describe the atomic composition that characterises an organism or species (Fernández-Martínez, 2022; Peñuelas et al., 2019) and hold potential for diverse ecological applications, ranging from understanding ecosystem functioning to advancing niche theories (Fernández-Martínez et al., 2021; Peñuelas et al., 2019).

Ecosystem elementomes change over time. Shifts in these elementomes can be caused by human-related impacts, such as the substantial increase in available C and N due to fossil fuel combustion and extensive fertilisation (Gruber & Galloway, 2008; Sundquist, 1993), or by major land use changes associated with agropastoral and mining activities. Similarly, climatic fluctuations and geological events, such as volcanic activity, play significant roles in shaping ecosystemelementomes (Rodríguez-Hernández et al., 2022; Sun et al., 2021; Waal et al., 2010). Given the potential risks of nutrient imbalances and/or stoichiometric disruptions (Peñuelas et al., 2020), enhancing our understanding on elementome shifts and its consequences is important.

Elementome analysis has proven valuable at the organismal level (Fernández-Martínez et al., 2021; Peñuelas et al., 2019; Sardans et al., 2021), but its application to soils, water bodies, and the whole ecosystem remains limited. This lack of ecosystem-scale data prevents us from fully understanding how shifts in elemental composition drive ecological changes in response to environmental perturbations. Addressing the elemental changes in ecosystems driven by climate, land-use change, and other anthropogenic factors requires an elementome assessment that extends beyond plant elemental composition. Estimating, however, the elementome of an entire ecosystem is a challenging task. Additionally, studying changes in the elementome requires time-series data, especially to understand the consequences of past events such as past climate changes or early anthropogenic impacts. To address these challenges, we propose analysing the elementome within palaeoenvironmental records by introducing the concept of the “palaeoelementome”.

Lake sediments serve as a natural archive, preserving evidence of past environmental conditions and providing insights into ecosystem responses over time (Birks, 2019; Williamson et al., 2009a). They are useful for studying the impacts of contemporary and past environmental change, as they record shifts in ecological and environmental processes (Catalan et al., 2013; Parducci et al., 2017). Each sediment layer represents a snapshot of the biotic and abiotic processes occurring in the lake, its catchment, and surrounding area at a

given time. Various methodologies facilitate the analysis of sediment layers, with fossil pollen providing critical insights into vegetation dynamics (Castilla-Beltrán, De Nascimento, et al., 2021; Nogué et al., 2021, 2022) and charcoal particles serving as indicators of fire dynamics (Kulkarni et al., 2021; Sayedi et al., 2024).

Elemental data also play an important role in palaeoenvironmental studies by providing complementary information to biological proxies. Traditionally, these studies have focused on geochemical profiles obtained through X-Ray Fluorescence (XRF) scanning, as well as measures of carbon (C), nitrogen (N) alongside stable isotopes analysis conducted using mass spectrometry. These analyses often focused to a subset of elements (e.g. N isotopes indicating changes in the source of N) (McLauchlan et al., 2013) or elemental ratios (e.g. Mn/Fe indicating lake oxygenation) (Makri et al., 2021). In addition, palaeolimnologists use elemental composition to define chemical or biochemical facies within the records (Giralt, Rico-Herrero, & Vega, 2011; Hernández et al., 2017), trace metal pollution (Granmo et al., 2020; Karlsson et al., 2015; Ladwig et al., 2017), and associate the different elements with the mineralogy of the record (Garcia-Oteyza et al., 2024; Giralt et al., 2007; Sánchez-López et al., 2016; Speranza et al., 2019). These diverse methods collectively enhance our understanding of how ecosystems have responded to past environmental changes, providing context for predicting future ecological trajectories, particularly under global change scenarios.

By examining (palaeo)elementome trajectories across five distinct lakes from four islands (Flores, Corvo, São Miguel and Pico) in the Azores archipelago (Figure 1), we aim to characterise significant shifts in elemental composition through trajectory analysis and identify their causes. Our goal is to contextualise palaeoelementome dynamics with relevant ecological changes that occurred in each island over the past two millennia, considering both anthropogenic and non-anthropogenic impacts (Hernández et al., 2017; Leeuwen et al., 2005; Raposeiro et al., 2017, 2024; Richter et al., 2022; Ritter et al., 2022; Rull et al., 2017; Skov et al., 2010; Vázquez-Loureiro et al., 2023).

The trajectory analysis aims to quantify the magnitude, direction, and graduality of the changes in elemental composition over time. While spatial trajectories in two-dimensional space are commonly applied in movement ecology, this concept has recently been extended to multivariate spaces in community ecology ((De Cáceres et al., 2019; Giguët-Covex et al., 2023; Matthews et al., 2013; Sánchez-Pinillos et al., 2023; Sturbois, Cáceres, Bifulchi, et al., 2023; Toumi et al., 2023) and has also been applied to other disciplines, such as studies of stable isotopic composition (Sturbois et al., 2021).

We hypothesise that:

- 1) Trajectory metrics (elemental turnover, directionality, and speed) will indicate the magnitude, graduality, and direction of changes in the elementome. These metrics might reveal shifts that align with human activities and/or climate-related events affecting the lakes and their catchments.

2) Distinct trajectory shapes reflect the characteristics of each lake catchment, including variations in size, depth, and other environmental factors.

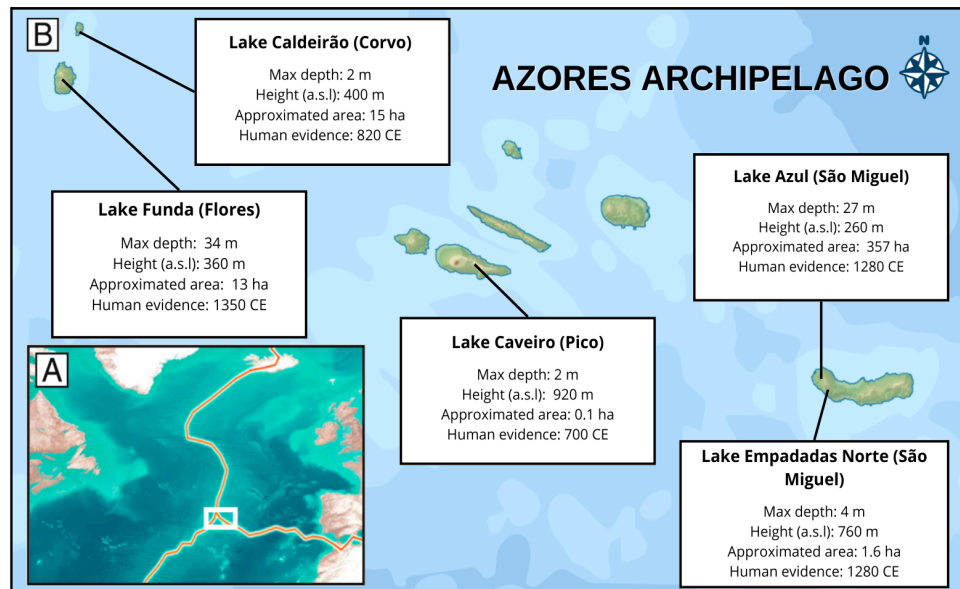


Figure 1. (A) Location of the Azores Archipelago in the North Atlantic. Red lines, triple junction between North American, the Eurasian, and the Nubian plates. (B) Map showing the selected lakes in each island. For each lake, it is indicated the maximum depth (in m), the height above the sea level (in m asl), the approximated area of each lake (in ha) and the year with first evidence of human presence (cal. CE). All information from Raposeiro et al 2021.

Materials and Methods

Study site

The Azores Archipelago is a group of volcanic islands situated between approximately 36°55'N and 39°43'N latitude and 24°46'W and 31°16'W longitude, 1500 km west to mainland Portugal. While the Portuguese claimed to be the first to arrive around 1427 CE recent evidence suggests that the first settlers arrived 700 years before (Raposeiro et al., 2021). The earliest explorers arrived at the end of the early Middle Ages (500 to 900 CE), when temperatures were higher than average, and the westerly winds were weaker, facilitating arrivals to the archipelago from northeastern Europe and inhibiting exploration from southern Europe. This is consistent with archaeological and genetic research suggesting the Norse were the first to colonise the Azores Archipelago. The onset of the Little Ice Age (1300 CE) triggered ideal climatic conditions for exploration from southern Europe, that might have resulted in the Portuguese colonisation of the Azores

Data extraction

We compiled elemental data from five lakes across the Azores archipelago: Lake Caldeirão on Corvo island (39.7023° N, 31.1080° W; Raposeiro et al., 2021); Lake Funda on Flores island (39.4475° N, 31.1939° W, Raposeiro et al., 2021); Lake Caveiro on Pico island (38.43° N, 28.18° W) (Benavente, 2024) and Lake Empadadas Norte (37.49° N, 25.75° W, Hernández et al., 2017) and Lake Azul on São Miguel island (37.7804° N, 25.4970° W, Raposeiro et al., 2021); (Figure 1). Lakes Funda and Azul are the deepest lakes, while lakes Empadadas Norte, Caveiro and Caldeirão are the shallowest (Pereira et al., 2014). Lakes Caldeirão and Caveiro presented the longest records. All lake records cover time-periods before and after the arrival of Portuguese settlers, however, the records of lakes Empadadas Norte and Azul are posterior to the first pre-Portuguese arrival (Pla-Rabés et al., 2024; Raposeiro et al., 2021)(Figure 1). We selected these five palaeoenvironmental records due to the extensive palaeoecological research and high-quality elemental data available for them.

The published sedimentary sequences from all lakes included in this study were dated using radiocarbon dating techniques (^{14}C and ^{210}Pb). We used the published age-depth models, with radiocarbon ages calibrated according to IntCal20 (Reimer et al., 2020)(Northern Hemisphere) to assign a calibrated year per each sample (presented in Common Era, CE). The individual sources are Hernández et al., (2017); Raposeiro et al., (2021), Benavente (2024) and Ritter et al., (2022). For additional methodological details, refer to Raposeiro et al., (2021).

We employed the following elemental compositions: Potassium; K, Silicon; Si, Calcium; Ca, Aluminum; Al, Sulfur; S, Titanium; Ti, Vanadium; V, Chrome; Cr, Manganese; Mn, Iron; Fe; Chlorine; Cl, Strontium; Sr, Bromine; Br and Zirconium; Zr; measured with an Avaatech XRF core scanner. These elements are expressed in counts per second (cps). We also incorporated total organic carbon (C) and total nitrogen (N) measurements, expressed as percentages of dry weight (wt %), into our analysis. We considered organic elements to C and N, and terrigenous elements to K, Si, Al, Mn, Fe, Ti, Zr, V, Sr and Ca. See Raposeiro et al., (2021) for further details on methods.

We complemented the elemental data with available palaeoecological data from the same lakes, including fossil pollen percentages of arboreal, shrub, and herbaceous taxa; charcoal particle influx ($\text{cm}^2 \text{ year}^{-1}$) as an indicator of fire activity; and coprophilous fungi spores influx ($\text{cm}^2 \text{ year}^{-1}$) as a marker of human and/or cattle presence. For further details, see Raposeiro et al., (2021).

Conceptualisation of the elementome and data transformation

All elemental data were first transformed using a square root function to minimise the effect of high variability in elemental records. Some elements were not present across all records due to concentrations under the limit of detection of analytical methods. Thus, individual lake elementomes were constructed using the elements present in each dataset. Subsequently, we applied a min-max transformation, which rescales the values of the minimum value to 0 and the maximum to 1 and allows us to compare between the elements, by standardising their

ranges. This double transformation reduces the weight of highly abundant elements in the dataset (Legendre & Legendre, 2012) very much in the direction of a recent proposed methodology (Bertrand et al., 2024). The values after transformation were interpreted with respect to their relative contents, not by their absolute value.

To understand the relationship between elements, we conducted hierarchical cluster analysis of each element time-series using the Ward method with Euclidean distances (Murtagh & Legendre, 2014).

To evaluate the robustness of our approach, we compared elementome analysis under two scenarios: (i) including both XRF and C/N data, and (ii) using XRF data alone, relying only on XRF data. This comparison aimed to assess the method's reliability in studies where only XRF analysis, but not C and N analysis, had been conducted.

Identification of elementome shifts

We first employed stratigraphically constrained cluster analysis of the elementome data, using the stratigraphic constrained incremental sum of squares (CONISS) method (Grim, 1987).

Second, we compared our identified palaeoelementome zones to the established phases from previous studies. The phases were delineated using multiple proxies, including pollen, spores, charcoal particles, biomarkers, and historical records, providing a detailed reconstruction of human-induced environmental changes over time (Raposeiro et al., 2021). The distinct separation between palaeoelementome zones, marked by identified breakpoints in the elemental composition timeline, highlights significant shifts in the elementome.

For Lake Caldeirão and Lake Caveiro, we compared the palaeoelementome zones with the four-phase classification of anthropogenic impacts proposed by Raposeiro et al., (2021). Thus, we highlighted the three main breakpoints from the CONISS palaeoelementome analysis.

Lake Funda was assessed against the three trophic phases identified by Ritter et al., (2022). Thus, we highlighted the two main breakpoint from the CONISS palaeoelementome analysis

For Lake Empadadas Norte, five climate-related lake phases were previously established through palaeoclimate analysis (Hernandez et al., 2017). Thus, we highlighted the four main breakpoint from the CONISS palaeoelementome analysis

Finally, for Lake Azul, we matched against a three-phase pollen-based phases derived from another sediment core collected in the same lake (Rull et al., 2017). Thus, we highlighted the two main breakpoint from the CONISS palaeoelementome analysis

Quantification of Elementome trajectories

We constructed elementome trajectories to represent the elementome temporal changes of each lake in a multivariate space (Figure 2). The temporal changes in the elementome can be understood as trajectories in a multivariate space, defined by the elemental composition of the

record. Each sample occupies a specific point in the multivariate space, and the trajectories from the position of each consecutive sample can be tracked to obtain information about the shifts in the elementome through time (Giralt et al., 2011).

Principal Component Analysis (PCA) was used to graphically represent the trajectories. To simplify the visualisation of the results, we highlight the trajectories between the centroids of the values for each period defined by a stratigraphically constrained CONISS analysis.

First, we estimated the trajectory shapes of each lake, enabling comparison between all of them. We generated a multivariate space using all the data from the five lakes, including only the elements common across the records (C, N, K, Fe, Mn, Ti, Zr, V, Si, Sr, Si, Ca). To describe the trajectory shape, we first calculated the explored area. This metric reflects the amount of the multivariate space explored by each trajectory by calculating the area of the ellipse, that encompassed approximately 95% of the data points of the record. Ellipses were generated using *stat_ellipse* function from ggplot2 package (Whickham, 2016)

Moreover, to address the similarity between the main clusters (zones) within each record, we calculated another metric, the three-centroid length, that was defined as the sum of the Euclidean distances, in the multivariate space, between the three centroids of the three main clusters of the record, defined by a stratigraphic constrained CONISS. Both trajectory shape metrics: explored area and three-centroid length, were developed for this study.

Secondly, we examined the internal structure of these trajectories by calculating the elemental turnover, directionality and trajectory speed using moving windows. To calculate those metrics, we first defined time-fixed moving windows. The moving windows were defined by a fixed time interval, representing 30% of total temporal sequence, and applied to each sample, with the year value of the sample as the center of the moving window. The size of the moving window was 581 years for Lake Caldeirão (that spans from 21-1986 CE), 533 years for Lake Caveiro (that spans from 7-1758 CE), 370 years for Lake Funda (that spans from 774-2009 CE), 196 years for Lake Empadadas Norte (that spans from 1353-2011 CE) and 194 years for Lake Azul (that spans from 1311-1960 CE). The size of the window was chosen to have enough samples ($n > 3$) represented in each moving window.

After, we calculated the elemental turnover using the beta diversity index (Legendre & Cáceres, 2013) to quantify the variability in elemental composition across time. High values indicate larger differences between samples for the period considered. In combination with moving windows elemental turnover was used to reflect the stability of the palaeoelementome across time, expecting low variability values during stable phases and high variability values in disturbance periods. Since sample sizes will not be equally distributed within each defined moving time window, we calculated intervals of confidence of the metric via bootstrap ($N = 999$) using the R package *boot* (Canty & Ripley, 1999).

For the same moving windows, we also calculated the directionality of the trajectory (De Cáceres et al., 2019) which describes how much a trajectory consistently follows the same direction on the multivariate space, as opposed to non-directional temporal changes. High values of the directionality index indicate that samples have consistently moved towards the

same direction for the period considered. We used bootstrapping to generate confidence intervals for elemental turnover, but this was not applicable for directionality, as it is defined as an ordered set of samples.

Finally, to detect the speed of elementome change, we used moving windows and calculated the Euclidean distance between the deepest and shallowest samples within each window, advancing by one sample at a time. We repeated that process for each of the samples between the deeper and shallower sample. Then, we calculated the mean value of all calculations and divided it by the size of the moving window. This was performed for each sample, and the trajectory speed value was assigned to the mean year of the corresponding moving window. Similarly to the directionality of trajectory, bootstrapping was not applicable. To calculate these metrics, we used R (R Core Team, 2023) packages, including, *zoo* (Zeileis & Grothendieck, 2005), *codyn* (Hallett et al., 2018), *adespatial* (Dray et al., 2012) *vegan* (Oksanen et al., 2024) and *ecotraj* (De Cáceres et al., 2019; Sturbois et al., 2021, 2023).

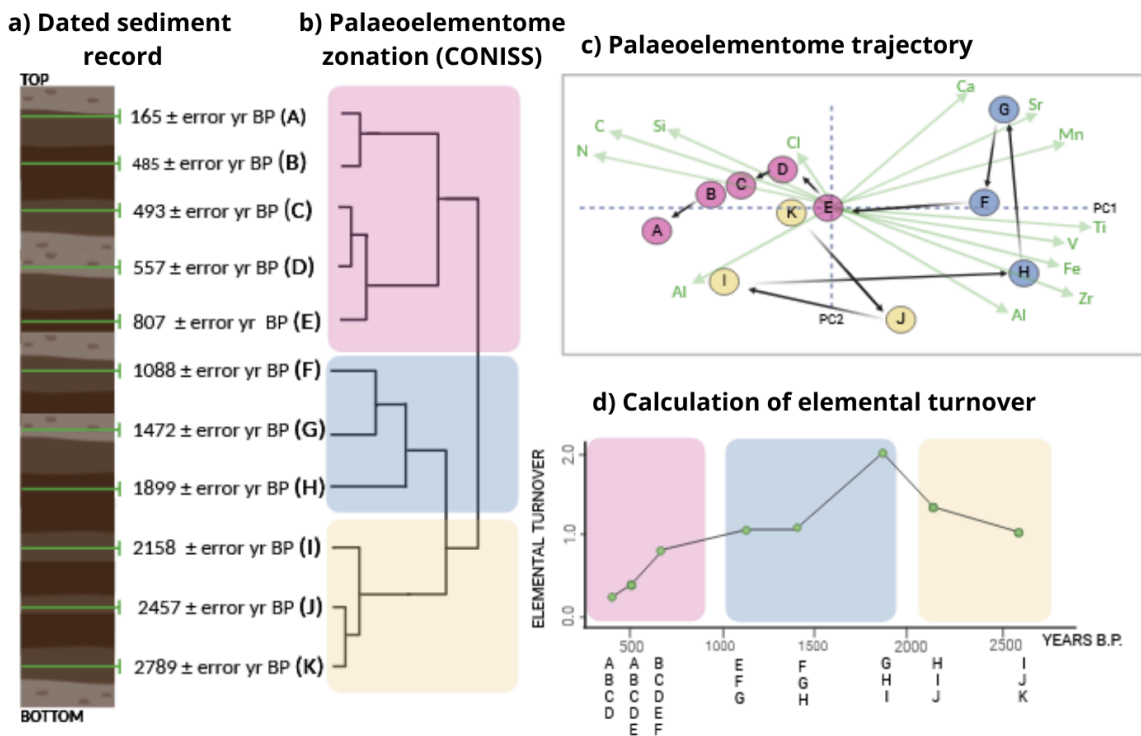


Figure 2. Schematic overview of the trajectory analysis of the palaeoelementome based on selected data from the record of Lake Caveiro. (a) Representation of the chronologically-dated sediment core (cal., years BP, Before Present). (b) The clustering of samples based on their elemental composition was represented using stratigraphically constrained CONISS, with different colors indicating distinct zones within the sediment record. (c) Trajectory of the palaeoelementome, from oldest to most recent samples, with each sample color-coded according to its CONISS zone. (d) Illustration of the calculation of elemental turnover. The number of samples included in each moving window is stated in the

X axis. This figure was created using selected data from the record of Lake Caveiro, as an example we used moving windows defined by the 35% of the temporal record.

Results

Trajectory shapes

We found a similar trend across all lakes. The first axis clearly separated the samples between organic (C and N), and terrigenous elements (K, Si, Al, Mn, Fe, Ti, Zr, V, Sr, Ca, with >70% variance explained in the first two principal components (Figure S3-S7, Table S1). We detected differences in the shapes of the trajectories (explored area and three-centroid length) between the lakes depending on their depth and area (Table 1). We found that deeper lakes displayed shorter values of three-centroid length. Lake Azul had the lowest value, followed by Lake Funda, Lake Caldeirão, Lake Empadadas Norte and Lake Caveiro. The explored area value of each trajectory did not show a similar trend (Table 1).

Table 1. Lake Characteristics and Trajectory Shapes. The explored area reflects the amount of the multivariate space explored by each trajectory. The three-centroid length addresses the similarity between the three main clusters of the trajectory.

Lake	Area	Maximum depth	Explored area	Tree-centroid length
Azul	357 ha	27 m	0.69	0.07
Funda	13 ha	34 m	0.91	0.16
Caldeirão	15 ha	2 m	0.32	0.19
Empadadas N.	1.6 ha	4 m	1.25	0.36
Caveiro	0.1 ha	2 m	0.59	0.66

Trajectory shifts and metrics

The results related to elemental turnover, speed and directionality differ between lakes (Figure 3).

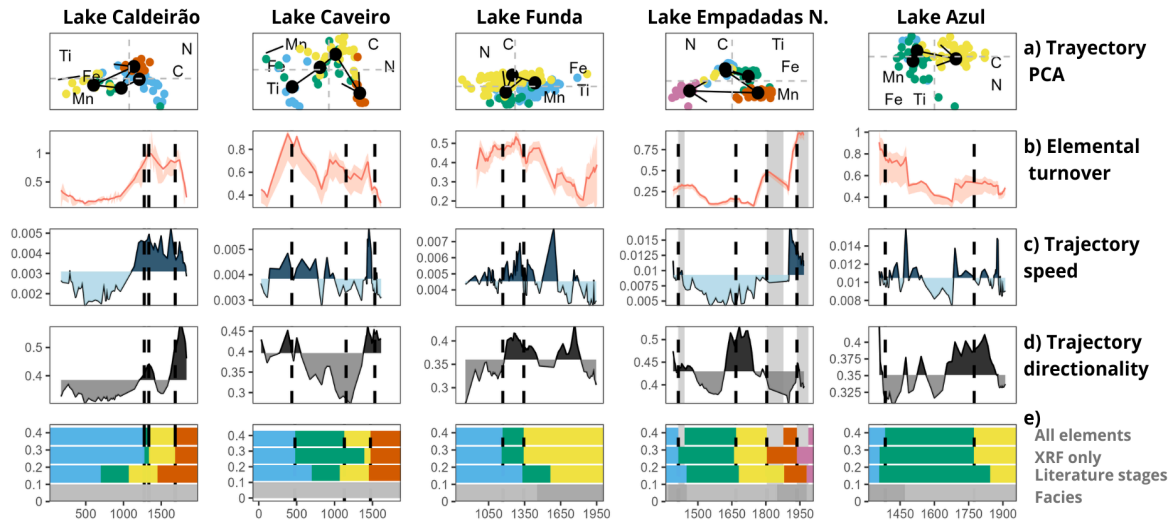


Figure 3. Summary of the Elementome trajectories for the five lakes analysed in this study. For detailed information of the trajectories of each lake see supplementary information (Figures S2 - S7). In (a) the trajectories within the multivariate space are represented with a PCA. Only C, N, Ti, Fe, and Mn are represented to help the clarity of plot, but the trajectories were constructed using all elements available in each record. The arrow represents the trajectory within the centroids of the different stages identified with stratigraphic constrained CONISS, also depicted by the colors. In (b) the elemental turnover calculated using centered moving windows restricted by time (red line) with confidence intervals calculated with bootstrap (red shade). In (c) the speed of change. Dark blue depicts directionality values above the mean, while light blue depicts values below. In (d) the directionality values. Dark grey depicts directionality values above the mean, while light grey depicts values below. In (e), we compared the three different zones of the palaeoecological record. At the top, we show the zones calculated using stratigraphically constrained CONISS with all available elements, followed by those calculated excluding C and N values. At the bottom, the previously identified zones for the same record are presented: the four-phase classification for Caldeirão and Caveiro (proposed in 2021), the three trophic phases for Funda (2022), the six climate-related phases for Empadadas Norte (2017), and the pollen-based phases for Azul (2017). The last bar represents the different sediment facies reported in the study, different by shades of grey. Dotted lines across the plots represent shifts in the elementome (identified with CONISS). The dark columns in Empadadas Norte represent data hiatuses

Lakes Caldeirão and Caveiro elementome aligned with some of the previously identified phases of human impacts for Azores (Raposeiro et al., 2021; Figure 3e). These stages were marked by three boundaries: 700 CE (the arrival of first settlers, which was not synchronic to

all islands); 1070 CE (the intensification of human activities); and 1450 CE (the arrival of Portuguese colonisers, coinciding with the onset of the Little Ice Age; LIA). High values of elemental turnover peaks coincide with elementome shifts in both lakes (Figure 3).

In Lake Caldeirão, any elementome shifts are directly associated with the arrival of Portuguese settlers or the Little Ice Age (LIA). However, around 1500 CE, elemental turnover and trajectory speed were notably high, while directionality remained low, indicating dynamic but non-directional changes in the lake's elemental composition during this period.

In Lake Caveiro, the impact of early settlers on the elementome is characterised by two distinct phases. The initial impact, evident around 900 CE, is marked by high elemental turnover and trajectory speed but very low directionality, signaling the onset of human influence. However, the major elementome shift, driven by intensified agropastoral activities, occurred approximately 430 years later, around 1330 CE. This delayed response suggests that while human presence was detectable early on, significant changes in Lake Caveiro's elemental composition took centuries to manifest, likely due to the gradual intensification of agricultural and pastoral practices (Raposeiro et al., 2021). The Lake Caveiro record has an elementome shift matching with the arrival of Portuguese and the LIA, with high values of directionality and trajectory speed. After the last elementome shift (1685 CE and 1473 CE, for Lakes Caldeirão and Caveiro respectively) in both lakes elemental turnover, directionality, and trajectory speed decreased.

Lake Funda elementome shifts were compared to the Ritter et al., (2022) palaeolimnological assessment, that differentiated three distinct trophic stages for the lake and considered a baseline mesotrophic stage from 950 to 1330 CE, a transition stage from 1330 to 1565 CE, and the stabilisation of a eutrophic stage from 1565 to 2009 CE. This classification was made considering biomarkers, pollen, spores, diatom assemblages, and sediment geochemistry. The second elementome shift matches with the boundary between the mesotrophic baseline and transition stages, drastically reducing the organic elements and slightly the terrigenous, and associated with agropastoral activities. Elementome turnover, directionality, and trajectory speed were high. No elementome shift matched the stabilisation of the eutrophic state of the lake, previously described. Instead, the first elementome shift appears coinciding with the abrupt changes on the vegetation pattern, a reduction of trees and shrubs (Ritter et al., 2022) that occurred around 1115 CE.

Lakes Empadadas Norte and Azul are located on the same island, São Miguel, and separated by 5.7 km. The palaeoelementome of Lake Empadadas is compared to five previous climate stages assessed by Hernandez et al.,(2017) that highlighted the climate conditions: first the MCA-LIA transition, a warm and wet phase from 1300 to 1450 CE ; secondly, the LIA first half (cold and dry) from 1450 to 1680 CE ; third, LIA second half (warm and wet) phase from 1680 to 1880 CE; fourth, the Industrial era, a cold and dry phase from 1880 to 1980 CE (IV) and the current stage, a wet and very hot phase from 1980 to 2011 CE (V). There are three hiatuses in the sediment record from 1414 to 1442 CE; 1804 to 1878 CE and 1937 to 1988 CE. The elementome shifts we identified align closely with the phases proposed by

Hernández et al. (2017), likely due to the shared use of biogeochemical proxies. Also, they match with the elemental turnover peaks, except for the second and third elementome shifts, that had low values of elemental turnover and trajectory speed but peaked on directionality. When the climate shifts towards colder and drier conditions, there is an increase in terrigenous elements (e.g., Ti, Zr) due to enhanced erosion and sediment transport from terrestrial sources. At the same time, organic elements (e.g., C and N). The opposite occurs in the transition from cold and dry to wet and hot phases; C and N increase while terrigenous elements decrease.

For Lake Azul, the elementome shifts and the peaks in elemental turnover match with previously described vegetation zones (Rull et al., 2017), but not to the stages by Hernandez et al., (2017) that were constructed with the neighbor lake, Empadadas Norte, and should reflect similar climate conditions. The palynological study found three different zones regarding the pollen composition in the sediments. The first pollen zones (1273 to 1358 CE), was dominated by native laurisilva forest. The second zone (1358 to 1845 CE), was characterised by the disappearance of the native laurisilva and the dominance of native shrubs and grass meadows. The last zone (1845 to 2010 CE) was marked by the introduction of commercial tree species and dominance of forestry activities (Rull et al., 2017).

Comparison between different elementome conceptualisations

No differences were observed in the trajectory analysis when comparing an elementome composed of XRF data combined with C and N to an elementome composed solely of XRF data. This indicates that the inclusion of C and N did not significantly alter the trajectory results (Figure S8). The elementome shifts were similar or slightly similar in most cases, except for the second elementome shift in Lake Caveiro. This shift occurs in the XRF-only approximately 260 years later. In Lake Caveiro, while the trend is maintained, the data range of both elemental turnover and directionality is slightly reduced in the XRF-only approach.

Additional analysis

Finally, an analysis of the trajectories of each lake, focusing on elemental turnover, directionality and trajectory speed, is provided in the Supplementary Information (Figures S3 – S7). Moreover, to aid in understanding the changes, we provide a detailed plot depicting the individual changes of all elements (including C:N ratio, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values), in the same timeline for all five lakes (Figure S1). Additionally, Figures S9 to S13, provide the resulting trees from the cluster analysis of the palaeoelementome by stratigraphic constrained CONISS.

Discussion

Elementome trajectories

It is important to note that the elements originate from diverse sources. Organic elements, particularly C and N, are primarily fixed through biological processes. These elements can

originate from the surrounding catchments, atmospheric deposition, or in-lake production processes (Einsele et al., 2001; Harrison et al., 2009). In addition, other elements such as K, Si, Al, Mn, Fe, Ti, Zr, V, Sr, and Ca usually have a lithologic origin. However, Ca and Si can also have a biogenic origin from siliceous and calcareous organisms. Across our records, the second axis of the PCA further differentiated the non-soluble elements, Zr and Sr, from the other terrigenous elements (Figures S3 – S7). This differentiation reflects their behavior as particles that require higher energy for transport to the lake center (Bertrand et al., 2024; Hernandez et al., 2017). However, Ti, which is also not soluble, does not exhibit the same pattern in the second axis of the PCA. Moreover, we calculated three numerical indicators on elementome trajectories that are already used in community ecology (De Cáceres et al., 2019; Sturbois et al., 2021) but, as far as the authors knows, are novel in the description of biogeochemical data: element turnover, trajectory directionality, and trajectory speed. These metrics provided insights into how lake ecosystems responded to external (e.g. increased runoff in the catchment) and internal disturbances (e.g. shifting algal community and eutrophication). Element turnover quantifies the rate of elemental change, trajectory directionality assesses the consistency of change, and trajectory speed evaluates how quickly the elemental composition changes. By applying these indicators, we can identify periods of rapid or slow change, determine if shifts are consistent or stochastic, and quantify biogeochemical transformations (Table 2).

Finally, the combined interpretation of the elementome trajectory metrics shows periods of stabilisation when all metrics (elemental turnover, directionality, and trajectory speed) are low or decreasing. This pattern is particularly clear in Lake Caldeirão after the last major shift around 1650 CE. During this time, land use changed toward pastures in Corvo Island (Raposeiro et al., 2021; Silveira & Dentinho, 2010). The start of this change was marked by an increase in elemental turnover, directionality, and trajectory speed. These findings suggest that land use changes can cause significant shifts in elemental dynamics, followed by stabilisation as the system adjusts to new environmental conditions.

Table 2. Theoretical Description of the Ecosystem Changes Through Trajectory Metrics.

Elemental turnover	Trajectory Speed	Directionality	Interpretation of elementome dynamics	Example
↑	↑	↑	Large and abrupt changes directed towards a new state	Caldeirão third elementome shift. Caveiro first shift.
↑	↓	↑	Large and gradual changes directed towards a new state	Empadadas fourth elementome shift; Azul after first elementome shift
↑	↑	↓	Large and abrupt undirected changes	Any examples found
↑	↓	↓	Large and gradual undirected changes	Caveiro second elementome shift
↓	↓	↑	Smooth and gradual changes towards a new state	Azul second elementome shift
↓	↑	↑	Smooth and abrupt changes directed towards a new state	Funda around 1762 CE
↓	↑	↓	Loose stability (Matthews et al 2013): Smooth and abrupt undirected changes	Funda around 1600 CE
↓	↓	↓	Stabilisation	Caldeirão and Caveiro after the last elementome shift

Note: ↑ symbol depicts high or increasing values while ↓ symbol depicts low or decreasing values.

Lake catchment influence on elementome dynamics

A comparison of palaeoelementome records from a small and shallow lake (Lake Empadadas Norte) with a large and deep lake (Lake Azul), reveals significant differences in their responses to environmental impacts, despite their proximity of just by 5.7 kilometers (Figure 1).

The geomorphological characteristics of these lakes clearly influence how their elementomes respond to climatic changes. Lake Empadadas Norte, with a maximum water column depth of four meters, showed a clear pattern. When the climate was wetter and hotter (second elementome shift: 1668-1677 CE; and fourth elementome shift: 1937-1986 CE), the

elementome was richer in C and N. Conversely, it was richer in terrigenous elements during colder and drier climatic conditions (first elementome shift: 1414-1442 CE; and third elementome shift: 1804-1878 CE, which also was a period of reforestation). This trend might be explained by an increase in temperature and humidity that could increase the net primary production in the lake and catchment, resulting in an increased accumulation of organic material in the lake sediment (Jiménez-Navarro et al., 2023; Mattsson et al., 2015).

Lake Azul, which has a maximum water column of 27 m, the three palaeoelementome metrics increased around 1700 CE. This shift coincides with climate changes in the island during this period, likely reflecting environmental responses to broader climatic shifts such as those associated with the LIA (Hernandez et al., 2017). Lake Azul's sedimentary record has been significantly influenced by volcanic activity and, uniquely among the five lakes studied, is situated within an urbanised area. These factors may confound the interpretation of climate signals by introducing geochemical inputs from volcanism and anthropogenic disturbances, potentially masking their effects on lake productivity and stoichiometry (Vázquez-Loureiro et al., 2019). The comparison of trajectory shapes among the lakes further highlights their geomorphological differences (Benavente 2024). For example, Lake Empadadas, with a three-centroid length value 0.36, displayed more dynamic elementome trajectories compared to Azul (0.07) that is considerably bigger and deep (Table 1, Figure S2). In addition, lake geomorphology plays an important role driving changes in the elementome, especially with climate. This suggests that small, shallow (and closed) lakes like Lake Empadadas are more sensitive to climatic changes, which tend to induce more pronounced shifts in such environments compared to larger, deeper lakes. (Table 1, Figure S2).

The differences in trajectory shapes between large and small catchments are influenced by multiple factors. The geomorphology of the catchment defines how the lake is going to expand or shrink with changes in precipitation (Hayashi & Kamp, 2007). Moreover, vegetation removal in steep catchments typically enhances erosion rates, as vegetation helps stabilise soils and reduce sediment transport. This process can destabilise steep catchments, leading to increased soil loss and altered geomorphic processes, as observed in previous studies (Xu et al., 2013). Another limiting factor is the amount of light reaching the bottom of the lake. In shallow lakes, light penetrates the lake bottom, increasing biological activity. In contrast, deep lakes may experience stratification (e.g. Lake Funda; Ritter et al., 2022), leading to anoxic conditions in the bottom. However, this stratification might enhance lake productivity due to P mobilisation (Catalan et al., 2024; Cohen, 2003; Tu et al., 2020)

Elementome shifts and anthropogenic ecosystem perturbation

Most of the elementome shifts assessed in this study (via stratigraphic constrained CONISS analysis of the palaeoelementome) paired with relevant palaeoenvironmental events (Hernández et al., 2017; Rull et al., 2017; Raposeiro et al., 2021; Ritter et al., 2022).

This raises the question of potential temporal mismatches. In Lakes Caldeirão and Caveiro, the elementome shift linked with the impact of first settlers (approximately 700 CE) was delayed by approximately 500 years. However elemental turnover and trajectory speed were

increasing since the arrival of first settlers, indicating an accumulation of anthropogenic impacts from the arrival of first settlers until the elementome shift occurred (Figure 3). Additional temporal mismatches between our observed elemental shifts and the previously established phases are evident in Lakes Caveiro and Funda. The first elementome shift in Lake Caveiro occurred before the arrival of the first settlers and coincided with a decline in tree species (e.g. mainly *Juniperus brevifolia*). This change is attributed to volcanic activity (Connor et al., 2012). In Lake Funda, only one elementome shift (the second: 1168-1178 CE) matches with a previously stated trophic stage (Ritter et al., 2022). The first elementome shift occurs between 1168-1178 CE, with a peak in elemental turnover and without a direct correspondence in previously identified phases (Ritter et al., 2022). The observed shift coincides with changes in multiple palaeoenvironmental proxies. For example, Raposeiro et al. (2021) reported on Lake Funda a sudden decrease followed by an increase in arboreal pollen, suggesting significant vegetation changes. Concurrently, Ritter et al. (2022) documented shifts in *Chironomidae* communities and diatom assemblages, indicating an increase in lake productivity.

Human impact in our records could be associated mainly with an increase in the fire regime and/or changes on land-use change (Nogué et al., 2017). Fire regimes played a role in influencing elementome shifts in Lake Caldeirão (first elementome shift: 1275-1278 CE), Caveiro (second elementome shift: 1129-1143 CE), Funda (1100-1200 CE) and Azul (first elementome shift: 1385-1391 CE and second: 1774-1799 CE) (Figures S1-S7). These shifts were shaped by variations in fire frequency, intensity, and seasonality, which impacted nutrient cycling and sediment composition (Raposeiro et al., 2021). Fire events in the lakes Caldeirão and Caveiro were characterised by a high elemental turnover and speed. Directionality was variable. This may be caused by a combination of increased erosion due to land degradation, leading to prevalence of terrigenous elements such as Ti or Zr, along with the input of charcoal ashes and wood debris, which can have high concentrations of C or other elements as K or Si (Smółka-Danielowska & Jabłońska, 2021).

Land use change is a major driver of change when humans arrive on islands (Nogué et al., 2017; Nogué et al., 2021). While we do not have historical information prior to Portuguese colonisation, later historical documents provide evidence of forest burnings, cereal cultivation, and animal husbandry on the islands following the arrival of the Portuguese (Frutuoso, 1981; Moreira, 1987). The introduction of pastures is one of the most relevant land use changes in the environmental records of islands (Walsh et al., 2020). In our analysis, land use changes are typically associated with increases in carbon (C) and nitrogen (N) concentrations (Hernández et al., 2013; Ritter et al., 2022). These elevated levels can be attributed to two primary sources: enhanced inputs from the catchment area or increased in-lake production. The former may result from soil disturbance and erosion following land conversion, while the latter could be a consequence of altered nutrient dynamics stimulating aquatic primary productivity. For example, the introduction of pastures in Lake Caldeirão increased trajectory speed, directionality, and elemental turnover, until a point (the third elementome shift: 1685-1715 CE) after they started decreasing, indicating certain stabilisation (Figure 3). This more stable period coincides with the onset of the dominance of

herbaceous taxa in the pollen composition (Figure S3) that represents the stabilisation of the pasture ecosystem (Raposeiro et al. 2021). In Lake Caveiro, the introduction of agropastoral activities led to an increase in directionality values, that was low, followed by an increase in trajectory speed and elemental turnover, which all peaked before the third elementome shift (year 1100 CE). After that, elemental turnover and trajectory speed decrease while directionality increases, smoothly shifting towards a more dominated C and N elementome (Figure S4).

Around 1350 CE, grazing activities in Lake Funda coincided with the second elementome shift, marked by a peak in all three metrics (elemental turnover, trajectory directionality, and speed). This shift, however, resulted in a reduction of both organic and terrigenous elements. The pollen diagram for Lake Funda indicates that agropastoral activities led to a shrub-dominated landscape (e.g., *Myrsine africana*) with a decline in tree cover (Figure S5). This contrasts with Lake Caldeirão, where the shrub ratio remained stable over time (Figure S3). The replacement of forests by shrubs and pastures, without an increase in fire regimes, suggests logging activities as the primary driver. This could explain why, despite agropastoral land use changes, the organic element signal did not increase.

Limitations and perspectives

Our study simplifies complex data on sedimentary elemental composition into quantitative metrics. These metrics facilitate tracking environmental changes over a span of two millennia. We believe this approach has potential to reveal how elemental dynamics in ecosystems have changed over time. However, we also understand that lake sediment records mainly reflect sedimentary processes. To get a fuller picture of how ecosystems change, future research should also include other natural archives like soil layers, peat deposits, or long-lived trees. These could help uncover changes in both the biotic and abiotic components of ecosystems. In this study, we constructed an elementome using all available elements and the C/N ratio. However, we acknowledge that some palaeoenvironmental studies rely solely on XRF data, excluding C and N measurements. To address this limitation, we conducted a parallel analysis using only XRF-measured elements, which yielded similar results (Figure S8). This suggests that our approach is robust even when C and N data are unavailable. It is important to note that we do not recommend substituting C and N measurements with loss on ignition (LOI) values. While LOI is sometimes used as a proxy for organic matter content, it can introduce bias in carbon content estimates, as previously demonstrated (Santisteban et al., 2004). This potential for inaccuracy underscores the importance of direct C and N measurements when possible.

While in this study we explored four metrics of elementome trajectories, there are additional possibilities that may be more suitable for other research questions. One metric that could also be explored is the trajectory distance toward a reference point (Starbois et al., 2021). This metric is potentially useful for ecosystem restoration purposes with a clear restoration baseline or when research questions focus on specific and detailed impacts. Additionally, working with smoothed trajectories from the package *ecotraj* (de Cáceres et al., 2019; Starbois et al., 2021, 2023), could help when dealing with noisy datasets from lake records.

Together, elemental turnover, directionality, and trajectory speed characterised the evolution of the ecosystem elementome through time and served as ecological indicators of the environmental changes in the lake and catchment. While we have proven its potential in palaeoenvironmental records, the scope of elementome trajectory analysis extends beyond. Elemental trajectory analysis demonstrates significant potential as a valuable tool for ecologists and palaeolimnologists to monitor the stability of elementomes in ecosystems or organisms, and to provide insights into biogeochemical dynamics over time.

Conclusion

Through the lens of "atomical ecology" (Sardans & Peñuelas 2024), we introduced and tested trajectory analysis for examining elemental data from sedimentary sequences, termed elementome trajectory analysis. This approach involved the trajectories of different samples within a multivariate space constructed from the elemental composition of the records. By utilising this method, we were able to track shifts in ecosystem elementomes, thereby inferring the link with different ecosystem perturbations. For example, C and N played a role when biological activity within the catchment or lake increases. In contrast, terrigenous elements (K, Si, Al, Mn, Fe, Ti, Zr, V, Sr, and Ca) reflect increased runoff and erosion, a pattern observable across all studied systems.

Our study demonstrates the effectiveness of this approach in revealing how ecosystems have responded to long-term environmental changes. Furthermore, we introduced trajectory metrics for interpreting elemental time series: elemental turnover, trajectory speed, and directionality. These metrics serve as proxies for changes in magnitude, graduality, and directionality of the changes occurring in the lake and catchment. We described and compared trajectory shapes by quantifying the multivariate space explored for each trajectory (explored area) and the distance between the major clusters in the record (three-centroid length). The three-centroid length is directly related to catchment area, indicating that small, shallow lakes experience larger shifts than larger, deeper lakes.

Finally we would like to encourage the use of elementome trajectory analysis in environmental reconstructions to optimise the potential of elemental databases, enhance the depth of interpretations, and assess the magnitude, graduality, and direction of the observed changes. Additionally, this method serves as a powerful tool to monitor and untangle the intricate relationships between the elemental structure of ecosystems and the fundamental processes driving natural systems.



hird Chapter:

Erosion and geochemical legacies of human colonisation on Atlantic islands



Each island has its own Anthropocene

R. Whitacker

Erosion and geochemical legacies of human colonisation on Atlantic islands

Javier de la Casa, Josep Peñuelas, Sergi Pla-Rabés, Inger G. Alsos, Elena Baños , Ívar Ö. Benediktsson, Anthony Brown, Alvaro Castilla-Beltrán, Lea de Nascimento, Jeffrey P. Donnelly, Egill Erlendsson, Christopher Evans, Patricia L. Fal , Wesley R. Farnsworth, José M. Fernández-Palacios, Santiago Giralt, Armand Hernández, Sofia E. Kjellman, Alistair J. Monteath, Joshua Mueller, Pedro M. Raposeiro, Anders Schomacker, Zoë Thomas, Peter J. van Hengstum , Jordi Sardans, Miquel de Cáceres, Sandra Nogué.

Abstract

The ecological consequences of human colonisation and resource extraction on island biodiversity during the historical period are well-documented. However, comparatively less is known about the extent of soil erosion and alterations in the geochemical composition of island ecosystems over the same timeframe. The onset and transformation of anthropogenic land-use may have altered the geochemical composition of island ecosystems by accelerating erosion and increasing the input of land-derived elements on the catchments. The European overseas expansion around the 15th century (CE) drastically changed the landscape of islands, expecting different effects between unsettled islands and the ones already settled.

We analysed the inorganic geochemical composition of 21 depositional records, across 19 Atlantic islands, using X-ray fluorescence (XRF) data spanning the past three millennia. To assess soil erosion, we combined sediment accumulation rate data with a novel metric developed for this study, the Titanium index (Ti-index), which reflects the relative dominance of land-derived inorganic elements in the geochemical composition of the deposited material. Additionally, we conducted trajectory analyses of the geochemical records to evaluate elemental turnover and the directionality of compositional change over time.

We found that both accumulation rates and Ti-index increased following human arrival. On islands colonised during the European expansion, these values rose by factors of 2.09 and 1.48, respectively. In contrast, islands anthropised prior to this period showed increases of 1.61 and 1.41 times, respectively. Human arrival generally triggered soil erosion, though its impact varied across different environmental contexts and waves of anthropisation, and is still increasing under postindustrial times.

Introduction

Soil erosion is among the most visible and measurable indicators of human-driven environmental change. These processes reflect broader transformations in ecosystems and are closely linked with land-use practices, making them essential for understanding long-term ecological impacts. In recent decades, the scale of anthropogenic influence has sparked debate around defining a new geological epoch, the Anthropocene (Chakraborty, 2024). Although this period remains informally defined, it is characterised by widespread human impacts on global ecosystems, with the extent and nature of these impacts varying across historical and sociopolitical contexts (Ellis et al., 2021; Ruddiman, 2018). Understanding how these impacts unfold across different environments and time periods is essential for identifying patterns of ecological change (e.g. such as increases in soil erosion, shifts in geochemical stability, and directional disruptions in sediment composition). In this context, oceanic islands offer ideal settings due to their geographic isolation, long periods without human presence, and sometimes well-documented settlement histories (Alsos et al., 2021; Nogué et al., 2021; Nolan et al., 2018; Pla-Rabés et al., 2024; Raposeiro et al., 2021). These characteristics allow for comparisons of ecological conditions before and after colonisation, and for analyzing how different societies have shaped environmental trajectories. For example, many Atlantic islands were rapidly colonised during the European overseas expansion in the 15th century (CE, 550–451 years before present) (Penrose, 1952), leading to major land-use changes and vegetation shifts (Castilla-Beltrán, De Nascimento, et al., 2021; Nogué et al., 2021; Raposeiro et al., 2021). In contrast, islands like the Canaries experienced earlier phases of human settlement, with each cultural wave leaving distinct environmental legacies (de Nascimento et al., 2020; Santana et al., 2024). Islands are particularly vulnerable to biodiversity loss, with endemic species accounting for approximately 60% of all recorded extinctions (Tershy et al., 2015; Whittaker et al., 2017). While the long-term impacts of human activity on island vegetation are often well documented (Strandberg et al., 2024b, 2024a; Walentowitz et al., 2023), other consequences of anthropogenic pressure, such as soil erosion, have received comparatively less attention. Like biodiversity loss, these processes pose serious threats to island ecosystems. Despite being globally recognised as major environmental challenges (Montgomery, 2007; Z. Wang et al., 2017), soil erosion is often overlooked in island contexts (Montgomery, 2012). On islands, soil loss contributes to habitat degradation, reduced water quality, diminished ecosystem carrying capacity, depletion of soil organic carbon, all of which further endanger their unique biodiversity (Pimentel & Harvey, 1999). Human-induced soil degradation has been globally assessed for the current century (Borrelli et al., 2017; FAO & ITPS, 2015) and during the Holocene on inland lakes (Jenny et al., 2019; Rapuc et al., 2024), indicating a positive correlation between human activity and increased erosion.

A comprehensive regional or global synthesis addressing the historical anthropogenic driven soil loss on islands, however, is still lacking. This knowledge gap includes changes in the elemental composition of ecosystems (i.e., their elementome) (de la Casa et al., 2025; Peñuelas et al., 2019). Early human arrivals and the initial land, potentially increased soil erosion and consequently, the mobilisation of terrigenous elements (Williams, 2008), such as titanium (Ti), zirconium (Zr), and strontium (Sr) (Boyle, 2001) and affecting biogeochemical cycles (Quinton et al., 2010). Agricultural practices and the introduction of livestock could also increase the availability of organic matter and modify biogeochemical cycles (McLauchlan et al., 2014). The intensity of resource extraction after the Industrial Revolution (around the late 18th and 19th centuries, CE) (Steffen, et al., 2015a; Vitousek et al., 1997)

globally disrupted elemental cycles, especially for carbon, nitrogen, phosphorus, and sulfur (Bobbink et al., 2010; Galloway et al., 2008; Steffen, et al., 2015b). These anthropogenic impacts on these elemental sources, both direct and indirect, jeopardise the stoichiometric stability that is strongly connected with biodiversity and biogeochemical niches (Peñuelas et al., 2019). Climate fluctuations affect the geochemical and sedimentary changes as well on islands. The input of organic and inorganic matter to sediments is controlled by climatic factors, with changes in temperature and the availability of water playing important roles in modulating ecosystem productivity and rates of soil weathering (Adrian et al., 2009; J. F. Boyle, 2001)..

To characterise changes in the geochemical composition of depositional sequences we applied a trajectory analysis (De Cáceres et al., 2019). This approach allowed us to quantify the magnitude and direction of geochemical changes in the depositional records and the tendency toward titanium and other terrigenous elements (i.e. Ti-index) over the last three millennia. Based on previous works (de la Casa et al., 2025; Jenny et al., 2019; Rapuc et al., 2024), we assume that erosion is reflected by increases in both accumulation rate and Ti-index), accompanied by high elemental turnover and low directionality. In this study, we aim to analyse the impacts of human arrival on soil erosion across Atlantic islands using 21 depositional records (Figure 1; Table S1). We used four metrics: accumulation rate, Ti-index, elemental turnover, and directionality (Table 1).

Table 1. Meanings and hypotheses, based on (de la Casa et al., 2025), for the impact of human arrival on accumulation rate, Ti-index, elemental turnover, and directionality.

Indicator	Description
Accumulation rate	Indicates the amount of material deposited in a time window. High values indicate a higher material supply.
Ti-index	Indicates the dominance of the terrigenous elements (based on titanium) in the geochemical composition. High values indicate a higher presence of terrigenous elements in the sediment.
Elemental turnover	Indicates the variability of geochemical data in a time window. Low values indicate stable geochemical composition, and high values indicate the opposite.
Directionality	Indicates to which extent geochemical composition changes in a particular direction consistently, using the angles between consecutive segments in the trajectory. Low values indicate non-directional (i.e. random) changes, and high values indicate directional changes in the geochemical composition.

We hypothesise that human arrival caused a marked rise in erosion signals due to landscape disturbance (e.g., deforestation, burning, etc). Additionally, we expect geochemical changes to be more pronounced on islands colonised more recently, reflecting the intensive land-use practices of European colonisers. Remote islands such as Svalbard, where human impact is expected to be minimal should not reflect an exception. This integrated approach aims to improve our understanding of human-driven environmental change on islands, revealing patterns of soil degradation and erosion across diverse ecological and cultural settings.

Results

Geochemical indicators of erosion

Ti-index correlated positively in most of the records (19 out of 21; Figure S1 & S2) with at least the land-derived elements: zirconium and strontium; and when those elements were not available, with iron. Together with the accumulation rate, an increase in both serves as a proxy of erosion in the catchments, whereas an increase in accumulation rate while Ti-index decreases reflects increases in catchment primary production, with geochemical trajectories shifting towards more organic compositions. Ti-index and accumulation rate were positively correlated (Pearson's coefficient = 0.66; $p < 0.001$), and where the only metrics with significant correlations. Ti-index and accumulation rate were calculated for the 21 depositional records (Methods and Figure 1). In 10 out of the 21 depositional records (two from the Canary Islands, two from Cabo Verde, one from the Azores, one from the Falkland Islands, two from Iceland, and two from Svalbard), both metrics clearly increased after human arrival. In seven records (one from the Canary Islands, one from Gulf of Guinea Islands, one from Cabo Verde, and four from the Azores), the accumulation rate increased, while Ti-index decreased or maintained similar values. In two records (one from the Azores and one from the Bahamas), the accumulation rate decreased while the Ti-index increased. The record from British Virgin Island and one record from Cabo Verde presented a strong oscillation of Ti-index and accumulation rates,

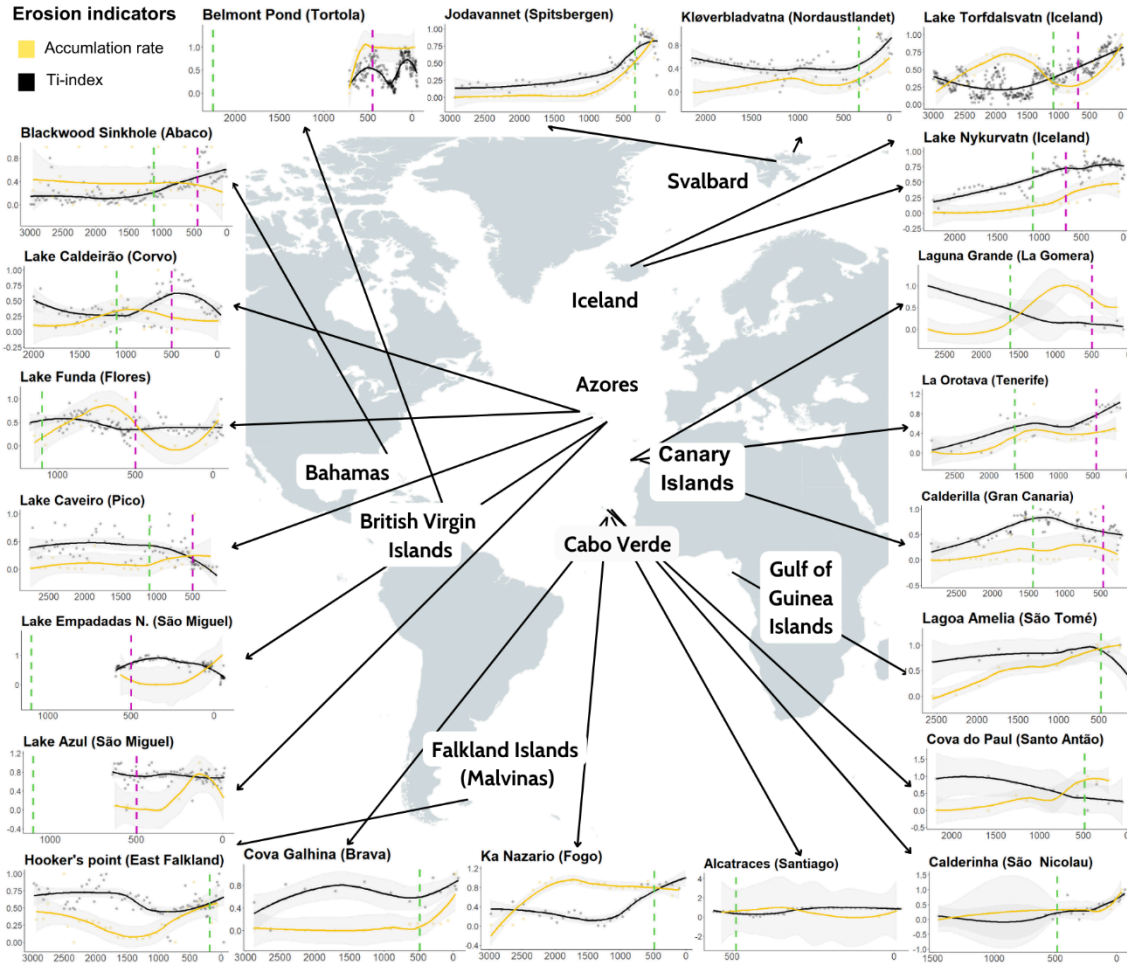


Figure 1. Map of the 21 depositional records in the analysis and the temporal trends for the accumulation rate (yellow) and Ti-index (black) using locally estimated scatterplot smoothing (LOESS). The X axes represent cal. yr BP while the Y axis is the 0-1 min-max transformed values of accumulation rate and Ti-index. The green dashed vertical lines indicate the first known arrival of humans to each island, while the purple dashed lines represent subsequent arrivals during the colonial era. The number of samples corresponding to each trend is detailed in Table S2.

We built general additive mixed models (GAMMs) to assess the trends across islands over time for the accumulation rate and Ti-index (Figure 2). Both metrics generally increased toward the present. Accumulation rate and Ti-index general models explained little proportion of the variance (8.0% and 18.0%; respectively), as expected due to the different anthropogenic and climatic history across records.

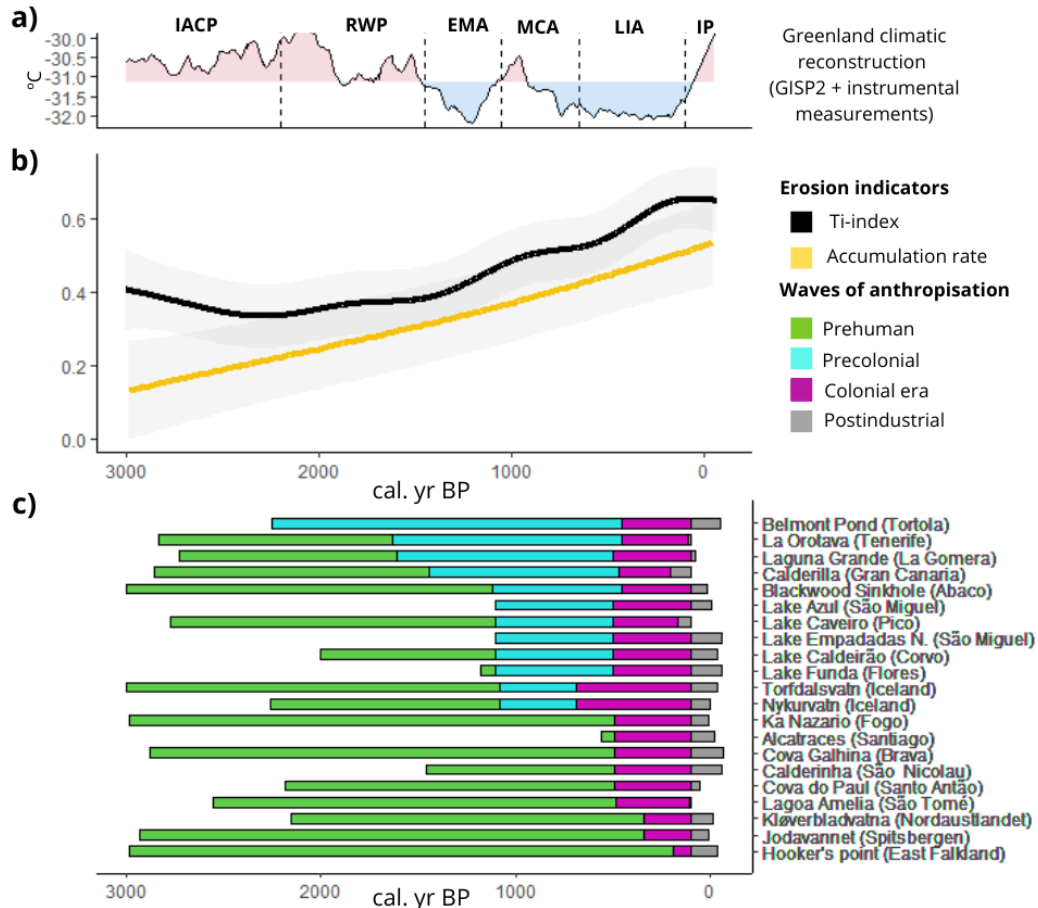


Figure 2. a) To illustrate the climatic context of the past 3000 years, we used temperature reconstructions from Greenland ice cores (GISP2) (Alley, 2004), complemented by modern temperature measurements from the same site for the period 2001–2010 (Kobashi et al., 2011). We also incorporated major past climatic periods relevant to the Northern Hemisphere, as identified in previous studies (Lapointe et al., 2020; Sánchez-López et al., 2016; Swindles et al., 2007). The Iron Age Climate Period (IACP; 3000–2200 cal. yr BP) was marked by generally warm and stable conditions. This was followed by the Roman Warm Period (RWP; 2200–1450 cal. yr BP), a phase of continued warmth that coincided with the expansion of the Roman Empire. A subsequent cooling phase, known as the Early Middle Ages (EMA; 1450–1050 cal. yr BP), then set in. A subsequent warming trend occurred during the Medieval Climate Anomaly (MCA; 1050–650 cal. yr BP), a time of notable climatic variability. This period was followed by the Little Ice Age (LIA; 650–100 cal. yr BP), a period of global cooling that affected agriculture and societies worldwide. Finally, the most recent phase, the Industrial Period (IP; from ~100 cal. years BP (1850 CE) to the present), was characterised by a rapid increase in global temperatures driven mostly by human activity. Red indicates temperature values over the mean while blue depicts the opposite. b) Temporal trends in accumulation rate and Ti-index across all records, modelled using generalised additive mixed models (GAMMs), with 95% confidence intervals shown in gray. Values were transformed to be between 0 and 1. c) Chronologies for each island, with distinct colours representing waves of anthropisation. The x-axis represents calibrated years before present (cal. yr BP) and is consistent across panels.

Geochemical trajectories after human arrival

We calculated elemental turnover and directionality for each record, as indicators of a stabilising elemental composition when both metrics present low or decreasing values (de la Casa et al. 2025). Both metrics were calculated for the 21 depositional records, but the records from La Gomera, Santo Antão, São Nicolau and Brava were not suitable for calculating elemental turnover and directionality due to their low temporal resolution (Table S2). Both metrics responded differently to individual trends depending on the island (Figure S3). From the 17 records suitable for the analysis, five showed an increase in both metrics after human arrival to the island (i.e. one from British Virgin Island, two from Azores, one from Bahamas and one from Iceland) indicating large and directed changes in the geochemical composition after human arrival. One record from Svalbard (Kløverbladvatna) also increased both metrics after human arrival to the island, but the metrics were already increasing ahead of arrival. In four records, elemental turnover increased while directionality decreased (i.e. two records from Canary Islands, one record from Gulf of Guinea Islands and two from Azores) indicating large but undirected changes in the geochemical composition. In three of the records (i.e. two from Azores and one from Iceland) elemental turnover decreased after human arrival while directionality increased, indicating stabilisation of the geochemical composition. In two records (i.e. one from Svalbard and one from Cabo Verde) both metrics were decreased after the first arrival of humans to the islands. The record from the Falkland Islands did not have enough data after the arrival of humans.

GAMMs were also built for elemental turnover and directionality, but explained only 0.69% and 5.99% of the variance, respectively (Figure S4). In contrast to accumulation rate and Ti-index, elemental turnover and directionality lack of trends when all records are considered together

Trends across waves of islands anthropisation

A comparison of various metrics across different waves of island anthropisation (Figure 3) reveals clear differences between islands first anthropised during European colonisation in the 15th century CE (i.e. Svalbard, Cabo Verde, São Tomé and Falkland Islands and Svalbard, although they were colonised later on) and those that experienced precolonial anthropisation prior to European overseas expansion (i.e. Bahamas, British Virgin Islands, Canary Islands, Iceland, Azores).

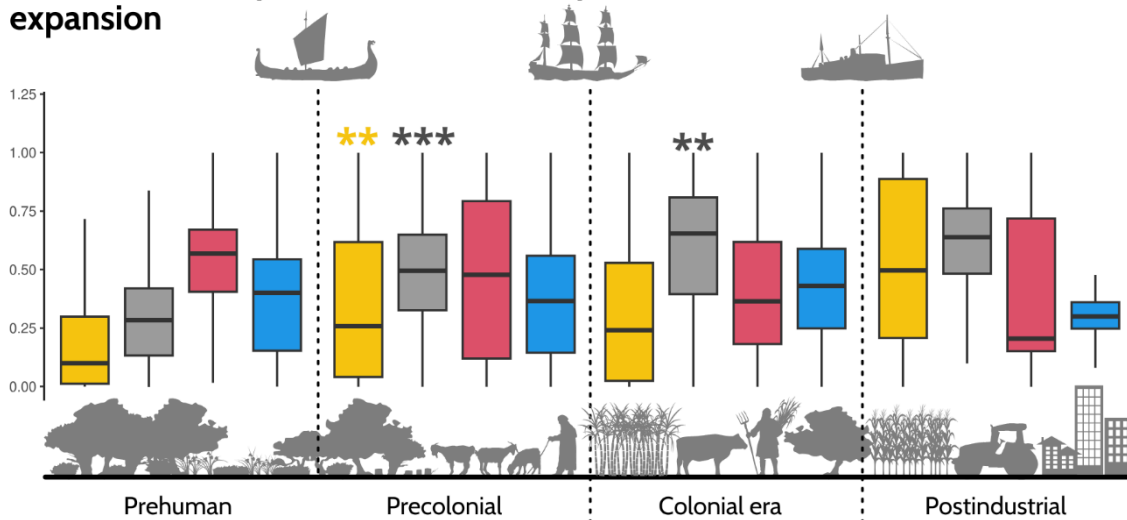
On islands with the early precolonial wave, accumulation rates increased significantly (1.61 times) between the prehuman era and the precolonial settlements ($p = 0.008$). No significant changes occurred between precolonial and colonial era ($p = 0.926$), or colonial era to post-industrial ($p = 0.456$). In contrast, on islands colonised during the 15th century CE, the accumulation rate increased significantly (2.09 times) between the prehuman era and the stages of the colonial era ($p < 0.001$) but did not change significantly between the colonial era and the post-industrial stage ($p = 0.864$).

Ti-index on the early anthropised islands strongly increased (1.40 times) between the prehuman era and the precolonial wave ($p < 0.001$), continuing significantly increasing (1.23 times) into the colonial era ($p = 0.003$), but did not differ significantly between the colonial era and the post-industrial stage ($p = 0.85$). Ti-index on islands colonised during the 15th century increased significantly (1.48) from the prehuman era to the stages of the colonial era

($p < 0.001$); and continued increasing significantly (1.19 times) between the colonial era and the postindustrial stage ($p = 0.19$).

For the precolonial anthropised islands, elemental turnover did not differ significantly between any of the waves of anthropisation ($p = 0.942$; $p = 0.991$; $p = 0.919$, respectively). However, on islands colonised during the European overseas expansion (15th century CE) elemental turnover increased significantly (2.05 times) between prehuman and colonial era ($p < 0.001$) and significantly decreased (0.34 times) between colonial era and postindustrial times ($p = 0.002$). Trajectory directionality did not present any significant differences between waves of anthropisation for precolonial anthropised islands ($p = 0.901$; $p = 0.820$; $p = 0.331$, respectively) or islands colonised during the 15th century CE ($p = 0.994$; $p = 0.224$, respectively).

a) Islands anthropised before the European overseas expansion



b) Islands anthropised during the European overseas expansion

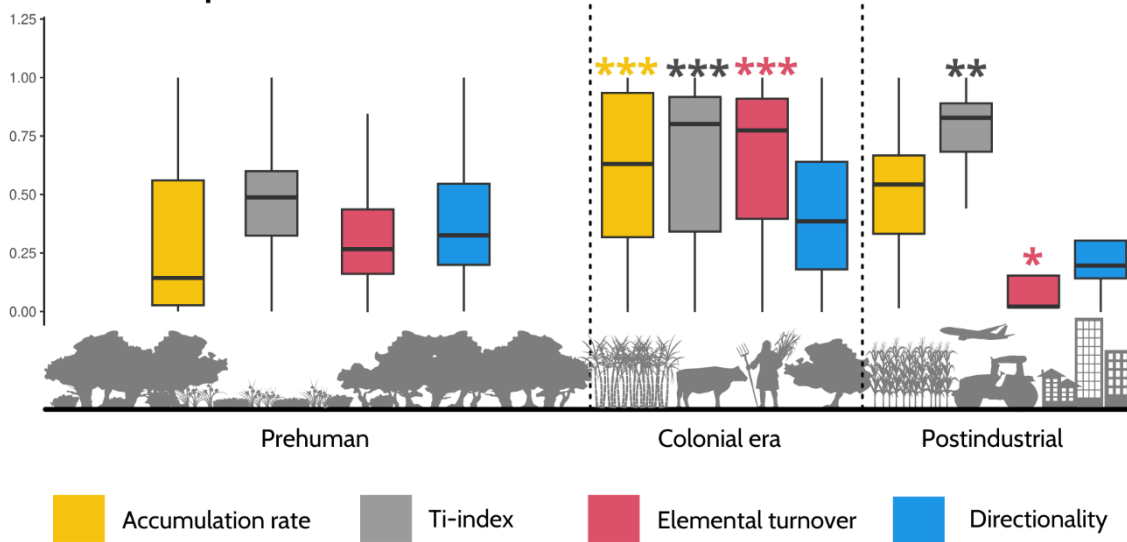


Figure 3. Changes in elemental turnover, trajectory directionality, accumulation rate, and Ti-index are shown for: (a) Early anthropised islands (Bahamas, British Virgin Islands, Canary Islands, Iceland, Azores), comparing different waves of human arrival. (b) Islands anthropised during the European overseas expansion (Svalbard, Cabo Verde, São Tomé, Falklands), also comparing successive waves of anthropisation. Each metric is normalised using min-max scaling (range 0–1) and plotted on the Y-axis. The letters above the boxplots are used to represent significant changes between waves of anthropisation. This was done independently for each variable. The asterisk above the boxplot indicates significant changes between this wave and the previous. The number of asterisks indicates the level of significance (** for $p < 0.001$; * for $p < 0.005$; * for $p < 0.05$)

Distinct responses to island anthropisation

We evaluated whether the time since human arrival, as well as the latitude and elevation of the sites, influenced the key environmental change metrics namely accumulation rate, Ti-index, elemental turnover, and directionality. To do this, we fitted regression curves spanning 250 years before and after human arrival and calculated the differences in the rates of change. All regression models showed acceptable root mean square errors (RMSE) (Legendre & Legendre, 2012)(Figure S8).

The rate of change of accumulation rate, Ti-index, elemental turnover, and directionality was generally higher at high-elevation sites compared to low-elevation ones, with a similar but less pronounced trend observed for Ti-index. In contrast, elemental turnover exhibited higher rates of change at low-elevation sites. Latitudinally, regions between 0–20° N and 70–80° N showed elevated rates of change in both elemental turnover and directionality. Islands that were anthropised more recently displayed higher rates of change in elemental turnover, while their accumulation rates changed more slowly, this was particularly evident in Svalbard, where human activity is reduced, and the Falkland Islands, whose flat geomorphological setting also should be taken into account. In contrast, earlier anthropised islands showed more variable patterns: for example, Tenerife exhibited a low rate of change, whereas Gran Canaria showed a high one.

Discussion

Accelerating trend of soil erosion following human arrival and settlement on islands

Our findings indicate a continuous and accelerating trend of soil erosion following human arrival and settlement on islands. Both the accumulation rate and Ti-index generally increased over time and were positively correlated (Figure S3), indicating an enhanced soil loss across the Atlantic islands (Figure 2). Our results align with previous research (Baud et al., 2021; Rapuc et al., 2024), which shows that human activities and subsequent land-use changes, such as deforestation (Jenny et al., 2019), agricultural intensification (Govers et al., 2017), burning, and the introduction of grazing animals, were major drivers of increased soil erosion and landscape transformation on islands.

The concurrent increase in accumulation rate and Ti-index suggests the increased deposition of land-derived material, indicating soil erosion. This pattern is evident in islands such as Canary Islands (Tenerife, Gran Canaria), Azores (Corvo), Cabo Verde (São Nicolau, Brava), Falkland Islands (East Falkland) and Iceland where both metrics sharply increase following human arrival, revealing a pattern of human-driven erosion (Figure 1). This can be explained by land-use changes and increased fire activity, both of which are associated with soil loss. The first settlers of Tenerife and Gran Canaria had a clear impact, as evidenced by vegetation changes and increased fire frequency, which help explain the observed soil erosion signal (de Nascimento et al., 2020; Ravazzi et al., 2021). On Corvo, land-use changes left a clear erosive signal in Lake Caldeirão, though this later diminished—700 years post-settlement—coinciding with rising lake productivity and system eutrophication (Raposeiro et al., 2021). The arrival of European colonisers to São Nicolau and Brava

triggered a distinct pattern of erosion, likely driven by the introduction of livestock and the establishment of commercial plantations (Castilla-Beltrán et al., 2021; Castilla-Beltrán et al., 2023).

In Iceland, human settlement during the Landnám period (870–930 CE) was marked by an abrupt population influx and drastic land-use shifts, leading to landscape destabilisation and extensive erosion (Vésteinsson & McGovern, 2012). The onset of land use practices radically altered vegetation composition and drove significant landscape changes, which help explain the observed erosion patterns (Alsos et al., 2021; Streeter et al., 2015). The record from East Falkland showed a clear erosive pattern after European arrival, which could also be attributed to previous settlements, although the evidence of earlier arrivals is still insecure (Hamley et al., 2021; Zangrando & Borrero, 2024). The two records from Svalbard showed increased accumulation rate and Ti-index in the last 500 years (Figure 1). However, since there is still no human activity in the vicinity of the studied lakes, these changes cannot be attributed to direct human impact. More plausible explanations involve aeolian deposition of glacial dust and glacial meltwater inputs, in addition to erosion driven by natural processes (Kjellman et al., 2024; Lapointe et al., 2023; Schomacker et al., 2019; Voldstad et al., 2020). Together, these case sites reveal a consistent pattern of human-driven soil erosion across diverse island environments, highlighting the profound and lasting impact of early land-use practices, while also emphasising the need to distinguish natural processes from anthropogenic signals in more remote regions like Svalbard.

An increase in accumulation rates accompanied by a decrease in Ti-index suggests that the accumulating material is primarily non-terrigenous, most likely organic matter. This may originate from enhanced organic matter build up in soils, or aquatic productivity, increased input from the lake catchment. This phenomenon was observed in sediment records from Canary Islands (La Gomera), Gulf of Guinea Islands (São Tomé), Cabo Verde (Santo Antão), Azores (Flores, Pico, and São Miguel). In particular, Lake Empadadas (São Miguel, Azores) and Lake Caveiro (Pico, Azores), both small and shallow lakes, are especially sensitive to eutrophication and shoreline changes (Hernández et al., 2017; Pla-Rabés et al., 2024) which is reflected in the dominance of organic components in their sediments (J. Zhou et al., 2022). Lake eutrophication was also observed in deeper lakes such as Lake Azul (São Miguel, Azores) and Lake Funda (Flores, Azores), which exhibited relatively stable Ti-index values but fluctuating accumulation rates. These variations coincided with shifts in in-lake productivity (Richter et al., 2022; Vázquez-Loureiro et al., 2019). Lagoa Amélia (São Tomé, Gulf of Guinea Islands), located in the afromontane belt, shows a decrease in Ti-index values that may be linked to the development of bogs in recent centuries (Castilla-Beltrán et al., 2023b)(Figure 1). Similarly, Laguna Grande (La Gomera, Canary Islands) showed limited evidence of human impact, which likely contributed to the minimal anthropogenic impact observed in its sediment record (Nogué et al., 2013). Finally, in Cova de Paúl (Santo Antão, Cabo Verde), a highland depositional site within a volcanic caldera, the erosive process that followed human arrival appears to have been mitigated, likely due to afforestation efforts and nutrient enrichment driven by increased livestock presence (Castilla-Beltrán et al., 2019). These examples highlight the importance of combined analysis of accumulation rates and Ti-index, as an increase in accumulation accompanied by a decrease in Ti-index often indicates the dominance of non-terrigenous, likely organic material. This combined approach provides a clearer understanding of erosion patterns and sedimentation dynamics.

The results from Blackwood Sinkhole (Abaco, Bahamas) show a considerable increase in Ti-index values. However, significant human impact is unlikely, as the Lucayan settlement in the area was likely limited due to poor agricultural potential stemming from minimal soil cover (Fall et al., 2021). Nevertheless, the Ti-index increase may be explained by wetland development in the epikarst surface around 1330-1410 cal. yr BP; and the following diagenesis of sediments (Tamalavage et al., 2018). Similarly, the record from Fogo (Cabo Verde) shows an increase in Ti-index over time, while accumulation rates remained stable or declined. Notably, this shift occurred around 2000–1500 cal. BP, which predates human arrival suggesting a predominantly natural origin for the observed changes. The volcanic activity on the island, which peaked around 1200 cal. yr BP. Seismicity and deposition of airborne volcanic particles can account for this signal. This natural disturbance may have masked the impacts of later human settlement around 488 cal. yr BP and the associated intensive land use (Castilla-Beltrán et al., 2023b). The record from Santiago is associated to an archaeological site, amongst the first settlement on the island (Evans et al., 2017, 2025). It showed an initial increase of accumulation rates after human arrival, but the increase in Ti-index was delayed. This can be explained by a strong accumulation of organic and charcoal material from the nearby settlement, and a posterior increase of Ti-index values when the vegetation cover was lost and thus erosion increased. Finally, European arrival to Belmont Pond (Tortola, British Virgin Islands), showed a constant trend of accumulation rates, but Ti-index first decreased to later increase; which could be attributed to the different land management and agricultural practices of European colonisers, as suggested by pollen and charcoal data (Mueller et al., 2019).

These diverse cases collectively show that natural disturbances, such as volcanic activity, hydrological shifts, wetland development, and sediment diagenesis, can generate sedimentary signals like those caused by human activity, which may obscure or overlap with anthropogenic impacts. This highlights the importance of contextual interpretation and multi-proxy approaches to accurately disentangle the environmental and human drivers of erosion and sedimentation.

Increase in elemental turnover coinciding with the onset of anthropisation

Elemental turnover and trajectory directionality captured both the magnitude and direction of geochemical transformations over time in the records where such analysis was feasible (17 of the 21 records, see Methods). Regardless of whether the geochemical changes were directional or not, most records showed an increase in elemental turnover coinciding with the onset of anthropisation. This pattern was observed in records from British Virgin Islands (Tortola), Bahamas (Abaco), Azores (Corvo, Flores and Lake Empadadas from São Miguel), Canary Islands (Tenerife, Gran Canaria), Gulf of Guinea Islands (São Tomé), and Iceland (Lake Nykurvatn) and Svalbard (Nordaustlandet) (Figure S3).

The high magnitude of geochemical transformations in the deposited material indicates the influence of intense land-use activities or, in some cases, non-anthropogenic factors such as aeolian deposition or glacier meltwater input Svalbard. However, several records, including those from Pico (Azores), Lake Azul (São Miguel, Azores), Lake Torfdalsvatn (Iceland), Spitsbergen (Svalbard), and Fogo (Cabo Verde), show decreasing elemental turnover values (Figure S3). This suggests that environmental changes following island anthropisation did not significantly destabilise the geochemical composition of sedimentary inputs in these locations, pointing to relatively low-magnitude impacts. This contrast highlights the variability in human-environment interactions across islands, suggesting that the magnitude

of anthropogenic impact is not uniform but instead shaped by local biophysical characteristics, land-use intensity, and pre-existing environmental conditions.

Waves of anthropisation

The anthropisation of Atlantic islands occurred in multiple waves throughout history. For islands that were settled earlier, the transition from prehuman conditions to precolonial settlements led to significant increases in both accumulation rates and Ti-index, indicating substantial environmental changes brought about by the first cultures to arrive (Figure 3).

The earliest human presence in the Caribbean dates back to over 7000 to 5000 yr cal. BP (Fitzpatrick, 2015), with subsequent expansions by various cultures, including the Caribbean, the Ciboney, and the Taíno, who settled areas such as the Bahamas and the British Virgin Islands. North African agropastoral groups settled the Canary Islands (La Gomera, Gran Canaria, and Tenerife) around 1800 years cal. BP (Santana et al., 2024). The early development of Norse seafaring skills in the Northern Atlantic enabled the settlement of Iceland around 870 CE and other remote islands such as the Faroes, Greenland and Newfoundland, Canada (Fitzhugh & Ward, 2000).

The colonial era was a period with high erosion (Figure 3). The islands colonised during the European overseas expansion were transformed into strategic areas for navigation, slave trade, and the production of goods such as cotton and sugar cane (Castilla-Beltrán et al., 2021; Crosby, 2004). European colonisation caused significant depopulation of earlier settlers in many islands. This trend was found in the Caribbean (e.g., Bahamas, British Virgin Islands) and Canary Islands. Factors included slavery, the introduction of diseases, violence, and forced displacement, leading to major demographic and cultural changes. Atlantic islands in the Southern Hemisphere such as St. Helena, Tristan da Cunha, and the Falkland Islands were first reported by European explorers and later colonised as strategic areas for trade, navigation, and military practices (Crosby, 2004), which also extended to remote Arctic islands such as Svalbard which main activities were hunting, trapping and coal mining (Kruse, 2016). In islands that were previously settled, European colonisation only drove increases in the Ti-index compared to the previous wave. However, islands that were first colonised during the European overseas expansion showed significant increases of Ti-index, accumulation rates and elemental turnover, compared to prehuman conditions. The onset of anthropisation led to accumulation rate impacts that were 1.29 times greater on islands colonised during the overseas expansions compared to those settled earlier. However, the impact on Ti-index was similar across both groups.

A major turning point in the ecological impact of human activity occurred after the Industrial Revolution (approximately 1850 CE). Although industrialisation may have reached many islands only recently, we consider the postindustrial era as a distinct wave of anthropisation. This is due to socio-political and historical differences that are also evident in land management practices, resource extraction, demographic pressures, and ecological footprints (Steffen et al., 2015a). From a geochemical perspective, postindustrial times are affected by the decoupling of the nutrient cycles such as carbon, nitrogen, and phosphorus (Steffen et al., 2015a), and the introduction of novel entities and pollutants (Persson et al., 2022). In our study, the limited amount of data for the last two centuries restricted an exhaustive assessment of postindustrial impacts (Figure 3). We observed significant changes only on islands colonised during the European overseas expansion. From the colonial era to postindustrial times, these islands experienced a marked decrease in elemental turnover and a

significant increase in Ti-index. These trends suggest that the geochemical composition is beginning to stabilise, in contrast to the highly disruptive effects of initial European colonisation on previously uninhabited islands. This could also be explained by a socioeconomical shift towards fishing and tourism as main economic activities, in contrast to land-intensive agriculture (e.g. Caribbean, Cabo Verde). However, the continued rise in land-derived elements in sediments indicates ongoing anthropogenic influence.

Our results suggest that the anthropisation of Atlantic islands left a unique ecological imprint across distinct historical waves. These findings highlight the long-term and evolving nature of human-induced environmental change across island ecosystems.

Natural drivers of the erosion signal

Environmental changes on islands over the past three millennia were shaped by human activity, climate, and also volcanic activity. Fully understanding the role of climate would require high-resolution reconstructions tailored to the specific conditions of each island. Disentangling human and climatic drivers remains challenging, as they often act simultaneously. For instance, the Norse expansion into Greenland and Iceland coincided with the Medieval Climate Anomaly (Streeter et al., 2015), while the onset of the Little Ice Age aligned with European colonisation of the Atlantic islands, likely facilitated by shifting wind patterns and cooler temperatures (Raposeiro et al., 2021). These overlapping factors may help explain why accumulation rates did not increase around 650 cal. yr BP, despite intensified human activity during that period. Similarly, the arrival of humans to Iceland is synchronous with higher temperatures that could enhance the mobilisation of elements (Streeter et al., 2015). This coincidence of human and climate relevant events is also present in other island records, i.e. in drought and human settlement in South Polynesia (Sear et al., 2020).

Erosion signals in our study were inferred from both accumulation rates and Ti-index values. While the records provide strong evidence of erosion, we also identified cases where the observed signals may not result from erosion alone. In some instances, other natural processes, such as changes in sediment transport or deposition, may contribute to similar patterns, highlighting the need for cautious interpretation (e.g., Svalbard). For example, in volcanic regions like Iceland or Cabo Verde, the deposition of tephra resulting from explosive volcanic eruptions can have a direct effect on accumulation rates and minerogenic composition of the sediments (Alsos et al., 2021; Castilla-Beltrán, et al., 2023b; Farnsworth, 2025).

We also found that sites at lower elevations exhibited a stronger response to human arrival, likely due to their greater accessibility (Figure S5). This pattern was expected, as low-lying areas are easier for humans to reach and modify. However, accumulation rates at elevations close to sea level did not follow this trend. This exception may be explained by the flat geomorphology of these areas, which can dampen the impact on external sediment accumulation.

Potential limitations and direction of future research

This study may be influenced by dating uncertainties and the inherent challenges of comparing data from diverse sources, which could introduce some bias to the results. The estimated dates for the arrival of humans were a simplification of a complex process of occupation. The year of arrival can be distinct from the onset of the impacts in the area. Moreover, human arrival is not necessarily impacting all parts of the island. New evidence for updated dates of arrival can also change, as for the Azores archipelago, where recent

findings suggest human arrival before the Portuguese colonisers (Raposeiro et al., 2021). We chose 1100 cal. yr BP as the first arrival time, but the evidence for human activity differed drastically across records: from 1100 cal. yr BP for Lake Caveiro (Pico Island) to 650 cal. yr BP for Lake Funda (Flores Island).

Accumulation rates were derived from the depth age models, which quality, although is high in all the records included in the analysis, is variable across studies. Moreover, in some settings the apparent increase in accumulation rate can also be a result of more compaction of deeper sediments, in comparison to softer and less dense surface sediments. Ti-index was assessed based on the dominance of titanium within the multi-elemental multivariate space (see Methods) and, together with accumulation rates, served as an indicator of erosion. While most terrigenous elements showed positive correlations with Ti, we also identified exceptions. For example, vanadium (V) on Tortola (British Virgin Islands) and strontium (Sr) on Santiago (Cabo Verde) were negatively correlated with Ti. These cases suggest that the elemental composition of land-derived inputs can vary in reflection of differences in local geology, hydrology, or sediment sources (Boës et al., 2011).

Elemental turnover and directionality were used to describe the magnitude and direction of geochemical changes. We calculated these metrics using time-fixed moving windows, with window widths based on the temporal resolution of each record. This method was best suited to our dataset, which includes records with varying sampling resolutions (Table S2). Ideally, a uniform window width would be applied across all records, but this was not feasible given the data resolution variability. This, together with the asynchrony of anthropisation waves, may explain the low global fit on elemental turnover and directionality GAMM (Figure S3).

Building on these findings, future research should aim to disentangle the effects of specific land-use changes, such as deforestation, burning and agricultural expansion, on soil loss dynamics in island environments. Disentangling those effects may require larger sample sizes and multiproxy global or regional databases. Integrating local palaeoclimate reconstructions with geochemical records also presents a valuable opportunity to understand how past climate variability has influenced sediment and elemental fluxes (Geirsdóttir et al., 2009; Raposeiro et al., 2021). Expanding these approaches globally will be essential for developing robust, transferable frameworks to inform land-use policy and climate adaptation strategies.

Final remarks

Our synthesis provides a multi-proxy perspective on long-term human impacts on island erosion, offering a valuable framework for future research and targeted land-use strategies. This signal of erosion in the island records was clear for some Atlantic islands and is consistent with broader global trends in anthropogenic erosion, which intensified by a factor of 1.48 to 2.1, depending on the wave of anthropisation. This generalised erosive legacy, should motivate urgent action (e.g. soil recovery, sustainable land management, policy frameworks) to avoid erosion-driven soil loss, especially on islands, which are particularly endangered by their limited amount of land.

Methods

History of human arrival on the Atlantic islands

The human colonisation of Atlantic islands occurred in different waves. The dates for human arrival were compiled from different sources (Table S3). Since settlement evidence is not

clear for all records, we consider the first evidence of human arrival to the island as the onset of the anthropisation of the island. We took into account European colonisation and the Industrial Revolution as milestones in the story of island anthropisation. Given that, we defined the following waves of anthropisation:

- (i) Prehuman, period without archaeological and historical evidence of permanent human presence on the islands.
- (ii) Precolonial anthropisation, period between the arrival of the first evidence of human presence and the European conquests during the overseas expansion around the 15th century CE (Penrose, 1952). This period was only defined for the islands that were anthropised prior to the European overseas expansion.
- (iii) Colonial era, period after the European overseas expansion and the start of the Industrial Revolution. For this study, Svalbard was considered to enter the colonial era with the start of whaling activities (338 cal. yr BP) (Arlov, 1989; Kruse, 2016). Iceland was considered to enter the colonial era around 688 cal yr BP, with the onset of Norwegian rule of the island. In the case of Falkland Islands, although there is debate suggesting precolonial human presence (Hamley et al., 2021), we considered the first arrival, and the introduction to the colonial era with the reported European arrival.
- (iv) Postindustrial times, period following the Industrial Revolution (1850 CE) to the present.

Geochemical data

We compiled 21 depositional records from lakes, soils, and wetlands across 19 islands (Table S2). These records were selected for their high chronological resolution and because they included data points from both before and after human arrival, either from initial settlement or, at minimum, from the European overseas expansion around the 15th century CE. Chronologies for each record, expressed in calibrated years before present (cal. yrBP), were obtained from the original studies using methods such as radiocarbon (¹⁴C) dating and lead-210 (²¹⁰Pb) dating (Table S3).

We obtained 18 geochemical datasets (XRF data) from published studies covering sites in Svalbard, Iceland, the Bahamas, British Virgin Islands, Azores, Canary Islands, Cabo Verde, São Tomé, and the Falkland Islands (Table S3) (Figure 1). In most cases, only a limited number of elements were reported in the original publication. Here, we compiled all available elemental measurements, including previously unpublished data.

Additionally, three new records, from La Orotava (Tenerife, Canary Islands), Calderilla (Gran Canaria, Canary Islands), and Alcatrazes (Santiago, Cabo Verde), were analyzed using a Niton™ XL3p+ handheld X-ray fluorescence (XRF) scanner with a test stand (Thermo Fisher Scientific, Massachusetts, USA). Analyses were conducted at the Universitat Autònoma de Barcelona (Catalonia, Spain; Table S3). Elemental concentrations were reported as proportional values (%) for elements detected above a threshold of 0.001%, with each sample measured for 180 seconds.

Curation of geochemical data

Our geochemical database contained the following elements: Aluminum (Al), Arsenic (As), Bromine (Br), Calcium (Ca), Chlorine (Cl), Chromium (Cr), Copper (Cu), Iron (Fe), Lead

(Pb), Magnesium (Mg), Manganese (Mn), Mercury (Hg), Nickel (Ni), Phosphorus (P), Potassium (K), Silicon (Si), Sodium (Na), Strontium (Sr), Sulfur (S), Titanium (Ti), Vanadium (V), Zinc (Zn), Zirconium (Zr).

For each record, we excluded elements that may present low quality results. We followed these criteria: i) If the source data had corresponding errors, only elements whose mean error was <0.6 were included. This threshold was selected to balance data completeness with analytical confidence, excluding low-quality measurements that could bias interpretations. ii) If the elemental data did not have a corresponding error, we applied an autocorrelation test using the *acf* function from the *stats* package in R Studio (Venables & Ripley, 2002) and selected only those with an autocorrelation >0.25 (Bishop, 2017).

Because the data were sourced from multiple studies and curators, we applied a square-root transformation to each element to reduce variability and minimise the influence of outliers that may not have been previously identified. We then applied a min-max normalisation to rescale each element's values between 0 and 1, setting the minimum to 0 and the maximum to 1. This standardisation allowed for direct comparison across elements (Legendre & Legendre, 2012).

Calculation of the accumulation rate

We calculated the sediment accumulation rate (Table 1) for each record as the difference in depth of two consecutive geochemical measurements with modelled ages (samples) divided by the difference in time of the same consecutive samples (Jenny et al., 2019). We then used the mean rates for data groups at a centennial scale (100 years) to facilitate the comparison between data sets with high and low resolutions (Table S2) and avoid issues such as the Sadler effect (Sadler & Jerolmack, 2015).

Characterisation of terrigenous elements in the trajectories (Ti-index)

To estimate the amount of land-derived elements in the geochemical composition we introduced a new indicator called Titanium-index (Ti-index). Titanium was chosen as the primary indicator of terrigenous elements due to its low reactivity, high abundance in terrestrial rocks, and strong association with sediment runoff (Croudace & Rothwell, 2015). The geochemical trajectories were assessed using a principal component analysis (PCA) and the elemental composition of each data set. To create an indicator that detected when the geochemical trajectory was heading toward terrigenous elements, we rotated all samples and element loadings in each record in the PCA, so that the angle of Ti loading with PC axis 1 (PC1) was 0° in all PCA plots (Figure S1). The PC1 value would then indicate the dominance of Ti in the trajectory and thus serve as an indicator of how strongly the terrigenous elements dominated the trajectory. The PC1 values of the Ti-rotated PCA were then called Ti-index (Table 1). We acknowledge, however, that not all terrigenous elements would be associated with Ti, so we calculated the correlation between all elements and the PC1 for each record (Figure S2).

Elemental turnover and trajectory directionality

We constructed time-fixed moving windows to calculate trajectory metrics for quantitatively describing the elemental trajectories. The temporal resolution varied across data sets, so setting a fixed time span for all data sets would not provide good-quality metrics. We instead defined moving windows for each data set representing 25% of the total time span of the

record, with a step size calculated as 2.5% of the time span of the record. A window size representing 25% of the total time span of the record was chosen to balance the need for capturing temporal trends with the need for maintaining sufficient data points within each window. Smaller window sizes would have reduced the statistical power of the analysis, while larger window sizes would have smoothed out important temporal variations (Table S2).

We calculated two trajectory metrics. First, the elemental turnover was used as a metric of the dissimilarity of the samples within the moving window. We used the beta diversity index (Legendre & Cáceres, 2013) to quantify the variability in elemental composition over time. Second, we calculated the directionality of the trajectory using the *ecotraj* R package (De Cáceres & Djeghri, 2025). This metric describes how much a trajectory consistently follows the same direction in multivariate space, as opposed to nondirectional temporal changes. The calculation of elemental turnover and directionality was not based on the PCA axes but on the distance matrix

Individual and general trends for erosion and geochemical transformations

We transformed the minima and maxima for all datasets of the four metrics: elemental turnover, directionality, accumulation rate, and Ti-index. The correlations between the four metrics were calculated by grouping all variables in time windows of 100 years and calculating Pearson's correlation coefficient.

Trend analyses were conducted as follows. First, we described the trends of all metrics in each data set using locally estimated scatterplot smoothing (LOESS) (Cleveland et al., 1988), with a confidence interval of 95%. Second, we calculated generalised trends for all metrics across all data sets of depositional records. We used generalised additive mixed models (GAMM) (S. N. Wood, 2017) as follows: each selected metric in the study (accumulation rate, Ti-index, elemental turnover, and directionality) was modeled as a smooth function of time (calibrated years BP), allowing for flexible, nonlinear trends. Random intercepts were included: archipelago and record name to account for spatial clustering and an unbalanced number of samples, respectively.

Third, we calculated the difference for all metrics within different waves of human anthropisation. We separated the analysis of islands that were settled before European overseas expansion (Penrose, 1952). The groups (waves) in this case were: prehuman, precolonial, colonial era, and postindustrial. The islands that were uninhabited until the arrival of Europeans during the overseas expansion were grouped as: prehuman, colonial era, and postindustrial.

Last, we calculated the effect of the environmental characteristics of the site that originated the records: latitude, elevation and number of years since island anthropisation started (Table S1 and S3). We calculated the difference between the rate of change of the four indicators for 250 years before and after humans arrived and modeled the difference with elevation, years since humans arrived, and latitude as response variables of the environmental characteristics using LOESS (Cleveland et al., 1988). We calculated single models with only one predictor (latitude, elevation and years since humans arrived) in each possible combination.



Fourth Chapter:

Biogeochemical and vegetation
coupling in the Alps: climate change
and livestock effects on alpine
ecosystems across the Holocene



*Do palaeoecologist
dream of ancient
sheep?*

Biogeochemical and vegetation coupling in the Alps: climate change and livestock effects on alpine ecosystems across the Holocene.

Javier de la Casa, Sandra Garcés-Pastor, Scarlett Zetter, Sandra Nogué, Miquel de Cáceres, Franka Gaiser, Jordi Sardans, Peter D Heintzman, Youri Lammers, Christoph Schwörer, Andreas Tribsch, Oliver Heiri, Eric Coissac, Sébastien Lavergne, Kevin Walsh, Willy Tinner, Anthony G. Brown, Inger G. Alsos, Josep Peñuelas

Abstract

The elemental composition of ecosystems (the ecosystem elementome) and its availability is a key factor shaping species composition and ecosystem functions. However, long-term studies addressing the temporal covariation between plant community composition and ecosystem elementomes are scarce. Lake sediments offer an ideal archive, preserving dated records of changes in vegetation and elementomes. The Alps have been influenced by humans since the Neolithic and are a well-studied region in palaeoecology. In this study, we explored spatiotemporal shifts between alpine vegetation and sediment biogeochemical composition, especially focusing on the effect of climate and livestock introduction as drivers of these shifts. Our database comprises 410 chronologically dated sediment samples from 12 lakes in the Alps, covering the last eight millennia to the present. Each sample contains independent measures of sedimentary ancient DNA (*sedaDNA*) for plants and mammals, along with the sediments biogeochemical composition (C, N and XRF data). We found that the coupling of ecosystem elementomes and vegetation decreased by 18% after 4k yr BP, with precipitation and sheep abundances negatively correlated with the coupling values. Alpine vegetation diversity generally increased with precipitation and with sheep and cattle presence, and decreased with temperature, when the sediments presented a more organic composition and the community had higher abundance of woody taxa. Our study concludes that the onset of pastoralism in alpine hills during the Mid-Holocene disrupted ecological coupling through the introduction of sheep, which, together with cattle, have been the main drivers of alpine vegetation diversity since the Bronze Age. Furthermore, our findings show that cattle and sheep negatively affect carbon and nitrogen stocks, an issue that warrants further investigation.

Introduction

The elemental composition of ecosystems (ecosystem elementomes) and the structure of plant communities are intrinsically linked, with each influencing the other and jointly

determining ecosystem functioning (Peñuelas et al., 2020; Welte et al., 2017). Since macronutrients (e.g. nitrogen, potassium, phosphorus, calcium...) and micronutrients (e.g. iron, manganese...) are essential for plant development, their availability and stoichiometric ratios can determine community composition and function. The biogeochemical niche theory (Peñuelas et al., 2019) proposes that species elemental composition (elementome) is linked to their elemental requirements to carry out their functions. The structure of plant communities and the elemental composition of ecosystems can be viewed as a dynamic equilibrium, constantly responding to internal and external drivers such as climate fluctuations, species interactions, and disturbances. Changes in the element availability on the ecosystem (ecosystem elementome) can drive significant shifts in species and function diversity. For example, eutrophication or addition of multiple limiting elements can cause losses of plant diversity (Fay et al., 2015; Harpole et al., 2016). In forb and graminoid communities, multi-element competition generates high diversity, but this effect collapses when nutrients are not limiting, and light becomes the primary limiting resource, allowing fast-growing taxa to dominate. Similarly, the enrichment of particular elements could lead to a limitation of others. This is the case for P-limitation under nitrogen enrichment scenarios (Luo et al., 2022), driving a shift in plant community and traits (Hou et al., 2020; Olde Venterink, 2011). Plant communities also regulate biogeochemical cycling through litter deposition, nutrient usage, element accumulation and nutrient uplifts (Hooper & Vitousek, 1998; Jobbágy & Jackson, 2004). Elementome shifts may disrupt the connections among species, while global change (i.e. climate change, livestock introduction) disrupts the connections among species and their environment, including the elementome (Ochoa-Hueso et al., 2021). Although understanding the relationship between ecosystem elementomes and plant communities is key for conservation and ecosystem management, most studies to date rely on modern experiments (Q. Chen et al., 2025; Y.-Y. Hu et al., 2020; Wijesinghe et al., 2005). Modern experiments, though valuable, may not fully capture the long-term dynamics and historical contingencies that shape ecosystem elementomes and plant community interactions over centuries and millennia. Moreover, the historical covariation between elementome composition and plant community composition remains largely unexplored. Incorporating long-term perspective is thus needed, especially focusing on climate trends and periods before and after human management.

Lake sediments offer a great opportunity to address ecological questions with a long-term perspective (Catalan et al., 2013; Williamson et al., 2009a). The biogeochemical composition of lake sediments reflects the catchment bedrock, material incorporated into the lake via runoff, biological inputs from catchment and lake organisms, and chemical processes at the bottom of the lake (Cohen, 2003). Sediment biogeochemistry can depict changes in the elemental composition of the terrestrial ecosystems, yet, the terrestrial input may be hindered by in-lake change dynamics. However, lake sediment biogeochemistry has shown strong potential for reconstructing past ecosystem elementomes, or palaeoelementomes (de la Casa et al., 2025). Since sediment biogeochemistry reflects changes in soil, lake waters, atmosphere and living organisms, it is overall a reflection of the environmental biogeochemical composition and fluxes, for now on, ecosystem elementomes. Using lake

sediments, this work aims to reconstruct the past vegetation and ecosystem elementomes, to study its evolution under the effect of climate change and pastoralism. In this study we combine 410 independent measurements for sediment biogeochemistry (carbon, nitrogen, aluminium, calcium, iron, potassium, manganese, phosphorus, sulphur, silicon and titanium) and sedimentary ancient DNA (*sedaDNA*) from plants and mammals from 12 lakes in the Alps; spanning eight millennia. Previous studies quantified plant and mammal species richness and relative abundance using *sedaDNA* (Garcés-Pastor et al., 2022, 2025; Zetter et al., 2025). They found that domestic herbivores, especially cattle, are related to high plant richness and diversity. We chose sheep and cattle abundances, obtained from *sedaDNA* as a key human impact in the catchments. Here we include the biogeochemical composition of the sediment in the same depths where the *sedaDNA* was taken from. Other studies in lakes from the region showed biogeochemical patterns, such as carbon storage in lake sediments linked to human-driven eutrophication (De Jonge et al., 2025; Haas et al., 2019) and warming-induced changes in the lake levels (Ammann, 1986). Temperature and precipitation were reconstructed for all lakes using CHELSA-TraCE21k v1.0 model (see Methods). Previous reconstructions of the climate in the region suggest warmer and wetter conditions across most of the pre-industrial Holocene (before 100 yr BP), with a thermal maximum around 7.5k to 5.7k yr BP in the Eastern Alps, and increased drought episodes during the Little Ice Age (especially between 50 to 249 yr BP) (Arosio et al., 2025; Vollweiler et al., 2006). With this study, we aim to understand plant communities and ecosystem elementome interactions in a long-term perspective; and under livestock management and climate change scenarios. We ask the following questions:

- How has the relationship between alpine vegetation and elementomes changed over the past eight millennia?
- What role have climate and livestock played in driving these changes?

Results & Discussion

A database to address ecosystem elementome and plant community feedback.

To better understand biogeochemical and vegetation dynamics, we built two multivariate spaces. One defined by the elemental composition of the sediments (elementome space; Figure S1 & S2) and other defined by the relative abundance index (RAI) of the plant taxa (taxa space; Figure S3 & S4). For each 12 lakes we recorded the temporal dynamics (approximately at a centennial scale) of the elementome space (elemental turnover), and the temporal dynamics of the taxa space (taxa turnover) (Figure 1).

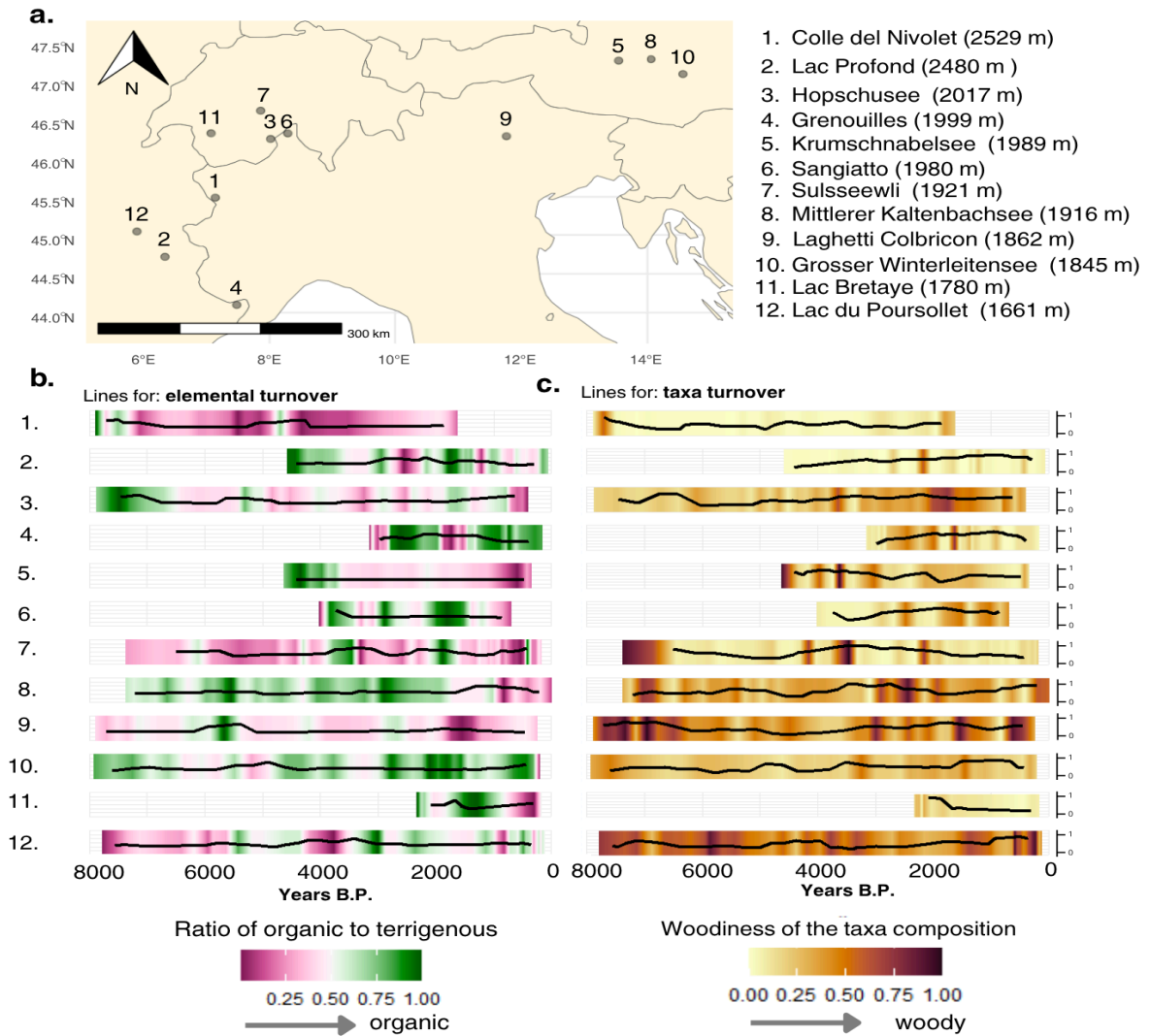


Figure 1. A. Map of the 12 lakes included in the analysis. B. Organic to terrigenous ratio (see Methods). Green colours depict sediment biogeochemical composition dominated by carbon and nitrogen, while purple depict dominance of terrigenous elements such as titanium. Black line represents the elemental turnover C. Woodiness of the taxa composition. Intense brown shows a taxa composition dominated by shrubs and trees. Black line represents the taxa turnover.

Sediment biogeochemistry showed a clear pattern distinguishing periods of more organic content, from others where terrigenous elements dominate (Figure S1), likely due to increased catchment erosion (Croudace & Rothwell, 2015). We use the organic to terrigenous ratio (see Methods) to characterise the elementome space across the 12 lakes (Figure 1). We found no common trend across all lakes, which showed diverse trajectories (Figure S2). While some lakes (i.e. Profond, Hopschusee, Sangiatto, Sulsseewli, and G. Winterleitensee) show synchronical increases of organic content around 2k yr BP; other like Grenouilles or Laghetti Colbricon showed the opposite, increasing of the terrigenous content. The lack of a consistent trend across lakes suggests that local factors, such as catchment lithology and

geomorphology, and land use history, may play a dominant role in regulating sediment biogeochemistry. Vegetation was characterised using the woodiness of the taxa composition, defined as the percentage of trees and shrubs (Figure 1). Again, no common trend was found across lakes. However, in the same lakes where the organic elements dominated during 2k yr BP, there were similar peaks in woodiness. Lake Grenouilles, on the other hand, had a parallel peak of terrigenous elements and a peak of woodiness at 2k yr BP. Around that time, Roman management of livestock magnified the presence of cattle in the region (Garcés-Pastor et al., 2025). While cattle density can lead to environmental eutrophication (Tiberti et al., 2014), opposite results have also been observed (Sitters et al., 2020). However, other processes different from livestock are playing important roles. Other factors as deforestation started gaining importance after 5k yr BP (Nicolussi et al., 2005; Wick & Tinner, 1997) Erosion rates increased in the European Alps after the Bronze Age (Bajard et al., 2017; Rapuc et al., 2024), specially, during the Late Iron Age and Roman Period due to deforestation and overgrazing by sheep and cattle (Giguët-Covex et al., 2014) Erosion has also shown decreases in available carbon at regional scales (J.-H. Park et al., 2014). Together, this can explain the lack of a general trend in taxa and elementome composition across the 12 lakes included in the analysis.

To determine the effects of biogeochemical traits over plant community traits, we built linear mixed models, using each lake as a random factor, and using as predictors temperature, precipitation, cattle and sheep abundances, elemental turnover, and the organic to terrigenous ratio. This model was tested to predict individually the woodiness of the taxa composition, taxa turnover and the richness of trees, shrubs, forbs, and graminoids (Figure S4). Similarly, linear mixed models were constructed to estimate the effects of plant community traits over biogeochemical variables. We used as predictors temperature, precipitation, cattle and sheep abundances, woodiness of the taxa composition, plant diversity (Hill N1), and taxa turnover. The models were tested to predict organic to terrigenous ratio, elemental turnover, the carbon, nitrogen and titanium content, and the sediment C:N, C:P, and N:P ratios (Figure S5). For this section we highlight that taxa turnover and elemental turnover both positively affect each other (t value = 4.47, p value < 0.001 taxa turnover over elemental turnover; t value = 3.73, p value < 0.001; elemental turnover effect over taxa turnover). The organic to terrigenous ratio is negatively affected by plant diversity (Hill N1) (t value = -3.21, p value < 0.001). This can point to less diverse communities associated to less productivity in the Alps system, although the relationship between biomass production and diversity is complex, usually representing hump-shaped relationships (i.e. diversity increases with productivity up to a point, then declines at higher productivity levels) (Cardinale et al., 2007; Grace et al., 2016; Willig, 2011). We did not find significant predictors for the woodiness of the taxa composition.

We observed a relationship between plant diversity and C:N:P ratios in lake sediments, but these results must be interpreted cautiously due to potential limitations in the XRF data for phosphorus. Therefore, we focus on describing the patterns and avoid drawing strong conclusions about nutrient limitation. We only found significant negative effects between plant diversity (Hill N1) and the N:P and C:P ratios (Figure S5). High N:P and C:P ratios are

indicators of P-limitation (Luo et al., 2022). We speculate that higher C:P and N:P, indicators of P-limitation, filter the community toward a few tolerant species, reducing diversity (Harpole et al., 2016). Lower ratios, however, would allow a greater variety of plant strategies to coexist, thereby increasing diversity. N:P and C:P ratios.

Climate and livestock influence the relationship between ecosystem biogeochemistry and vegetation

The Mantel correlation between distance matrices of vegetation trajectories (taxa space) and biogeochemical trajectories (elementome space) was evaluated through time using moving windows to assess the temporal series in the degree of coupling between both spaces. We found that the Mantel correlation oscillated between 0.4 and 0.65 (Figure 2). In the Mesolithic (8000 - 7500 yr BP) and Neolithic period (7500 - 4400 yr BP) the correlation was relatively high. However, after the Bronze age (4400 - 2600 yr BP) the correlation values dropped. We detected through stratigraphically constrained cluster analysis (CONISS) that the breakpoint Mantel correlation was at 4k yr BP (3965 yr BP). Mean values before and after this breakpoint are 0.55 and 0.45 respectively, which represents a relative decrease of 18%. In the Middle Ages (1500 – 500 yr BP) and Modern Era (500 – 0 yr BP), the Mantel correlation values start to increase

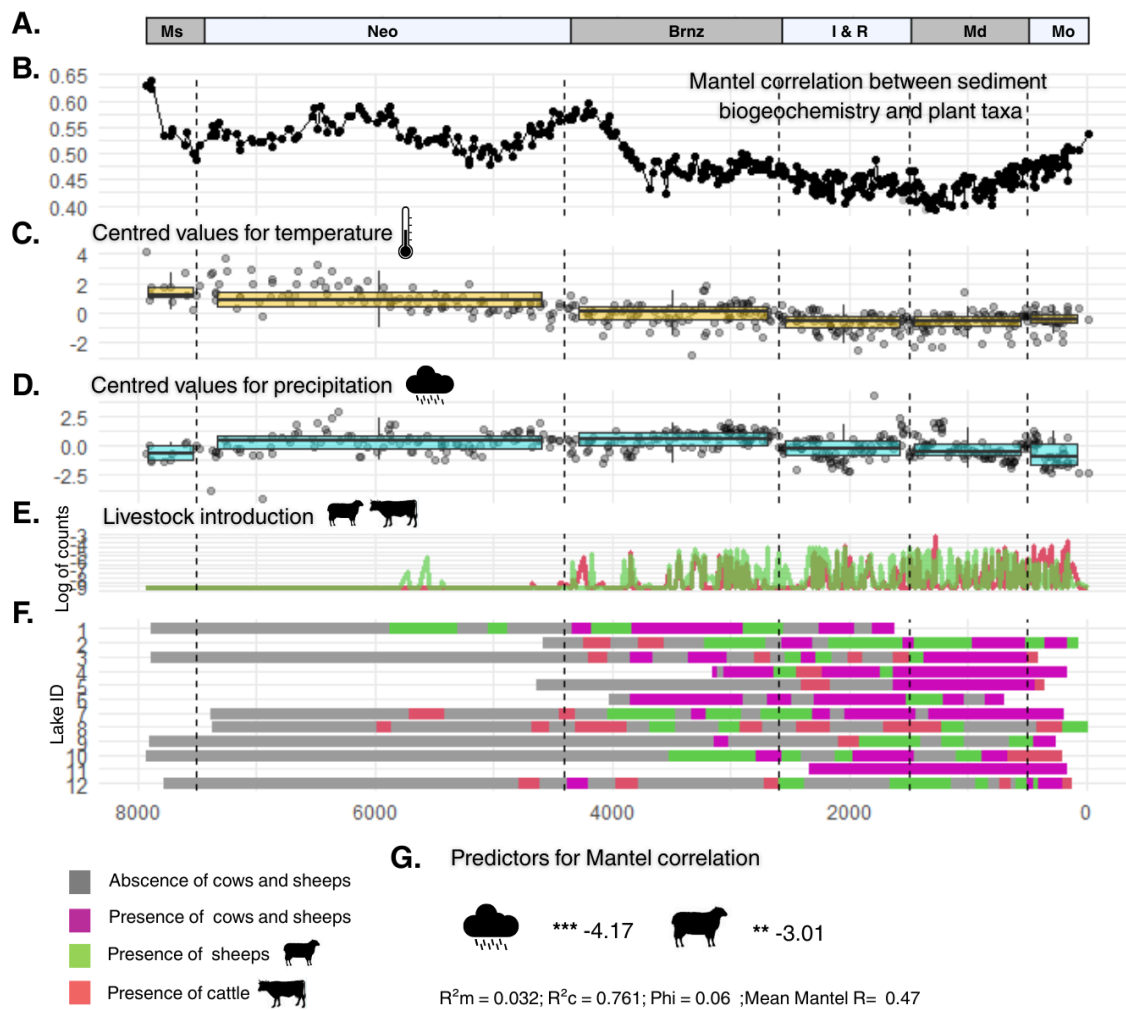


Figure 2. A. Archaeological periods from the last eight millennia: Ms= Mesolithic (8000 - 7500 yr BP); Neo= Neolithic (7500 - 4400 yr BP); Brnz = Bronze Age (4400 - 2600 yr BP); I&R = Iron Age & Roman Period (2600 - 1500 yr BP); Md= Middle Ages (1500 - 500 yr BP) and Mo = Modern Era (500 - 0 yr BP) B. Mantel correlation between the elementome space trajectories (Figure S2) and the taxa space trajectories (Figure S4). Only significant (p value < 0.05) values are represented. C. Temperature trends across lakes. They are centred to reduce spatial noise, as they were used for the Mantel models. D. Precipitation values across lakes. They are centred to reduce spatial noise, as they were used for the Mantel models. E. Logarithmic transformed abundances of sheep and cattle. F. Timelines of livestock across the 12 lakes. G. Summary of the models for Mantel correlation test R^2m (marginal) is the variance explained by the predictors of the model, while R^2c (conditional) is the variance explained by the predictors considering the random factor. The fixed factors of the models are temperature (centred), precipitation (centred), cattle abundance (log-transformed) and sheep abundance (log-transformed). The random factor is the combination of lakes used to calculate the Mantel correlation.

To better understand the drivers of the decreasing coupling of taxa and elementome dynamics, we modelled the effect of temperature, precipitation and cattle and sheep abundance over the Mantel correlation values. The *phi* value of the model was 0.06, indicating a weak effect of temporal autocorrelation. Since lakes have distinct timespan, we used the combination of available lakes as a random factor. We found a negative effect of precipitation (t value = -3.26; *p* value = 0.001) and a negative effect of sheep abundance (t value = -2.08 *p* value = 0.037). The predictors explained only 8.2% of the variance. However, the model explained 77.3% of the variance when including the effect of the random factor, indicating the relevance of between-lake comparisons driving distinct coupling values.

Precipitation negatively affected the coupling between plant communities and ecosystem elementomes. However, the wetter period of the Holocene (early to mid Holocene) (Arosio et al., 2025) coincides with the highest coupling values. This is potentially explained by extreme (high or low) values of precipitation rather than overall the reconstruction across periods. Heavy rainfall events increase the leaching of bedrock material and the runoff of deposited material on the catchment (Croudace & Rothwell, 2015), considerably altering the sediment elemental composition independently from plant communities. Moreover, severe drought episodes may increase the coupling of ecosystem elementomes and vegetation communities

Sheep abundance reduced the coupling between plant community composition and ecosystem elementomes, likely because sheep grazing alters vegetation in ways that are not directly linked to biogeochemical processes. Sheep grazing may decouple vegetation and elementome trajectories through several mechanisms. Selective grazing can alter plant community composition without proportionally affecting soil nutrient availability (Su et al., 2023). Additionally, sheep may translocate nutrients by grazing in one area and depositing faeces and urine elsewhere. Finally, sheep grazing may increase erosion rates, altering sediment biogeochemistry independently of vegetation changes. Grazing by sheep significantly increased both taxa turnover (Figure S4; t value = 1.97, *p* value = 0.049) and elemental turnover (Figure S5; t value = 2.75, *p* value = 0.01), indicating greater dynamism in both taxa and elementome space. Although sheep grazing amplified the magnitude of changes in both spaces, the directions of taxonomic and elemental change may not align, thereby weakening the correlation between biodiversity shifts and biogeochemical change (Lavorel & Garnier, 2002).

Plant diversity under climate change, livestock and shifting ecosystem elementomes

Alpine ecosystems host rich and unique biodiversity but shifts in climate and patterns of human land use are increasingly threatening their persistence. To better understand the fate of plant diversity we modelled alpine vegetation diversity (Hill N1). Similar models have been tested in the same lakes (Garcés-Pastor et al., 2025), but without including biogeochemical variables. Here we constructed a structural equation model (SEM) explaining alpine vegetation diversity (Hill N1) using as predictors precipitation, temperature, abundances of cattle and sheep, organic to terrigenous ratio, elemental turnover, taxa turnover and

woodiness (Figure 3). The model structure (Table S16) was built under the premise that biogeochemical variables have an effect over vegetation variables; and that climate and livestock variables affect both biogeochemical and vegetation variables. We tested if the model under the assumption of biogeochemical traits affecting vegetation traits were better than the opposite assumption comparing the AIC of both models (Figure S6). We found that the ΔAIC was -18.27 across all periods, and had a similar magnitude across the different archaeological stages, indicating that the models assuming that plant traits were mediated by biogeochemical traits were fitter. The model was constructed for all period, but also for the Neolithic & Mesolithic (8000 – 4400 yr BP), the Bronze Age (4400 – 2600 yr BP), The Iron Age & Roman Period (2600 – 1500 yr BP), the Middle Ages (1500 – 500 BP) and the Modern Era (500 – 0 BP)

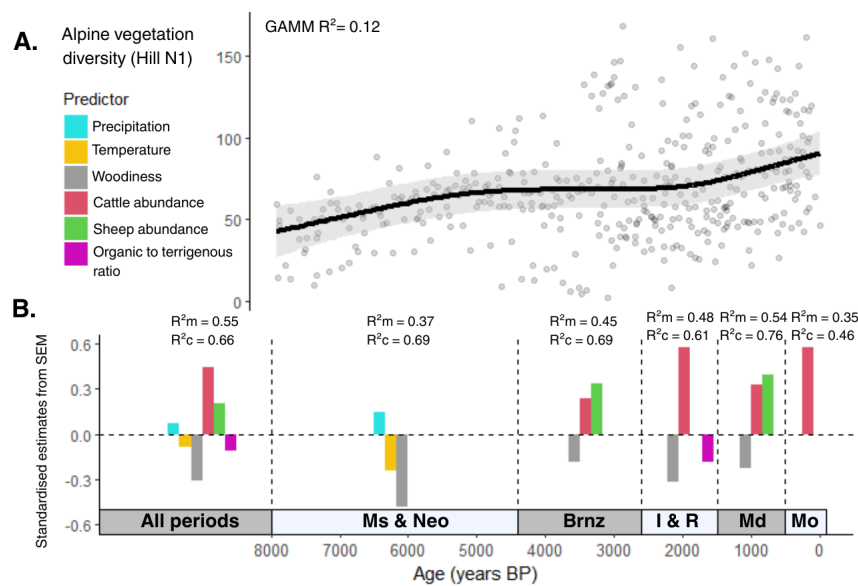


Figure 3. Structural equation model explaining alpine vegetation diversity (Hill N1). A. is the GAMM of the temporal trend of Hill N1 across time. GAMM R^2 is the variance explained by the fitting of the model. B. is the standardised estimates of the predictors with significant (p value < 0.05). The model was done for all periods and replicated across all archaeological periods (Mesolithic and Neolithic were merged, see Figure 2 captions for the acronyms). R^2m (marginal) is the variance explained by the predictors of the model, while R^2c (conditional) is the variance explained by the predictors when taking into account the random factor.

Alpine plant diversity increased through time, especially in the Middle Ages (1500 - 500 yr BP) and Modern Period (500 – 0 yr BP), as expected from previous studies (Garcés-Pastor et al., 2022, 2025; Zetter et al., 2025). When looking at the model from all periods, cattle abundance was the main driver (Figure 3), followed by sheep abundance and precipitation. On the contrary, we found that the increasing woodiness of the taxa composition decreased plant diversity, which aligns with previous studies assessing the effect of encroachment in grassland communities (Wieczorkowski & Lehmann, 2022). Higher temperatures and organic to terrigenous ratio also decreased plant diversity. Temperature increases may be promoting

the dominance by fewer, faster-growing species (S. Liu et al., 2021; Steinbauer et al., 2018) (e.g. ruderals, thermophiles or light-competitive taxa). When looking at archaeological periods independently, we highlight that after the Bronze Age, the only direct drivers increasing plant diversity (Hill N1) were cattle and sheep abundances. Precipitation and temperature were only predicting plant diversity in the Mesolithic & Neolithic era, before livestock intensification, supporting previous studies (Garcés-Pastor et al., 2022, 2025; Zetter et al., 2025). The woodiness of the taxa composition reduced alpine diversity in all periods but the Modern Era, possibly because forest and shrublands lead to habitat loss for graminoids and forbs (Dirnböck et al., 2011; S. Liu et al., 2021). Lastly, the organic to terrigenous ratio decreased plant diversity in the Iron Age & Roman Period. The negative feedback between plant diversity and the organic to terrigenous ratio, was also found for graminoid and forb richness. Our results are consistent with the hypothesis of ecosystem eutrophication leading to a simplification of the flora, but with grazing counteracting the effect of eutrophication (Borer et al., 2014).

To add on diversity descriptions, richness (Hill N0) of forbs, graminoids, shrubs and trees were recorded and modelled (Figure S4). Temperature reduced tree and graminoid richness, which can be associated with a thermophilisation event, with few taxa more adapted to warmer conditions dominates the system (Borderieux et al., 2024; Brice et al., 2019). Temperature also decreased elemental turnover values (Figure S5), pointing to the idea of less dynamic elemental compositions under warmer environments which can also control biogeochemical processes (e.g. higher nutrient uptake, faster litter turnover) (de la Casa et al., 2025). Cattle had a positive effect over tree, shrub, graminoid and forb richness while sheep had it for shrub, graminoid and forbs. While cattle and sheep clearly had an effect, the different result for each domestic herbivore opens questions about their different ecological implications.

Cattle vs. sheep shaping alpine ecosystems

We found contrasting effects for cattle and sheep. Cattle was the main driver of alpine diversity, followed by sheep. By trampling, selective grazing, altering soil nutrients and relocating seeds, cattle and sheep create heterogeneous habitat mosaics and facilitate a broad range of plant species, particularly those associated with open habitats. Cattle and sheep positively affected shrubs, forbs and graminoid richness positively, but the effect was around two times stronger in cattle than sheep across the models (Table S11 – S14 & S16). Cattle abundance presented also positive effects over tree richness, possibly because grazing preferences of sheep exclude forested areas, (Putfarken et al., 2008), while cattle show preference for grazable woodlands (Pinchak et al., 1991). Beyond this and other regional studies (Garcés-Pastor et al., 2022, 2025; Zetter et al., 2025). A recent meta-analysis (Su et al., 2023) shows that cattle are more beneficial to biodiversity and ecosystem functions. The study also highlights that cattle grazing had a positive effect on soil organic carbon. However, our results show that increased abundances of cattle and sheep reduced the sedimentary content of carbon and nitrogen (Figure S4). Nutrient translocation could be responsible for the decrease of carbon and nitrogen in the lake sediments. Cattle and sheep

may be grazing closer to the lake but urinating and defecating outside of the lake catchment area (Sitters et al., 2020; Svensk et al., 2023). However, the potential of grazing for inducing carbon dioxide, methane and nitrous oxide emissions, and therefore C and N stocks, should not be overlooked, specially in alpine systems (Abdalla et al., 2018; Deng et al., 2023; Gao et al., 2018; Liu et al., 2020; Ren et al., 2024; Yin et al., 2020). Our results pointed to sheep grazing as a key driver decoupling of biogeochemical and vegetation trajectories after 4k yr BP. Sheep abundances increased both taxa and elementome turnovers, while cattle did not present any effect. The fact that sheep are associated with higher magnitudes of taxonomic and biogeochemical change may be associated with the grazing behaviour. While cattle tend to graze in areas closer to water bodies, sheep show affinity to dry and nutrient-poor habitats (Putfarken et al., 2008). To compensate for the nutrient-poor environments, sheep are more selective compared to cattle (Abaye et al., 1997) excluding non-nutritious species such as *Nardus stricta* while selecting nutritive species like *Poa alpina* (Wild et al., 2023). These differences between cow and sheep could result in the cow perturbations being more stable close to the lake, since it is the preferred location for cowherds. Sheep, however, may exert unsteady and unpredictable perturbations, which would increase ecosystem temporal complexity (Fernández-Martínez et al., 2025), explaining the increased magnitude of change in both vegetation and ecosystem elementomes.

Our findings reveal livestock as a major driver of alpine ecosystem dynamics. Sheep and cattle have increased plant diversity and species richness since its introduction. However, it is also associated with a nitrogen and carbon depletion at least at a lake-catchment scale, which could point to nutrient translocation outside the catchment, or to atmospheric release. Warming and ecosystem eutrophication resulted in less diverse plant communities, with temperature reducing also the magnitude of change of ecosystem biogeochemical composition (elemental turnover, Figure S5). Sheep grazing on the other hand increased the magnitude of the changes in plant communities and ecosystem elementomes, reducing the coupling between these two ecosystem aspects. Our study shed light to the relationship between plant communities and biogeochemical cycling in a much-needed long-term approach, ranging from the Mesolithic to the present. Moreover, our results suggest contrasting effects of livestock in the studied catchments: increasing plant diversity but reducing carbon and nitrogen stocks. Further research is needed to explore livestock management strategies that can balance biodiversity conservation with the maintenance of soil carbon and nutrient stocks.

Methods

Study sites and data acquisition

The records used for this study were obtained from the Alps region. The data was obtained from a recent publication (Garcés-Pastor et al., 2025), which includes 14 lakes. However, the lack of geochemical data in two of them reduced to 12 the number of lakes included in this analysis. All information regarding the lake core sample and the construction of the

chronologies can be consulted in that publication. We decided to filter the data from 8000 to 0 BP, for two reasons: only two lakes presented data before 8000 BP, and to avoid the effect of the 8.2K cooling event. All cores were stored at 4°C in the cold room of The Arctic Museum of Norway (TMU, Norway). Temperature and precipitation were retrieved from CHELSA-TraCE21k v1.0 model (Karger et al., 2023)

SedaDNA database construction

SedaDNA data was retrieved from (Garcés-Pastor et al., 2025). Sediment samples for plant and mammal sedaDNA analysis were subsampled in the ancient lab at TMU. One cm-thick longitudinal sample was retrieved every 4-12 cm, depending on the core length. The first 4-10mm of exposed sediment were avoided for contamination. Cores were again stored in the cold room of TMU at 4°C. The sedaDNA results are expressed as the relative abundance index (RAI), which integrates information from the relative proportion of reads and replicability of metabarcoding PCRs. The RAI is a proportional index that is constructed by multiplying the proportion of obtained reads and the proportion of weighted PCR replicates.

Cattle (*Bos taurus*) and sheep (*Ovis* sp.) abundances (RAI), the composition of each plant functional type (forbs, shrubs trees and graminoids), the plant functional type richness (Hill N0), plant diversity (Hill N1) and other functional traits (i.e. light preference, continentality, human influenced and grazing tolerance were retrieved from (Garcés-Pastor et al., 2025). The woodiness of the taxa composition was calculated as the sum of the proportions of shrubs and trees.

Biogeochemical database construction

Aluminium, calcium, iron, potassium, manganese, phosphorus, sulphur, silicon and titanium were obtained for all lake cores using X-Ray fluorescence (XRF) analysis, that was previously analysed (Garcés-Pastor et al., 2025; Zetter et al., 2025) but not published for all lakes. Cr and Cl measurements were excluded due to the low autocorrelation values across lakes (under 0.1). In November 2024, 3g of sediment samples were obtained for C and N analysis from the similar spots where sedaDNA samples were retrieved from the core. Samples were lyophilised and sent to Laboratório de Isótopos Estáveis LIE - Stable Isotopes Analysis Facility, at the Faculdade de Ciências, Universidade de Lisboa - Portugal. C and N were obtained from mass spectrometry. The samples for the C analysis were previously decarbonised. The XRF values corresponding to the sedaDNA and C, N samples were obtained using the nearest neighbour interpolation, excluding data with more than 0.1 cm gap.

Multivariate spaces and trajectories for taxa and elementome

Trajectory analysis describes and quantifies temporal patterns of change within a multivariate space, and its application is increasing for ecology (De Cáceres et al., 2019), with applications also for elemental (de la Casa et al., 2025) and taxonomic (Giguët-Covex et al., 2023) composition across palaeoecological scales. In our case we applied trajectory analysis

to a multivariate space defined by the elemental content (carbon, nitrogen, aluminium, calcium, iron, potassium, manganese, phosphorus, sulphur, silicon and titanium) of the sediment: the elementome space. Similarly, we constructed the taxa space, with the taxa identified through sedaDNA analysis (Garcés-Pastor et al., 2025).

For the elemental space, all elemental data were first transformed using a square root function to minimise the effect of high variability in elemental records, and subsequently, we rescaled the values between 0 and 1, allowing us to compare between the elements, by standardising their ranges, and reducing the weight of highly abundant elements (de la Casa et al., 2025). We calculated the distance matrix of the elemental space using Euclidean distances. For the taxa space we used the RAI values of each taxa to define the multivariate space, and calculated the distance matrix using Bray-Curtis distances (Legendre & Legendre, 2012). For the visual description of the taxa trajectories we created a NMDS non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarities with two dimensions, and fitted taxa trait vectors (i.e. continentality, light tolerance human influence, grazing tolerance and the proportion of tree, shrub, graminoid, forb, moss and ferns) with 999 permutations. Significant vectors ($p < 0.05$) were displayed as arrows in the NMDS ordination biplot, with arrow direction indicating the gradient of maximum correlation and arrow length proportional to the strength of the correlation with the ordination axes.

We constructed moving windows of 500 years to quantify the magnitude of the change for each space, which we call elemental turnover for the elementome space, and taxa turnover for the taxa space. The windows and calculations were generated using internal variance values from the *ecotraj* package (De Cáceres & Djeghri, 2025), that generates, in this case, a window 250 years before and after the age of the sample. For each window we also recorded the number of samples per window. We used Principal Coordinate Analysis (PCoA) to represent both elementome and taxa trajectories (Figures S1 to S4).

Organic to terrigenous ratio

We determined the carbon (C) and nitrogen (N) contents, and calculated the C:N ratios from the raw contents of both elements. C:P and N:P, however, were calculated from the min-max standardised values of each element. This is because phosphorus was retrieved from XRF analysis, measured in counts per second. Titanium (Ti) content was also determined. In order to describe broad directions in the trajectories of the biogeochemical composition of the sediments, we developed a metric called organic to terrigenous ratio. Since the PC1 values of the elementome space clearly separated organic and terrigenous inputs (Figure S1), we created an indicator that detected when the geochemical trajectory was heading toward terrigenous elements (See Third Chapter). We rotated all samples and element loadings in each record in the PCA, so that the angle of Ti loading with PC axis 1 (PC1) was 0° in all PCA plots. The PC1 value would then indicate the dominance of Ti in the trajectory and thus serve as an indicator of how strongly the terrigenous elements dominated the trajectory. Independently, we repeated the same process but using C instead of Ti. Then we got an index that describes terrigenous inputs on the lake (Ti rotated), and another that does it for organic matter (C rotated). By dividing the organic matter index with the summatory of the

terrigenous input index and the organic matter index, we obtain an organic to terrigenous ratio, which ranges from 0 to 1.

Mantel correlation test

To assess the coupling between the spatiotemporal dynamics within the elementome and taxa spaces, we performed Mantel correlation analysis of the distance matrices (Mantel, 1967). For each sample age, we defined a 1000-year window (± 500 years) and selected all available samples within this interval. Windows containing at least 10 samples were subjected to a bootstrap resampling of 999 iterations, where each iteration randomly drew 10 samples (with replacement) and computed a Pearson Mantel test (999 permutations) between the taxa and elementome distance matrices. The *boot* package was used for the iterations (Canty & Ripley, 1999). For each window, we recorded the mean and standard deviation of the Mantel correlation coefficient and p-values across all bootstrap replicates. Only significant results (p value < 0.005) were included in the analyses. Windows with fewer than 10 samples were excluded (assigned NA values). This approach allowed us to evaluate temporal changes in spatial-environmental relationships while accounting for sampling uncertainty through bootstrapped confidence intervals. To identify the principal breakpoint of Mantel correlation values across time we applied constrained hierarchical clustering (CONISS) (Grim, 1987).

Model construction

We used different models to explain the interactions between climate change, livestock pressure, plant community and ecosystem elementomes (Table S1-16). We gathered all variables in a single data frame. To do so we interpolated data using the closest neighbour, but in case of elemental turnover and directionality, we had to extrapolate 14 values. This is because the calculation of the turnover left gaps in the beginning and end of the records. Cattle and sheep abundances were log-transformed. Temperature and precipitation were transformed using the mean centering for each lake (Legendre & Legendre, 2012). Taxa and elementome turnover were also transformed using mean centring by lake when they were used as predictor. But not when used as a response variable.

Generalised additive mixed models (GAMM) (S. N. Wood, 2017) were constructed to describe the temporal trends (variable $\sim$ age) of the following variables: plant Hill N1, forb Hill N0, graminoid Hill N0, shrub Hill N0, tree Hill N0, woodiness of the taxa composition, taxa turnover, carbon, nitrogen, titanium, organic to terrigenous ratio, C:N ratio, C:P ratio, N:P ratio and elemental turnover. The random factor was the lake. Linear mixed models (LMM) (Laird & Ware, 1982) were used to estimate the effect of different predictors over vegetation and biogeochemical variables. LMM were constructed using lake as the random factor. However, for the LMM of Mantel we used the combination of lakes used for the Mantel test calculation as the random factor. Since Mantel correlation values come from moving windows, the temporal autocorrelation was considered using a first-order autoregressive correlation structure (AR(1)) (Pinheiro & Douglas, 2000). To facilitate estimation of temporal autocorrelation within lakes, the age of each sample was standardised (z-scored) within each lake combination. This ensures that the AR(1) correlation structure is

centred and scaled consistently across groups. We filtered the observations, selecting only lake combinations that had at least three Mantel correlation measurements. For more information consult Figure S4, S5 and Table S1. Finally, we wanted to pay special attention to plant diversity (Hill N1) dynamics across the Holocene. We built structural equation models (Kline, 2023). For all the period, but also at different archaeological stages, retrieved from several papers (Garcés-Pastor et al., 2025; Giguët-Covex et al., 2023; Rapuc et al., 2024). The structure is available in Table S16. The model was constructed under the premise that biogeochemical variables affect the vegetation, to follow the structure of previous models in the same lakes (Garcés-Pastor et al., 2025). Moreover, we compared the AIC of simple structural equation models (Figure S6). One under the premise that vegetation (Hill N1) affects biogeochemistry (organic to terrigenous ratio); with the opposite: biogeochemistry affects vegetation. We calculated the difference between the AIC of models across all records and across the different archaeological stages; to see which one was the fittest.



ifth Chapter:

soundtraj: Ecological trajectories
through sonification and animation of
multivariate environmental data



***soundtraj*: Ecological trajectories through sonification and animation of multivariate environmental data**

Javier de la Casa, Lina Bautista, Julia Música, Miquel de Cáceres, Sandra Nogué, Josep Peñuelas.

Abstract

Multivariate analysis is widely applied in ecology, allowing the exploration of complex sets of variables into a simplified representation of the data. While multivariate analysis is frequently quantitative, one of its most frequent uses is for descriptive exploration of the data.

Generally through a visual interpretation of two dimensions in Principal Coordinate Analysis (PCoA) and its variants. When time is included in the analysis, the trajectory of the consecutive samples within the multivariate space helps to identify trends and patterns, and construct ecological trajectories. Here we present “*soundtraj*” an alternative to the visual exploration of data, using sound instead of graphical inputs. We create a “note” for each principal component included in the analysis, whose timbre is defined by the loadings of each variable in the PCoA, and the variance depending on the variance explained by each component. Then, the frequency of each “note” is modulated depending on the position of each consecutive sample in each of the principal components. Moreover, we also included animations of the trajectories to help on the interpretation of sound. We provide a replicable open-source approach for the sonification of any trajectory within multivariate spaces that reflects the speed of the changes, that can help on the interpretation of visually saturated PCoA plots and that fosters the use of audition/hearing for science. More than that, the sonification of multivariate datasets opens great opportunities for science communication and art-science collaborations.

Introduction

Ecosystems preserve within their various components the imprints of environmental change, serving as testimonies to the passage of time. Lake sediments, in particular, bear witness to the continuous transformations to which ecosystems are subjected, encapsulating evidence of what they once were (Catalan et al., 2013; Williamson et al., 2009b). palaeoecology is the scientific discipline devoted to reconstructing past ecosystems through the interpretation of sediments and other natural archives. Studying environmental variables through time allows the construction of ecological trajectories that describe the temporal patterns of change across a set of environmental variables. Analyses of fossil pollen or sedimentary DNA, for example, make it possible to reconstruct past vegetation with high temporal resolution (Garcés-Pastor et al., 2025; Nogué et al., 2024). Depending on the research question, the temporal scale of these reconstructions may span from centuries to millennia, enabling the identification of ecosystem responses to major climatic fluctuations, as well as to the arrival and intensification of human activities (Raposeiro et al., 2021).

Multivariate analyses enable the detection of patterns in large datasets by considering multiple variables simultaneously (Legendre & Legendre, 2012). Methods like principal coordinate analysis (PCoA) reduce data dimensionality, identifying the main axes of variation in ecosystem composition over time (CITE). In this way, trajectories of change can be reconstructed. Despite its usefulness, PCoA interpretations have its drawbacks, especially in the context of temporal trajectories. Each sample is ordered in the multivariate space, representing a specific time. The distance between consecutive samples depicts the difference in the set of variables, but nothing indicates the time interval between the samples. Without animations, visual representations are ordered by time, but lacking time dynamics. This allows the description of the magnitude of change between two samples, but not the speed of the changes. Moreover, large datasets saturate the PCoA plot, and data simplification approaches (e.g. using time bins) need to be done before any description.

Sonification of ecological trajectories offers a complementary approach of exploring changes patterns through listening, which has been tested in several scientific fields (Lindborg et al., 2023; Russo et al., 2024; Zanella et al., 2022) and social sciences (Dayé & De Campo, 2006). Sound possesses an intrinsic temporal dimension, which facilitates the perception of data evolution over time, something that, as previously discussed, PCoA plots do not explicitly convey. The sonification of multivariate data allows a deeper exploration of data structure, incorporating temporal variations audible to the listener (Walker, 2023). Sonification diversifies how we interpret data, opening new possibilities for data interpretation, exploiting the ability of the human auditory system to recognise temporal changes and patterns and offering data-interpretation opportunities for those with visual impairments (Flowers & Hauer, 1995; Russo et al., 2024). Sonification strategies differ from disciplines and aims of sound production. Direct sonification implies the manipulation of oscillatory data into audible parameters of frequency and speed. This sonification approach belongs to the widely used Geiger counter, to test radiation levels; or in the beeps of the hospital heart rate monitors

(Bornmann, 2025). The artist and environmentalist Paula Bruna used the ultrasound produced by the embolism of tree vessels under drought conditions, direct sonification, and used it to create a conversation between the sound of trees and flamenco singers (Bruna, 2024). Indirect sonification, however, translates different attributes of the data into parameters of sound such as pitch, timbre and volume (Kramer, 1994). Any sonification approach is free from aesthetic choices (Lenzi & Ciuccarelli, 2020), but those should be carefully justified and performed to respect data structure. Sonification can then serve as a foundation for data-based music, which incorporates data-driven sounds with musical patterns or prerecorded sounds to create an immersive and appealing experience. This is the case of the work of Loud Numbers, which does sonification of different science topics, such as insect decline (Load Numbers, 2025; Møller, 2019). The work of Frank Pattyn on data-driven cryosphere changes in music creations is also noteworthy (Pattyn, 2025). Data has been also used to build musical sheets, to be played with orchestras in outreach events (Observatorio Pirenaico de Cambio Climático, 2025). More sonification examples can be explored in recent initiatives such as the Sonification Archive (Data Sonification Archive, 2025). Lastly, we would like to highlight the work of Than van Nispel and Karin Rebel (Van Nispen & Rebel, 2025) with the sonification of carbon dioxide and temperature anomalies in the last century, which produced an appealing, overwhelming and purely data-driven sound experience, with minimum external additions.

In this study, we developed an indirect sonification approach for ecological datasets, which can be extended to any data of a multivariate nature. We design the sonification process following three premises:

- 1) Data faithfulness: creating sound that reflects the real structure of the data preserving relationships among variables.
- 2) Interpretability: sonification strategy will aim for the interpretation, prioritising sound interpretation over sound aesthetics
- 3) Open source: all tools developed are open source, ensuring transparency in the process and providing detailed documentation for their use and reproduction.

Sonification workflow

Our aim is to translate two-dimensional PCoA plots into sound. So, the principal components (i.e. PC1 and PC2) will be the ones that will be generating sound. PC1 and PC2 are obtained using principal component analysis, with the preferred distance metric that better adjusts the data. The database consists of an identificatory of each sample (e.g. 1,2,3..), a time value, and the value for PC1 and PC2. Since our aim here is to sonificate PCoA plots, we decided to only make sound out of PC1 and PC2, to match the sonification with the graphical representation. However, more principal components could be added, to the real structure of the data

Within Plug data, the samples are linearly interpolated, to each time unit from the oldest to the youngest. The values of PC1 and PC2 will be transformed into two parallel notes respectively, and its values will represent different frequencies for each note. The maximum and minimum PC1 and PC2 values are transformed to be between 1000 and 100 Hz, to ensure that the data is within the audible range of frequencies. Each note (PC1 note and PC2 note) has a unique timbre. For this experiment, the timbre of each note is preset, to facilitate the differentiation between the two notes. However, the definition of timbre of each note can be data-driven. The PC1 and PC2 values for each variable loading (e.g. elements, species) can be turned into partials or harmonics to shape their timbre. The proportion of the variance explained by PC1 and PC2 is transformed into the volume of each note. With a high proportion of variance explained by higher volume. The tempo is constant and can be modulated by the user. For the entire duration of the record, the number of milliseconds that we recommend for each time unit is 0.05 times the total time span (i.e. for a time series of 2000 years, 100 ms per year). An additional metronome sound can be added to the sound to indicate the interval between units of time.

Sonification is accompanied by a visualisation of the ecological trajectories using Processing software (Processing Foundation, 2025), which represents the sample's trajectory within the multivariate space at the time of the generated sound.

To exemplify the potential of *soundtraj*, we show the sonification of the elemental composition of lake sediments across time (Figure 1).

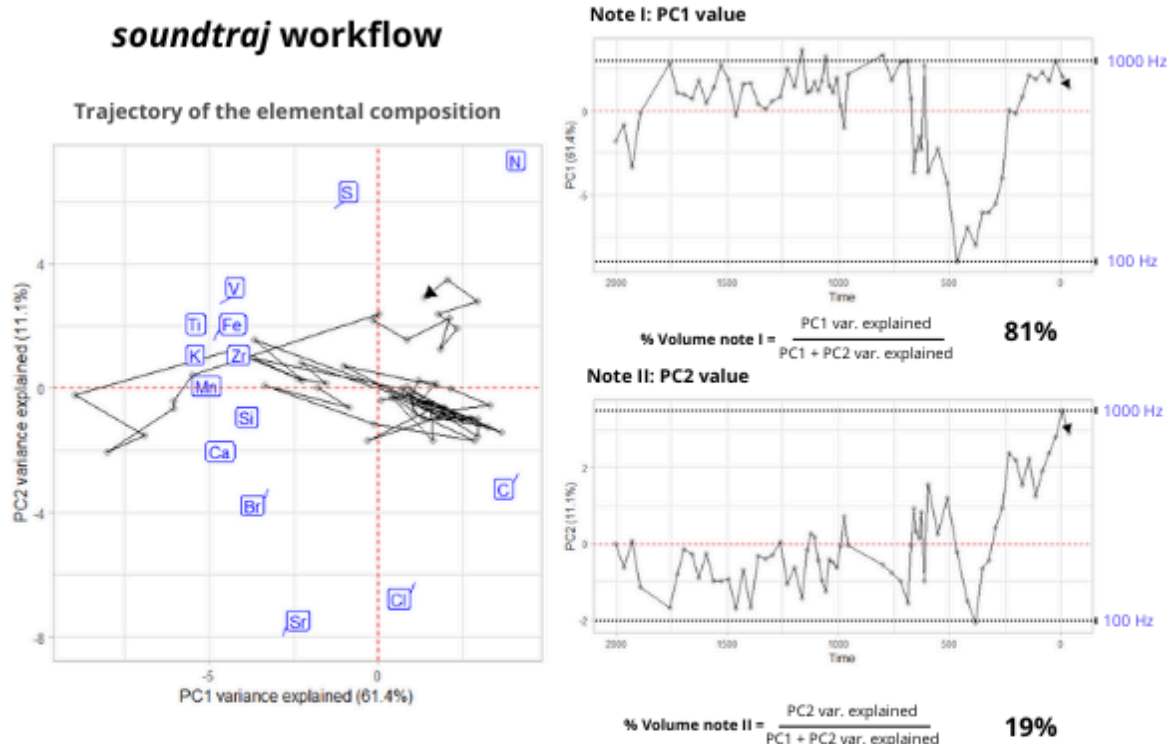


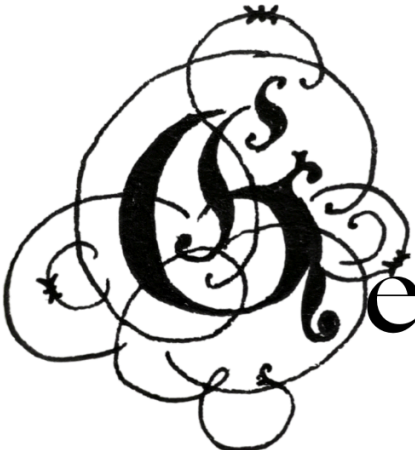
Figure 1. Workflow of *soundtraj* for the selected example: changes in the elemental composition of a chronologically dated lake sediment.

The elemental composition of lake sediments can reveal long-term ecosystem dynamics (de la Casa et al., 2025). In the case of Lake Caldeirao (Raposeiro et al., 2021) the trajectories of the elemental composition across time narrates distinct stages of the lake, which was dominated by organic elements before humans arrived (Figure 1), and shifted to a composition dominated but erosion-related elements. In recent years the lake shifted towards an organic composition again, due to eutrophication of the waters. The sonification (Movie 1 in de la Casa et al., 2025b) is recommended at 30 milliseconds each year of the trajectory.

Final remarks

Data sonification is a technique that complements data visualisation by adding an auditory dimension. By using sound, it expands the possibilities for human-computer interaction. In this context, we present *soundtraj* as a sonification tool specifically designed to represent PCoA plots of temporal trajectories through sound. This differs *soundtraj* from other open-source sonification tools such as Twotone (Twotone, 2025), which have a wide range of uses, but are less specific. In next steps of development, *soundtraj* will include more options to customise the sound mapping across the multivariate space. For instance, the atomic mass could be considered for elemental data; or the plant functional traits in trajectories of plant communities. Beyond the interpretation of data, *soundtraj* has potential to enrich science

outreach and to navigate the possibilities of connecting data interpretation from scientific and artistic perspectives.



General Discussion:

General Discussion

Elementomes shifting across peaks and islands

The five chapters of the thesis (Table 1) represent a journey through both time and space, spanning from the present day back to the last eight millennia, and from oceanic islands across the Atlantic to mountain lakes throughout the European Alps. The **First Chapter** discusses the potential and limitations of analysing ecosystem elementomes using different palaeoenvironmental archives: lake sediments, soil profiles, peat records, and tree-rings. The **Second Chapter** used five lakes in the Azores archipelago to introduce and validate two key concepts: the concept of ecosystem elementome modelled using multivariate analyses of lake sediment elemental composition across time (palaeoelementome); and the use of Elementome Trajectory Analysis to describe and quantify the palaeoelementome dynamics across time. The **Third Chapter** upscaled the research of the Azores archipelago to 19 islands across the Atlantic Ocean. The **Fourth Chapter** was based on mountain lakes from the European Alps. By combining biogeochemical data with sedimentary ancient DNA (*sedaDNA*), we assessed the feedback between shifts in the elementome and plant diversity under the influence of climate and livestock. And finally, the **Fifth Chapter** consists of an alternative approach to describe Elementome Trajectories using sound (i.e. sonification). This analysis allows the speed of changes, which graphs usually do not portrait, to be perceived qualitatively without the need of precise numerical quantification. The sonification pack is open source and available (de la Casa et al., 2025b) for all researchers that want to make sonification of any kind of temporal trends of multivariate data. Moreover, it opens the doors for alternative interpretation of the data, outreach activities and collaboration in the art-science interface.

Table 1. Specification and contributions of each chapter of the PhD thesis

	First Chapter	Second Chapter	Third Chapter	Fourth Chapter	Fifth Chapter
Type of study	Methodological review	Scientific paper	Scientific paper	Scientific paper	Methodological approach
Main contribution	Review of limitations and opportunities of different archives to assess ecosystem elementome	Validation of Elementome Trajectory Analysis	Assessment of the impact of human arrival and developments in Atlantic islands	Assessment of the feedback of ecosystem elementome and plant diversity under the effect of climate and livestock	Open source tool to transform into sound shifts in multivariate data (i.e. elementome) into sound
Type of record	Lake sediments, soil profiles, peat records, and tree-rings	Lake sediments	Lake sediments, soil profiles, and peat records	Lake sediments	Lake sediments (elementome and plant taxa trajectories)
Data complied	-	Five lake records from 4 islands	21 records from 19 islands.	12 lakes. 410 elementome measurements, taken from the same sediment depths as <i>sedaDNA</i> samples	Palaeoelementome from Lake Caldeirão (Azores). Plant <i>sedaDNA</i> from Lake Sulsseewli (Alps)
Data generated	-	None	A Total of 21 geochemical datasets (XRF). 3 of them generated in this PhD.	410 C and N samples; 12 XRF profiles	No data, but the sonification tool is open and available (de la Casa et al., 2025b)
Time span	-	2000 yr BP to present	3000 yr BP to present	8000 yr BP to present	-
Spatial span	-	Azores Archipelago	Atlantic Ocean (from Svalbard to Falkland Islands)	European Alps	-
Elementome	-	C, N, and XRF data	XRF data only	C, N, and XRF data	-
Other Proxies	-	Charcoal, coprophilous fungi and pollen	Accumulation rates	<i>SedaDNA</i> from plants and mammals	-

The initial research questions, highlighted in the General Introduction, can be addressed now with the findings of each of the chapters:

Q1: Can palaeoenvironmental records (e.g. lake sediments) be a good source describing ecosystem elementomes using elementome trajectory analysis?

Through all the chapters, we have used palaeoenvironmental records as information sources for past ecosystem elementomes. The analysis shows that palaeoenvironmental records are excellent describing elementome changes. The palaeoecological field has extensively used the elemental composition of lake sediments to describe past ecosystems, such erosion and the accumulation of heavy metals (Giralt et al., 2008; Granmo et al., 2020; Sánchez-López et al., 2016; Speranza et al., 2019). Therefore, the robustness of using lake sediment elemental compositions as a proxy is well established (J. F. Boyle, 2002). Nevertheless, in the **Second Chapter**, we used five lake sediments in the Azores archipelago to test lake sediments as information sources to depict changes in ecosystem elementomes. Unlike previous work, based on single elements or elemental ratios (Croudace & Rothwell, 2015; Makri et al., 2021), we developed a framework inspired from atomic ecology (Sardans & Penuelas, 2024) and the increasing attention of trajectory analysis in community ecology (De Cáceres et al., 2019). Multivariate analyses have long been applied to sediment biogeochemistry to describe sediment composition (Garcia-Oteyza et al., 2024; Giralt et al., 2011). However, we studied applied Trajectory Analysis to multielemental temporal series (Elemental Trajectory Analysis) to quantify and describe changes in the elemental composition of ecosystems across time.

Elementome Trajectory Analysis builds on this tradition by explicitly describing and quantifying the palaeoelementome as trajectories in a multidimensional space defined by elemental composition. If lake sediments are good sources for inferring palaeoelementomes, then we would detect coherent feedback between shifts in the elementome and other palaeoecological variables such as fires or shifts in vegetation. Because the five selected lakes had already been subject to high-quality palaeoecological assessments (Raposeiro et al., 2021, 2024; Richter et al., 2022; Ritter et al., 2022; Rull et al., 2017; Vázquez-Loureiro et al., 2019), they provided an ideal context in which to test the Elementome Trajectory Analysis. Shifts in the ecosystem elementome matched with historical and ecological shifts already highlighted in the previous works. Elemental signals were also coherent across lakes, which responded similarly to similar impacts. For instance, in the **Second Chapter**, fire events in the lakes Caldeirão and Funda were characterised by a high shift towards terrigenous elements like titanium or zirconium, indicating increased erosion.

In the **First Chapter** we discuss the challenges and opportunities of using lake sediments, and other natural archives like soil profiles, peat records and tree-rings to depict past ecosystem elementomes. Meanwhile lake sediments and soil profiles had a greater effect on

sedimentary processes. Peat records and tree-rings offer the possibility to capture elementome shift from a biospheric perspective. Ombrotrophic bogs specially capture the signals from atmospheric deposition. Tree-rings on the other hand reflect the element uptake from the soil, except for elements that are sourced from the stomata (atmospheric) such as carbon, mercury and small quantities of nitrogen and sulphur (Binda et al., 2021). However, nutrient transport between plant tissues complicates the construction of a chronology of element uptake from the soil. So affirmatively, natural archives can reflect shifts in the elemental composition of ecosystems, but in the case of tree-rings nutrient transportation needs to be considered before any assumption of change in the palaeoelementome. Elementome Trajectory Analysis provides a useful framework, but it is important to consider that the choice of elements included in the analysis can influence the results. Therefore, further research is needed to explore the sensitivity of the method to different elemental suites

Q2: How can we represent and quantify ecosystem elementomes?

One of the advantages of Elementome Trajectory Analysis is that different aspects of the trajectories can be quantified. We built elementomes with data from different methods (i.e. XRF and elemental analysers). To merge all elemental data into a common elementome, we transform each element measurement using min-max transformation. This rescales the minimum value to 0 and the maximum to 1 and allows us to compare between the elements, by standardising their ranges. Prior to that, square root can be used to minimise the effect of high variability in elemental records. This data transformation understands elementome data as a flow of elements relative to the record itself, with elemental values interpreted with respect to their relative contents, not by their absolute value. This equals the importance of each element for driving shifts in the elemental composition. Although XRF data is not strictly compositional, (i.e. data is relative to a sum), other transformations of the data, such as centred log-ratios, can be performed to fit into compositional standards (Bertrand et al., 2024). However, since our conceptualisation of the elementome mixes data (i.e. C, N and XRF measurable elements) from different measurement techniques (i.e. XRF, elemental analysers), data units (i.e. counts per second, parts per million), and scales (thousands/million scale vs decimal scale), centred log ratios are discouraged.

After transforming the data, we can proceed with quantification. One interesting analysis is the detection of elementome shifts. Stratigraphically constrained clustering (CONISS) can detect different ages at which the elementome changed drastically. This should always be checked against sedimentary facies. Some metrics use moving windows. For each window, we calculated three metrics: elemental turnover, trajectory directionality, and trajectory speed (**Second Chapter**). The windows can be calculated using a fixed number of samples, or a fixed time span. In the **Second Chapter** we explored both approaches. While both are valid, we encourage the use of time-fixed moving windows, aiming for shorter time spans when possible. Element-index can describe the dominance of one element in the elemental composition in comparison with (Box 1; **Third and Fourth Chapters**). Since lake sediments usually have a bipolar distribution of the elements in the multivariate space, we also defined a ratio, organic to terrigenous, to describe the dominance of erosion and organic accumulation

in the trajectory (Box 1; **Fourth Chapter**). Finally, we developed two metrics that describe a whole trajectory, with the aim to compare within trajectories: explored area and three-centroid length (Box 1; **Second Chapter**). Elementome trajectory analysis enabled the use of a variable set of metrics, which offer insights belonging to biogeochemistry, detailing the dynamism of the ecosystem to natural and anthropogenic transformations.

Box 1. Elementome Trajectory related metrics used across the chapters of the thesis.

Elemental turnover:

Measures the internal variance of the elemental composition of samples within a moving window. High values indicate abrupt changes and lack of elementome stability

Trajectory directionality:

Measures the angle of consecutive samples within a moving window. Lack of variation in the angles depicts changes towards a similar direction in the multivariate space

Trajectory speed:

Measures the distance between the consecutive samples within a time window and then is divided by the span of the time window.

Element-index:

Measures the dominance of the signal of a single element in the elementome of a sample. They are calculated by rotating the PCoA so the X axis is parallel to the loading of the desired element. Hence, the first principal coordinate (PCo1) value represents the dominance of that element. For example, Ti-index measures the dominance of titanium while C-index the dominance of carbon

Organic to terrigenous ratio:

Measures, on a scale of 0 to 1, the dominance of organic accumulation versus land-derived sedimentary inputs. Is calculated by dividing C-index by the sum of C-index and Ti-index, and the suitability of this metric should be validated before, Ti-index and C-index are not universal metrics to define erosion and organic accumulation.

Explored area:

Measures the area of all the elementome trajectory in the multivariate space, which is calculated using an ellipse. Compared to other trajectory, high values indicate that the variability of the trajectory is higher

Three-centroid length:

Measures the length (Euclidean distance or others) between the three main centroids of the trajectory. The centroids are defined using CONISS analysis. Compared to other trajectory, high values indicate that the elementome has stabilised across the record in more diverse elemental compositions

The visual description of the trajectories, generally through the use of biplots and principal coordinate analyses (PCoA), offer a robust source for describing trends of the elementome.

The position of the lodgings (elements), reveal information about the association of the elements, and the dominance of those elements across the trajectory. We found that most of our PCoA plots separated carbon and nitrogen (often accompanied by other elements such as bore or sulphur), from the rest of the elements, especially the land derived such as zirconium or titanium. Although visual description is a useful tool by itself, we wanted to go further on the sensorial description of the data: going from sight to hearing. We developed a sonification algorithm, to transform two-dimensional PCoA plots of Elementome Trajectories into sound. The first and the second coordinates produce an independent note independently, which frequency depends on their value. While visual description is good showing the magnitude of the changes and the different clusters of data across time; sonification allows one to sense speed, a metric that is impossible to describe visually in traditional PCoA plots. We consider sonification as an interesting tool for data interpretation. It may not be crucial to the analysis of elementome data, but it provides alternative and complementary insights that enrich the description of palaeoelementomes.

Q3: How does the onset of human activities affect ecosystem elementomes?

Palaeoenvironmental records from isolated areas, such as islands and mountains, allowed the identification of the first impact of human-related disturbances in the ecosystem. In the **Second Chapter** we studied how elementomes shifted after humans arrived at the Azores. The charcoal count allowed the reconstruction of fire regimes, coprophilous fungi helped to infer grazing intensity and lastly, changes in the pollen composition revealed deforestation episodes and land use changes. Elemental turnover, speed and directionality (Box 1) were sensitive abrupt and continued perturbations. In Lake Caldeirão, the values of elemental turnover slightly increased after human arrival and peaked associated with strong registered fires. However, in sustained impacts like the land use change towards pastures in the same lake directionality increases while elemental turnover and speed decreases over time, indicating a stabilisation of the geochemical composition. However, notable differences were observed for similar human activities depending on the lake geomorphology. Shallow lakes for instance, were more affected by perturbations compared to lake sediments. Stronger elemental turnover responses to human impacts, and higher three-centroid length values (Box 1) indicate that perturbations exert greater shifts in the elementomes of shallow waters, which is consistent with recent literature (Pilla et al., 2020; Qin et al., 2020)

The **Third Chapter** focused on arrival dates of the first settlers and European colonisers during the European overseas expansion. We gathered 21 palaeoenvironmental records across the Atlantic, that consisted of geochemical measurements (XRF) and accumulation rates. Further proxies were not considered as they were not present in all records. We detected a generalised trend of increased erosion after human arrival to the islands, indicated by parallel increases of Ti-index and accumulation rates. While we did not focus on the specific human activities carried out after colonisation, we can say that overall, human arrival shift elementome towards erosion-related elements, as they remove stabilised vegetation and actively use land (CITE). Coming from the undetailed “colonisation” as a human activity, in

the **Fourth Chapter** the onset of a concrete anthropogenic disruption was successfully calculated: the introduction of sheep and cattle. The study comprises 12 lakes from the Alps region and eight millennia of elementome changes. Thanks to *sedaDNA*, the introduction of livestock can be recorded in the alpine mountain region, which is around the detected 5.8K yr BP for sheep and 4.2K yr BP for cattle. We found that sheep and cattle exerted a negative effect on nitrogen and carbon stocks. This should shift the elementome away from the organic elements, but have no effect on the organic to terrigenous ratio. While further analysis should be carried out to define the mechanisms of the effects, the result is in line with vast literature (Abdalla et al., 2018; Deng et al., 2023; Gao et al., 2018; Liu et al., 2020; Ren et al., 2024; Yin et al., 2020) showing the negative effect of carbon and nitrogen stocks under grazing systems, especially in high intensities, and the livestock intensification of erosion (Li et al., 2019).

Overall, our results confirmed the hypothesis highlighted in the General Introduction about the potential responses of the ecosystem elementome to different human impacts (General Introduction Figure 2) and that is summarised here in Table 2. Further research should examine not only how human activities drive shifts in the elementome, but also how those elementome shifts determine ecosystem resistance, recovery and long-term resilience.

Table 2. Examples found in the thesis chapters validating the hypothesis of elementome shifts under different anthropogenic impacts.

Anthropogenic impact	Effect on the elementome	Examples
Settlement	Increase in erosion-associated elements due to human land transformations	Third Chapter: Although the effect of settlement is not isolated. The increased erosion after human settlement is clear
Settlement	Increase of organic content from sewage inputs and lake eutrophication	No examples found
Deforestation	Increase in erosion-associated elements	Second Chapter: Lake Caldeirão after 1275 CE.
Deforestation	Increase of organic input from the eroded soil (Kastowski et al., 2011)	No examples found
Livestock	Increase of organic input due to increased in-lake activity	Second Chapter: Lake Caldeirão after 1685 CE.
Livestock	Reduction of organic content due to volatilisation, and increase in erosion associated elements	Fourth Chapter: Generalised negative effect of cattle and sheep over carbon and nitrogen stocks
Agriculture	Increase in organic input from increases in-lake productivity	None. Single effect of agriculture could not be discriminated from other impacts
Mining/ industrial	Increase in trace-metals	No examples found

Q4: Are ecosystem elementomes shifting more dramatically in post-industrial times or with the onset of human activities?

In this thesis, we do not aim to endorse any definition of the Anthropocene. Our aims are to fill the knowledge gap of anthropogenic impacts on ecosystem elementomes at long time-scales. As highlighted in the **First Chapter**, the top samples (i.e. younger samples within the record) are sometimes problematic and frequently are not included in palaeoenvironmental assessments. For this reason, records that capture both pre-historic and post-industrial times with high resolution are scarce. The alpine lake sediments from the **Fourth Chapter** arrived in 1950 CE, capturing only the initial century after the Industrial

Revolution. However, several records from the Atlantic islands arrive to the twenty-first century, allowing the comparison between the onset of human activities (e.g. settlement, livestock introduction). The **Third Chapter** particularly explores the effect of human arrival to islands across different cultural and historical events. The generalised trends indicate that the erosion rates in post-industrial times are higher, and elemental turnover increases. However, the biggest differences in erosion indicators (accumulation rates & Ti-index), and in elemental turnover happened between prehuman and the after human arrival, especially in islands first settled during the European overseas expansion. In those islands, elemental turnover decreased after post-industrial times, indicating that the magnitude of the elementome changes was lower when compared to the arrival of Europeans.

Rather than downplaying the impacts of post-industrial societies, these results highlight that the generalised narratives of the Anthropocene differ in isolated areas such as oceanic islands. Relevant perturbations like soil erosion, biodiversity loss through extinctions and invasive species (Russell et al., 2017; Nogué et al., 2021) are linked to the onset of human dominance of ecosystems, with more abrupt responses to European settlement in the islands studied. Post-industrial times continue the legacy of those perturbations (Fernández-Palacios et al., 2021) and introduce new anthropic signals like heavy metal (Cipro et al., 2018; Rahman et al., 2024; Toro-Valdivieso et al., 2023;), radionuclide (Williams-Hoffman et al., 2025) or novel entities pollution (García-Regalado et al., 2024; Ríos et al., 2018). Further research comparing the differences between post-industrial and early human impacts on ecosystem elementomes should also contemplate the effect of ecosystem isolation (e.g. elevation, connection with the continent) and historical land use changes.

Q5: Can human impact on ecosystem elementomes be discriminated against other factors like climate or vulcanism?

A common challenge in the analysis of the dataset is that correlation of events may not imply causality. One great example occurs in the **Second Chapter**. Around 1450 CE, the Portuguese arrived on the islands and began to settle. Shifts in elemental composition or other proxies occurring soon after, such as those detected in Lake Caldeirão, Lake Funda or Lake Caveiro can therefore be linked to the impact of the Portuguese. However, the arrival of the Portuguese is contemporary with the onset of the Little Ice Age, which shifted the climate across the Atlantic. This also changed the wind patterns in the Atlantic (Raposeiro et al., 2021), which potentially explains the arrival of Portuguese boats. Thus, the observed environmental changes likely reflect a combination of human settlement impacts and concurrent climatic variations, making it important to consider both drivers in interpreting the elementome record.

Statistical analysis can shed light to the relative importance of climate and humans driving ecosystem changes. For example, in Lake Funda, redundancy analysis for the last 500 years showed that climate explained more variance in the lake trophic than humans (Ritter et al., 2022). However, the robustness of the results depends on which variables are considered exclusively indicative of human or climate impacts. Another approach to compare the effects

of climate versus human activity is to examine long-term climate oscillations. If the ecosystem elementome shifts consistently in the same direction during similar climate fluctuations, regardless of indicators of human disturbance, this suggests that climate is the dominant driver of elementome trajectories. The climate effect on Lake Empadadas Norte supports this idea. The major elementome shifts matched with major shifts in the climate. Wet and hot periods matched with elementomes dominated by organic elements (e.g. C and N), while cold and dry periods shifted the elementomes towards land-derived elements (e.g. Ti, Zr). However, the effect of climate was not the same in Lake Azul, which is only 5.7 km away. This lake, 6.75 times deeper than Lake Empadadas Norte, reinforces the idea that lake geomorphology plays a major role determining elementome responses to natural and anthropogenic variables. Volcanic activity also interacts with the responses of ecosystem elementomes in lake systems, which can induce persistent oligotrophic conditions that mask the effects of human and climatic perturbations (Vázquez-Loureiro et al., 2019).

In the **Third Chapter**, the three-millennia generalised trends for erosion (Ti-index and accumulation rates) increased over time, ignoring strong fluctuations in the climate (e.g. Medieval Climate Anomaly, Little Ice Age). This evidence indicates that human activities have been the primary drivers of erosion in the Atlantic Islands.

However, it is important to note that the increases in erosion in some areas are also linked to the deposition of volcanic materials, as observed in records from Iceland (Alsos et al., 2021) and Fogo (Castilla-Beltrán et al., 2023b). This highlights the complex interplay between volcanic activity and erosion in shaping the landscapes of Atlantic islands. Having a clear record of the volcanic activity is thus crucial for geochemical interpretations. In the **Fourth Chapter**, we modelled together the effect of climate (i.e. reconstructed temperature and precipitation) and livestock introduction as anthropogenic impact (i.e. abundance of sheep and cattle). This allowed us to see the effect of each one on elementome patterns. For instance, warming was negatively associated with elemental turnover, while sheep abundance (human associated impact) has a positive effect. Another clear example is when looking at plant diversity under the effect of climate, livestock and biogeochemical changes. Models for each archaeological stage reveals which variables have a greater effect. From the Mesolithic to the Neolithic climate was the main force driving plant diversity, but after that, livestock mainly dominated the patterns of plant diversity in the European Alps.

Q6: How shifting ecosystem elementomes interact with biodiversity patterns?

Across the thesis, questions about how humans shape ecosystem elementomes across temporal scales have dominated the narrative. In the **Fourth Chapter** we wanted to study the implications of elementome shifts on plant communities, and *vice versa*. The structure of the data (i.e. independent samples of elementome and plant community at same depths) allowed the comparison of the trajectories of the elementome and the plant composition. Plant communities, assessed through *sedaDNA*, were analysed using trajectory analysis, in an

analogous way as elementome Trajectory Analysis, but using Bray-Curtis distances instead of Euclidean.

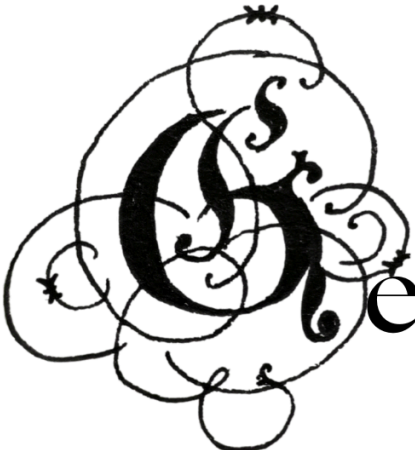
The coupling between plants and elementomes was assessed, which decreased after livestock introduction (especially sheep). This indicates a disrupted connection between biotic and abiotic factors (Ochoa-Hueso et al., 2021) driven by anthropogenic factors. Moreover, we studied specific effects of shifts in the elementome over plant communities. The organic to terrigenous ratio had a decreasing effect over plant taxa diversity (Hill N1). Eutrophic conditions lead to simpler plant communities because competition for biogeochemical resources is reduced. As light becomes the limiting factor, light-demanding taxa dominate the community composition (Fay et al., 2015; Harpole et al., 2016). On the other hand, elementomes dominated by land-derived elements may reflect a more heterogeneous environment, which potentiates plant diversity (Daleo et al., 2023). We conclude that elementomes and vegetation are coupled systems, which are subject to decouple when new perturbations introduce complexity into the system (Fernández-Martínez et al., 2025). For instance sheep grazing and extreme precipitation events were associated with the decreasing coupling of vegetation and ecosystem elementomes. Vegetation and elementome decoupling is concerning because ecosystem function efficiency is diminished (Ochoa-Hueso et al., 2021) until new stages of coupling arise. Although not explored in the thesis, elementome feedback on biodiversity extends beyond plants (Ferrín et al., 2025). Further research incorporating the interactions across ecosystem and trophic levels would shed light to potential cascading effects on the decoupling of elementome and biodiversity patterns. For instance, investigating the role of elementomes in regulating microbial communities

Steps towards “palaeoelementomics”

From ecosystem (Fernández-Martínez et al., 2014; Ma et al., 2021; Ochoa-Hueso et al., 2021; G. Zhou et al., 2025) to plants (Chilaka et al., 2025; Peñuelas et al., 2019; Sardans et al., 2021), and to cells and tissues (Wei et al., 2024; Zhang et al., 2023), the comprehensive analysis of elemental composition (i.e. elementomics) has consolidated as a valuable indicator of their functional roles or to identify relevant structural shifts. Coming from the atomic ecology (Sardans & Penuelas, 2024), studying ecosystems and organisms based on their atomic composition will open the doors to fundamental questions about the functioning and traits of the biosphere. The “elementomics” of the past works under different rules than current-time elementomics, since the source of information, palaeoenvironmental records, need specific interpretations. In that sense, palaeoelementomics should stand by its own feet, as the systematic study of elemental distributions in ancient biological and geological materials (e.g. sediments, wood, fossils, archaeological artifacts) to infer past ecological, environmental, and biogeochemical conditions.

Palaeoelementomics would focus on elemental composition rather than palaeobiochemistry (Dayhoff & Eck, 1969) which focuses on relic organic molecules and compounds of life; or palaeobiogeochemistry (Prentice & Raynaud, 2001), which focuses on relict molecules with importance in biological and geological processes (i.e. greenhouse gasses). Further research

is needed to define a common ground for palaeoelementomics, but the reward is promising, as I hope to have demonstrated across the words of my thesis. Coming back to the quote that closed the Author Statment, *I hope that this thesis is used to think other thesis with*; and that it contribute to a fruitful and harmonised future of palaeoelementomics.



General Conclusions:

- I. Natural archives (i.e. palaeoenvironmental records) are ideal sources to assess the effect of earlier manifestations of the Anthropocene in the elemental composition of ecosystems (ecosystem elementome). Surface effects (e.g. topsoil, acrotelm or sapwood-hardwood effects) should be considered in each natural archive, as they drive important errors constructing palaeoelementomes.
- II. Palaeoelementomes from lake sediments and soil profiles are more affected by sedimentary processes, while peat records (especially from bogs) and tree-rings reflect patterns of biospheric acquisition of elements from the atmosphere, pedosphere and hydrosphere.
- III. Elementome Trajectory Analysis generates a multivariate space with elemental data from the palaeoenvironmental records, which enables the combined use of all elementome data for descriptive analysis; and the quantification of trajectory metrics
- IV. The combined analysis of elemental turnover, speed and directionality, metrics derived from Elementome Trajectory Analysis, offer insights in the dynamics of past ecosystem elementomes (i.e. palaeoelementomes)
- V. The first human settlements in Atlantic islands had a strong effect on the ecosystem elementome of pristine ecosystems, increasing the dominance of erosion-related elements and elemental turnover values. The effect was greater in islands first settled during the European overseas expansion (500 yr BP) than in islands settled before by different cultures
- VI. The introduction of livestock in the European Alps weakened the coupling between the ecosystem elementome and plant communities. Although it led to increased plant diversity, it simultaneously reduced carbon and nitrogen stocks in alpine lake sediments.
- VII. The sonification of elementome trajectories (or other multivariate data) provided an alternative to traditional visual data representation, enabling a sensory perception of the speed and dynamics of change. Moreover, it opens new possibilities for outreach and art–science collaborations.
- VIII. The findings of this PhD thesis contribute to advancing the study of ecological stoichiometry and ecosystem elementomes at long-term scales. They provide element-based tools for ecological studies at palaeoecological scales, further contributing to the development of the palaeoelementomic framework



Appendix I:

Other contributions beyond
the thesis

Research papers (related to the thesis)

- **de la Casa, J.**, Sardans, J., Galindo, M. *et al.* Stoichiometry of litter decomposition under the effects of climate change and nutrient enrichment: A meta-analysis. *Plant Soil* **506**, 709–726 (2025). <https://doi.org/10.1007/s11104-024-06718-3>
- Wu, Y., Tie, L., Huang, C., Sardans, J., **de la Casa, J.**, Bose, A. K., Ouyang, S., Duan, H., Wang, J., & Peñuelas, J. (2025). The effects, patterns and predictors of phosphorus addition on terrestrial litter decomposition. *Global Ecology and Biogeography*, **34**(6), e70057. <https://doi.org/10.1111/geb.70057>
- **In Preparation.** Casabas, G., de la Casa, J., Lapiedra, O. et al., Cascading effects over soil nutrients driven by the invasion of *Hemorrhoids hippocrepis* in the island of Ibiza.
- **In Preparation.** Brown, A., van Hardenbroek, M., Mackay, H., Fonville, T., Pedersen, M. W., Langdon, P. G., Whitehouse, N., McCormack, F., Murray, E., Barratt, P., McCann, M., Henderson, A. C. G., Ficetola, F., Gielly, L., Davies, K., Crone, A., Cavers, G., **de la Casa, J.**, Hudson, S., Edwards, K., Alsos, I. G. Molecular, isotopic and ecological proxies show human activity is the dominant driver of lake conditions.

Scientific congresses

- EGU 2025: de la Casa et al. (2025). *Elementome trajectories: a framework for studying ecosystem biogeochemical shifts in palaeoenvironmental records*. Vienna, Austria.
- SIBECOL 2025: de la Casa et al. (2025). *Shifting elementomes: addressing long-term changes in the biogeochemical composition of ecosystems from palaeoenvironmental records*. Pontevedra, Spain.
- IPA-IAL 2025: de la Casa et al. (2025). *Elementome Trajectories reveal long-term ecological and biogeochemical shifts in ecosystem history*. Aix-les-Bains, France

Other activities

- COST Action PalaeOpen: XRF data harmonisation and data stewardship initiative



Appendix II:

Supplementary Materials for:

Unveiling two millennia of ecosystem
changes in the Azores through
Elementome Trajectory Analysis

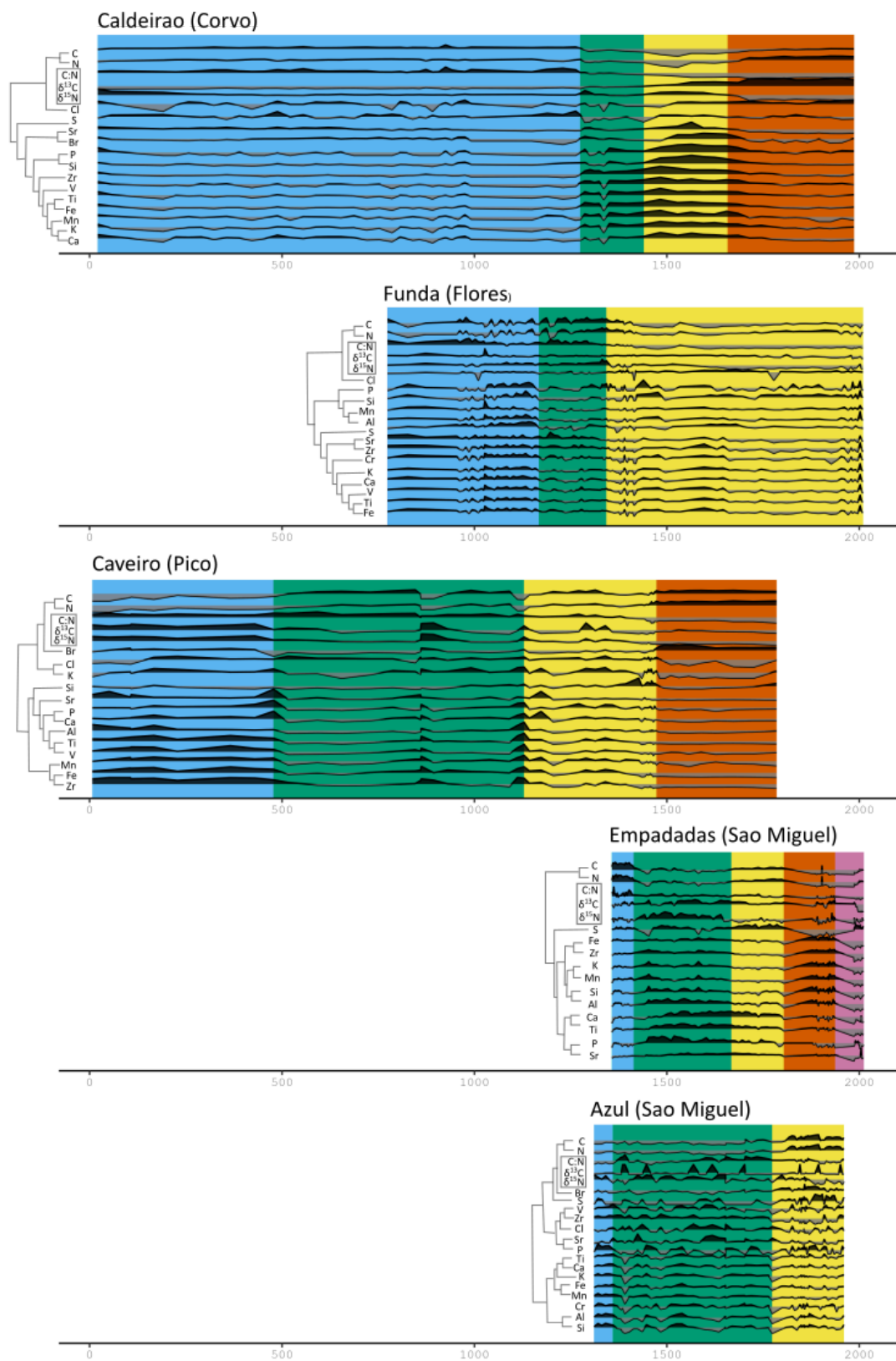


Figure S1. Evolution of the relative content of each element for the five lakes. The values of elements are standardised data. Although P was rejected for the trajectory analysis due to low resolution with the XRF analysis, we include the data here for anyone interested.

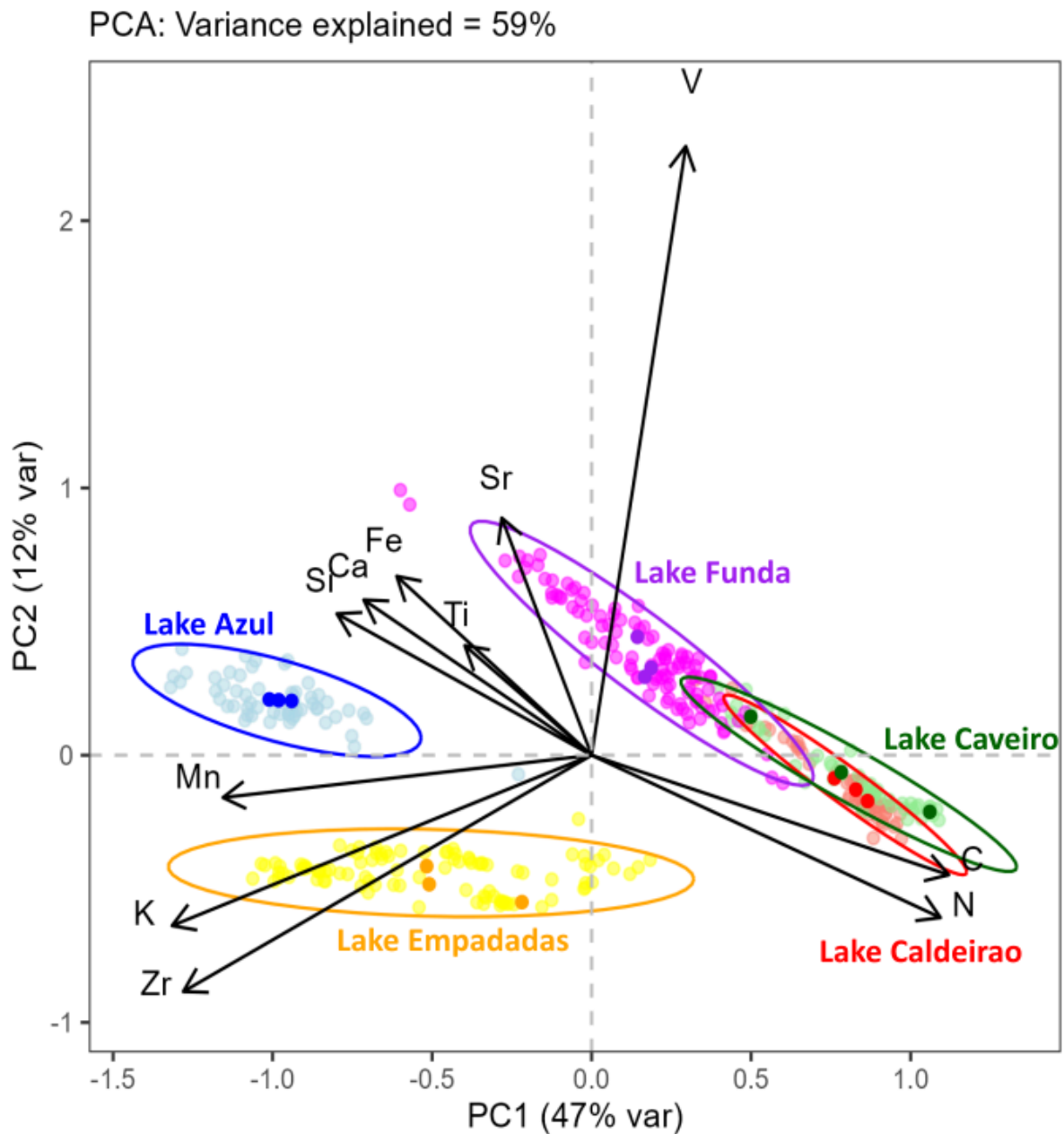


Figure S2. Trajectories of the five lakes in a shared multivariate space. Darker dots represent the three main centroids of each record. Three-centroid length was calculated as the sum of the lengths between the centroids. The ellipse represents the area occupied by the 95% of the samples. The explored area was calculated using the area of the ellipses.

Lake Caldeirão: trajectory analysis

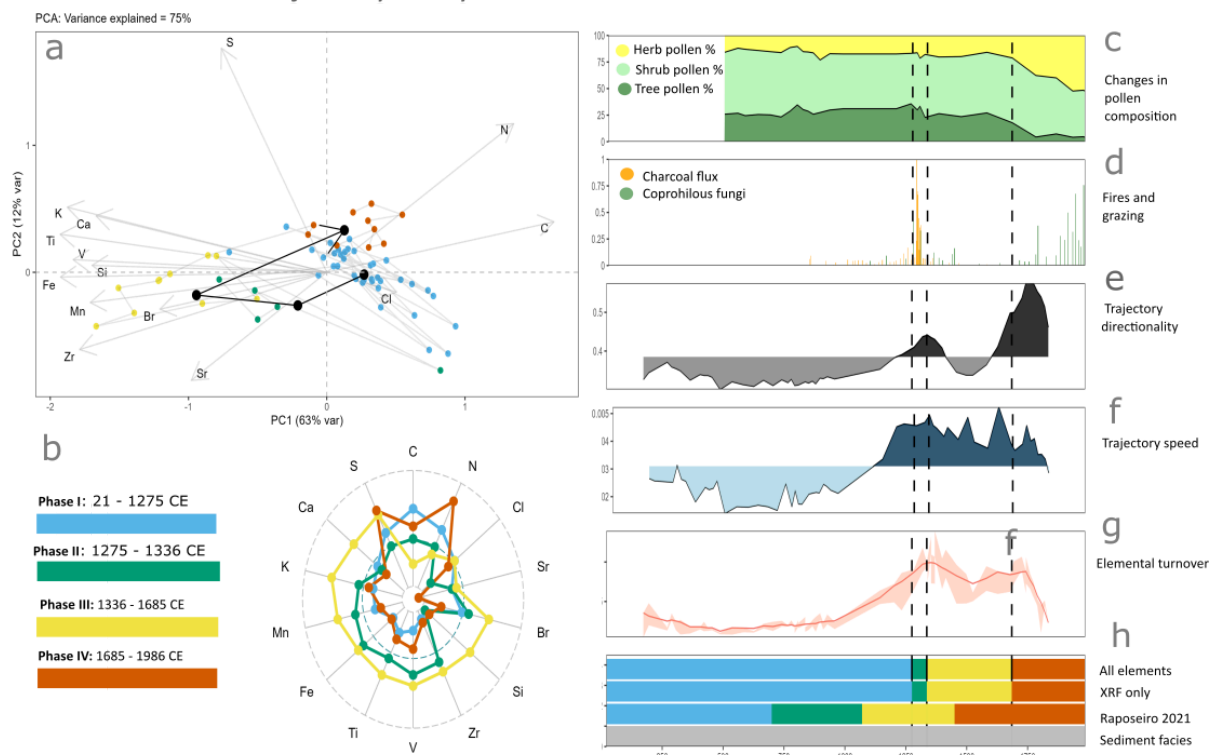


Figure S3. Lake Caldeirão palaeoelementome and palynology analysis. (a) is the palaeoelementome trajectory represented in a PCA plot. (b) is a spider plot of the characterisation of the elementome during the different zones. The elements are ordered following the Ward analysis (Figure S1) (c) is the change in pollen composition of herb (yellow), shrub (light green) and tree (dark green) species, in % (axis from 0 to 100%). (d) indicates the fire regimen (orange) by the charcoal flux and the cattle presence (green) by coprophilus fungi spore flux (rescaled values from 0 to 1). (e) is the trajectory directionality. Dark gray depicts values over the mean of the trend; while light gray indicates values under the mean. (f) is the trajectory speed. Dark blue depicts values over the mean of the trend; while light blue indicates values under the mean. (g) is the elemental turnover and its confidence interval generated via bootstrap. In (h) are the different temporal zones constructed with the palaeoelementome (all elements, and XRF only), and the ones previously determined by Raposeiro (ref) taking into account the anthropogenic stages of the lake. The colors of a, b and e (only the upper zonation) correspond to the palaeoelementome zonations: blue for the first (500 – 1275 CE), green for the second (1275– 1336 CE), yellow for the third (1360 - 1685), and orange for the last (1685– 1937 CE). On gray, the sedimentary facies. In this case it only presented one facies: reddish brown mud. The dotted line in c-g represent the elementome shift (the oldest date from the interval)

Lake Caveiro: trajectory analysis

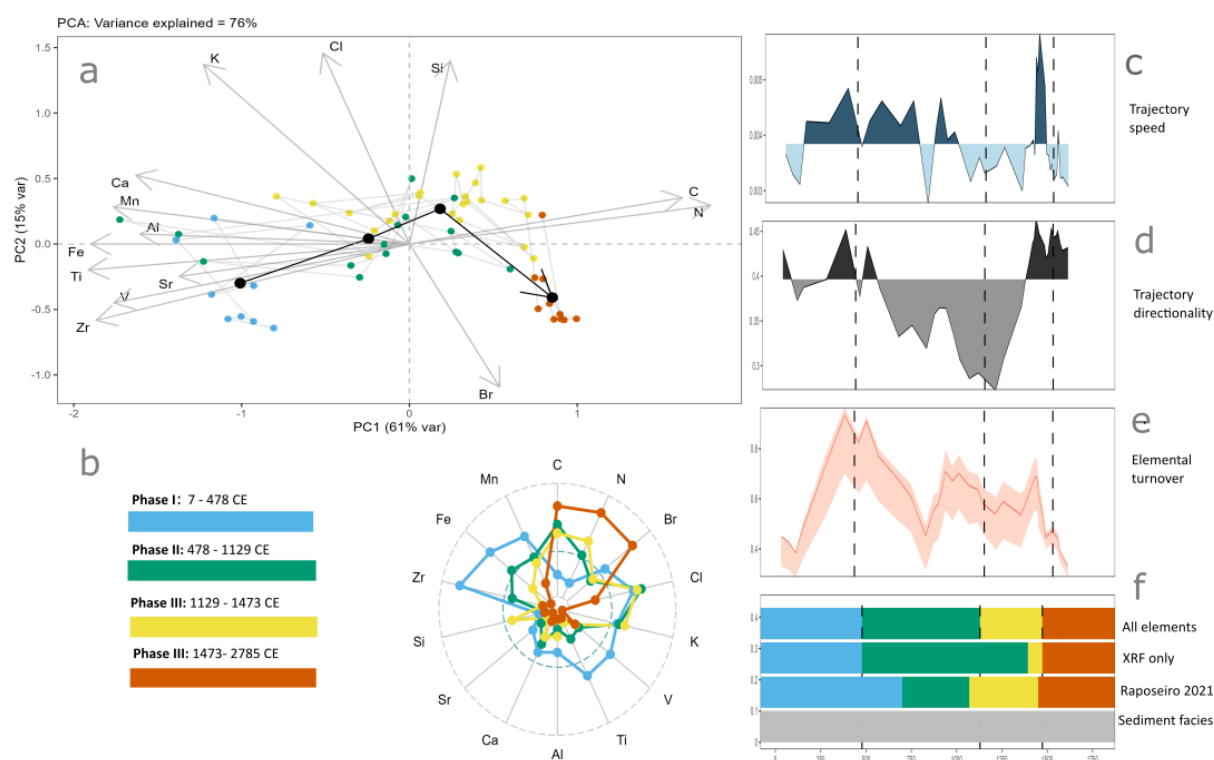


Figure S4. Lake Caveiro palaeoelementome analysis. (a) is the palaeoelementome trajectory represented in a PCA plot. (b) is a spider plot of the characterisation of the elementome during the different zones. The dots over the element name indicate a significant difference between this zone (the one of the color) and the previous. The elements are ordered following the Ward analysis (Figure S1). (c) is the trajectory speed. Dark blue depicts values over the mean of the trend; while light blue indicates values under the mean (d) is the trajectory directionality. Dark blue depicts values over the mean of the trend; while light blue indicates values under the mean. Dark grey depicts values over the mean of the trend; while light grey indicates values under the mean. (e) is the elemental turnover with a confidence interval generated via bootstrap. In (f) are the different temporal zones constructed with the palaeoelementome (all elements, and XRF only), and the ones previously determined by Raposeiro (ref) taking into account the anthropogenic stages of the lake. The colors of a, b and e (only the upper zonation) correspond to the palaeoelementome zonations: blue for the first (7 – 478 CE), green for the second (478 – 1129 CE), yellow for the third (1129 – 1434 CE) and orange for the last (1434 – 1785 CE). For this record, we didn't set a ceal sediment facies classification. The dotted line in c-e represent the elementome shift (the oldest date from the interval)

Lake Funda: trajectory analysis

PCA: Variance explained = 75%

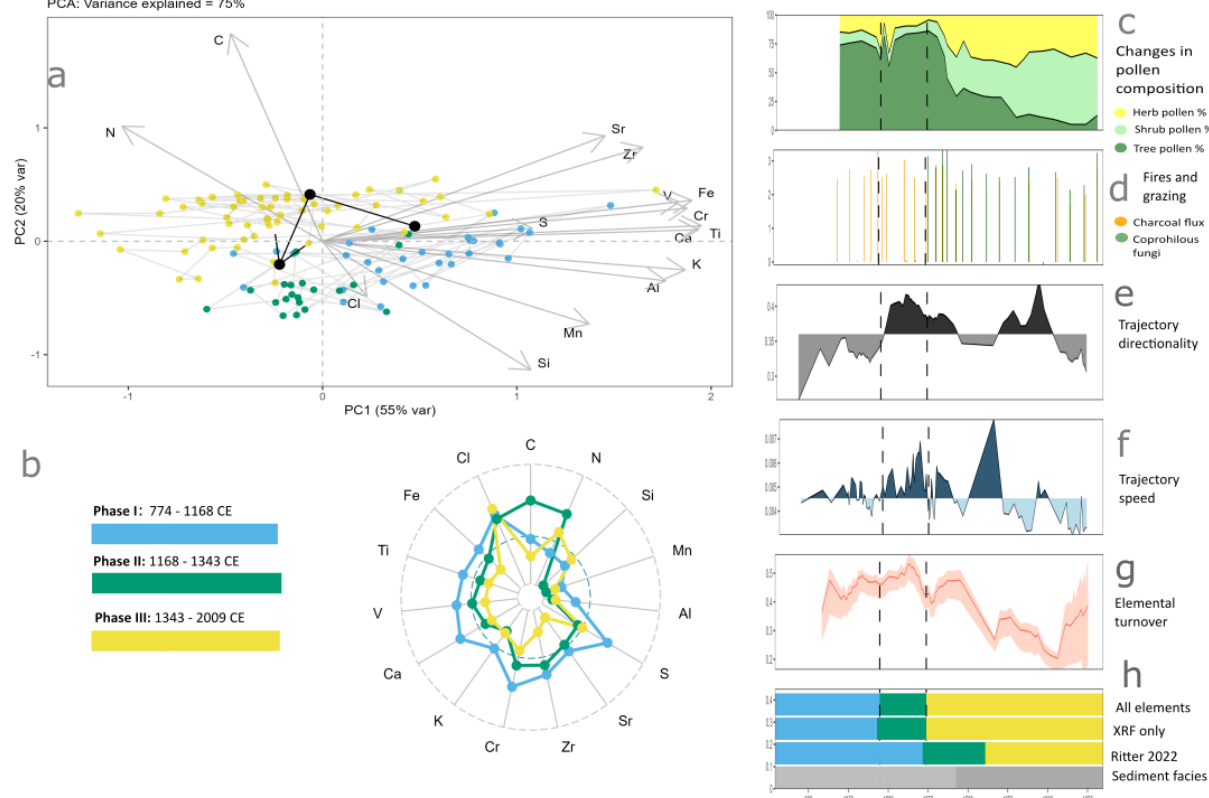


Figure S5. Lake Funda palaeoelementome and palynology analysis. (a) is the palaeoelementome trajectory represented in a PCA plot. (b) is a spider plot of the characterisation of the elementome during the different zones. The dots over the element name indicates significant difference between this zone (the one of the colour) and the previous. The elements are ordered following the Ward analysis (Figure S1). (c) is the change in pollen composition of herb (yellow), shrub (light green) and tree (dark green) species, in % (axis from 0 to 100%). (d) indicates the fire regimen (orange) by the charcoal flux and the cattle presence (green) by coprophilous fungi spore flux (rescaled values from 0 to 1). (e) is the trajectory directionality. Dark gray depicts values over the mean of the trend; while light gray indicates values under the mean. (f) is the trajectory speed. Dark blue depicts values over the mean of the trend; while light blue indicates values under the mean. (g) is the elemental turnover and its confidence interval generated via bootstrap. In (h) are the different temporal zones constructed with the palaeoelementome (all elements, and XRF only), and the ones previously determined by Ritter (ref) taking into account the lake trophic stages. The colors of a, b and e (only the upper zonation) correspond to the palaeoelementome zonations: green for the first (776 – 1668 CE), yellow for the second (1668 – 1434 CE) and orange for the last (1434 – 2009 CE). In gray/dark gray the different facies: first one (776 – 1455 CE) mud, sand and gravels; the second (1455 – 2009 CE) laminated deposit. The dotted line in c-g represent the elementome shift (the oldest date from the interval)

Lake Empadadas: trajectory analysis

PCA: Variance explained = 85%

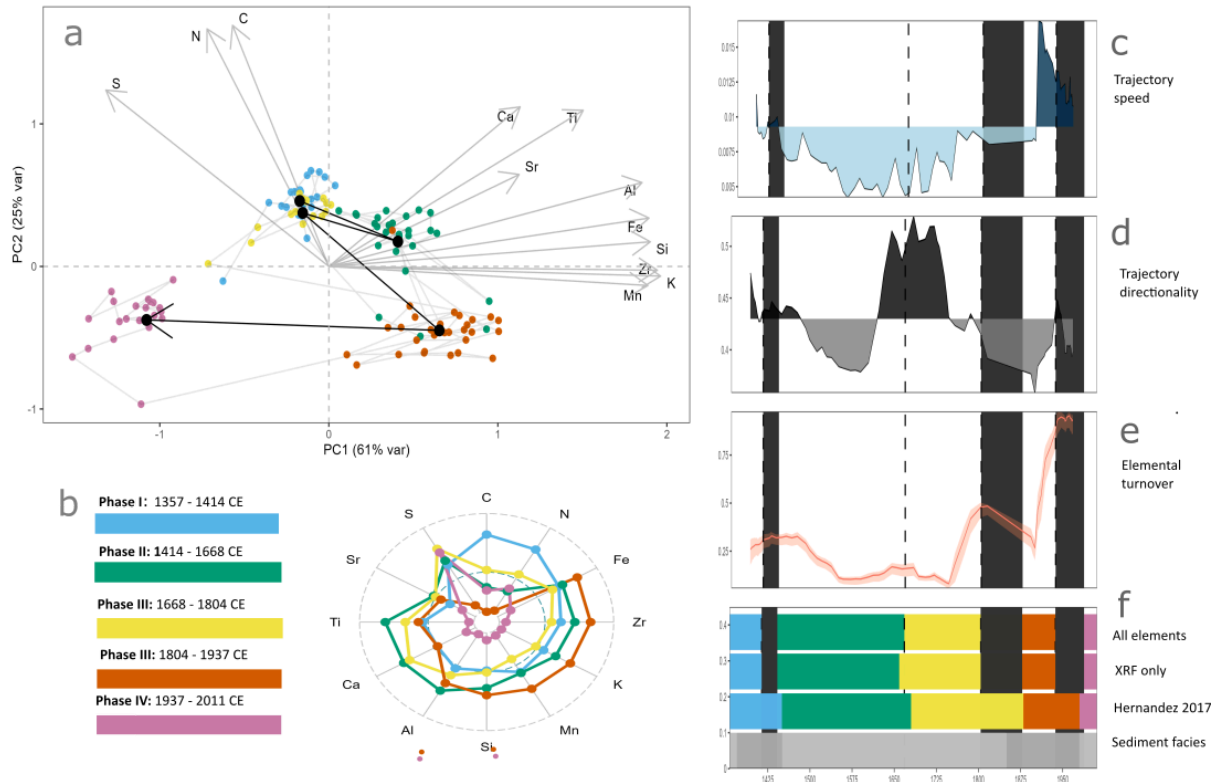


Figure S6. Lake Empadadas palaeoelementome analysis. (a) is the palaeoelementome trajectory represented in a PCA plot. (b) is a spider plot of the characterisation of the elementome during the different zones. The dots over the element name indicate a significant difference between this zone (the one of the color) and the previous. The elements are ordered following the Ward analysis (Figure S1). (c) is the trajectory speed. Dark blue depicts values over the mean of the trend; while light blue indicates values under the mean (d) is the trajectory directionality. Dark blue depicts values over the mean of the trend; while light blue indicates values under the mean. Dark grey depicts values over the mean of the trend; while light grey indicates values under the mean. (e) is the elemental turnover with a confidence interval generated via bootstrap. In (f) are the different temporal zones constructed with the palaeoelementome (all elements, and XRF only), and the ones previously determined by Hernández et al. 2017 (ref) taking into account the climate. The colors of a, b and c (only the upper zonation) correspond to the palaeoelementome zonations: blue for the first (1357 – 1414 CE), green for the second (1414– 1668CE), yellow for the third (1668 – 1804 CE), orange for the fourth (1878 – 1937 CE) and pink for the last (1988 – 2011 CE). In gray/dark gray the different facies: first one (until 1350 CE) volcanic clastic deposits; the second (1450 – 1450 CE) dark-brown muddy sediments; third one (1450-1850 CE) banned brown mud and silt, fourth one (1850 – 1980 CE) dark to pale brown silts, with a sand band at 1890 CE; and fifth one (1980 – 2011 CE) brown to ochre mud very rich in diatoms. Black boxes depict hiatus. The dotted line in c-e represent the elementome shift (the oldest date from the interval)

Lake Azul: trajectory analysis

PCA: Variance explained = 68%

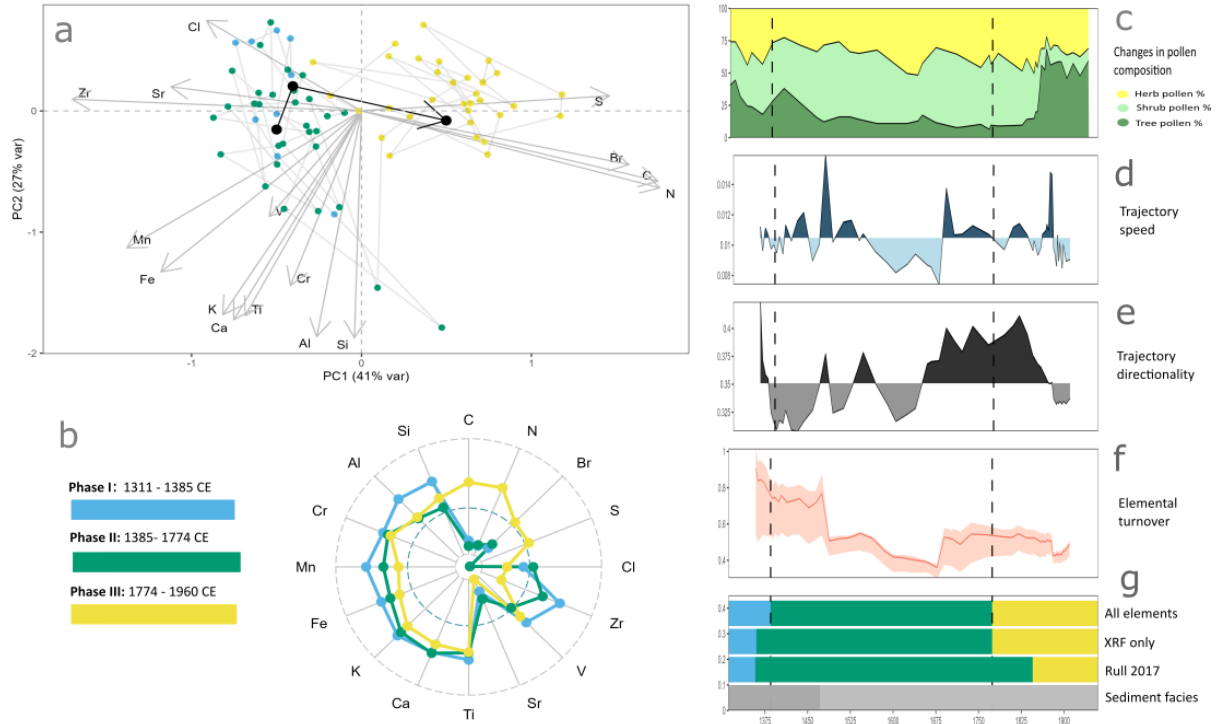


Figure S7. Lake Azul palaeoelementome and palynology analysis. (a) is the palaeoelementome trajectory represented in a PCA plot. (b) is a spider plot of the characterisation of the elementome during the different zones. The dots over the element name indicate a significant difference between this zone (the one of the color) and the previous. The elements are ordered following the Ward analysis (Figure S1). (c) is the change in pollen composition of herb (yellow), shrub (light green) and tree (dark green) species, in % (axis from 0 to 100%) This data is not from the same core, but from a previous publication (Rull et al 2017 ref). (d) is the trajectory speed. Dark blue depicts values over the mean of the trend; while light blue indicates values under the mean (e) is the trajectory directionality. Dark blue depicts values over the mean of the trend; while light blue indicates values under the mean. Dark grey depicts values over the mean of the trend; while light grey indicates values under the mean. (f) is the elemental turnover with a confidence interval generated via bootstrap. In (g) are the different temporal zones constructed with the palaeoelementome (all elements, and XRF only), and the ones previously determined by Rull (ref) taking into account the pollen record. The colors of a, b and d (only the upper zonation) correspond to the palaeoelementome zonations: blue for the first (1331 - 1385 CE), green for the second (1385 - 1774 CE) and yellow for the last (1774 - 1960 CE). In gray/dark gray the different facies: first one (1331 - 1471 CE) gray to brown laminated silty mud; the second (1471 - 1960 CE) is brown mud. The dotted line in c-f represent the elementome shift (the oldest date from the interval)

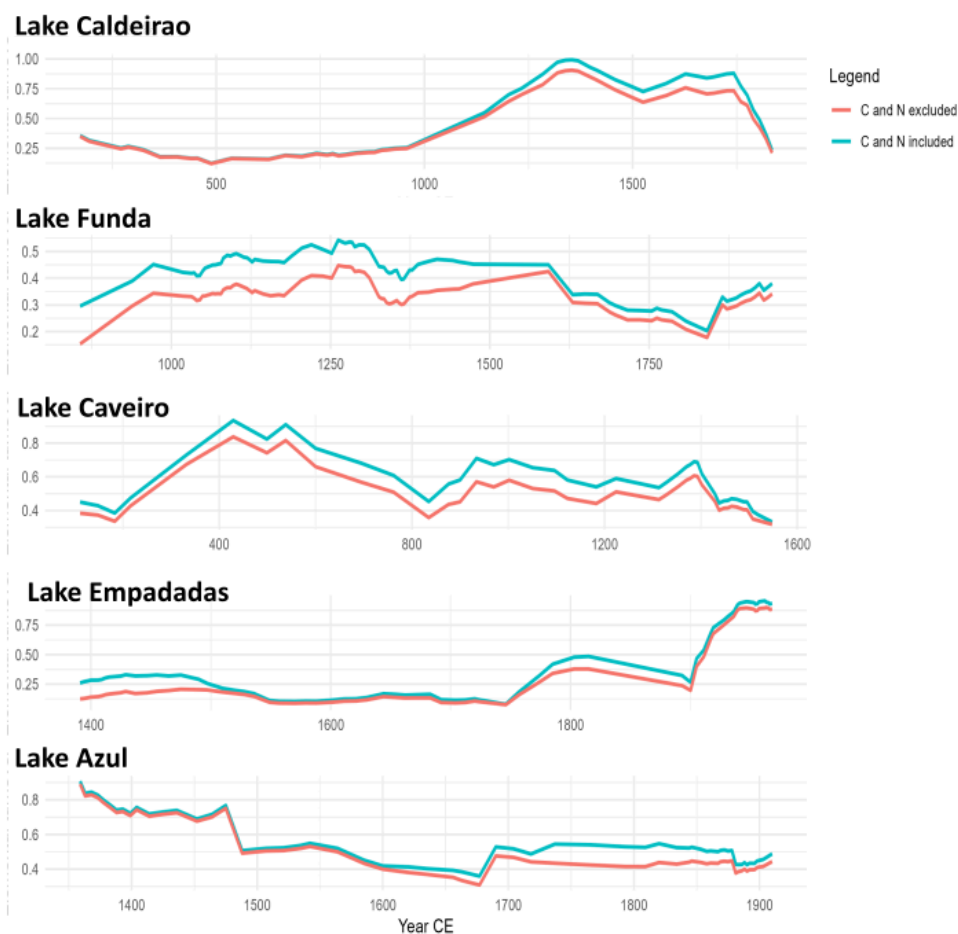


Figure S8. Comparison of elemental turnover with and without excluding C and N from the analysis. Blue lines represent C and N included, while red lines represent C and N excluded. Most of the elementome shifts were similar in both approaches. The general trends for elemental turnover and directionality were also similar (Figure S3-8). The most relevant difference is in the second elementome shift of Caveiro (1129-1143 CE), which occurred around 260 years later in the XRF-only elementome. This evidence shows the strong opposite correlation between organic and terrigenous elements. Even without the data for the C and N, the trajectories of the XRF-only palaeoelementome are alike because instead of going to the C and N direction in the PCA, they are following the opposite direction to the terrigenous signal. However, we encourage the inclusion of C and N when building elementomes as they provide key information for the ecosystems. The trajectory analysis of Lake Empanadas is one example. After the third shift in the complete elementome approach (1804-1878 CE; Fig S8), there is a reduction of both terrigenous and organic elements. This is not evident when looking only at the XRF elementome. In this case for XRF-only elementomes, this could be interpreted as an increase in the organic proportion of the palaeoelementome. Also, the oscillation between the first (1414-1442 CE) and second (1668-1677 CE) elementome shifts is not present when C and N are not considered

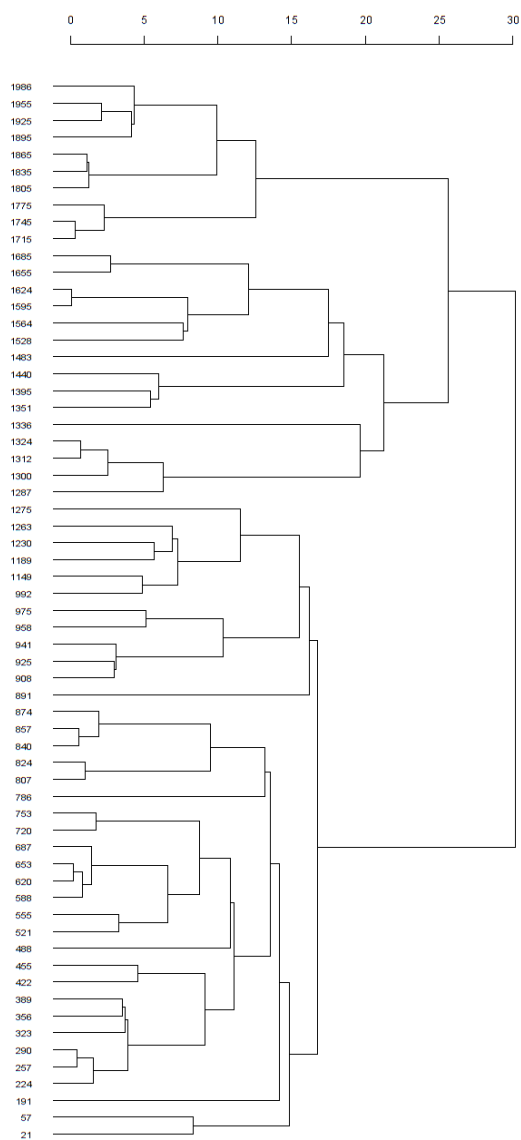


Figure S9. Dendrogram of the CONISS analysis of the palaeoelementome of Lake Caldeirao.

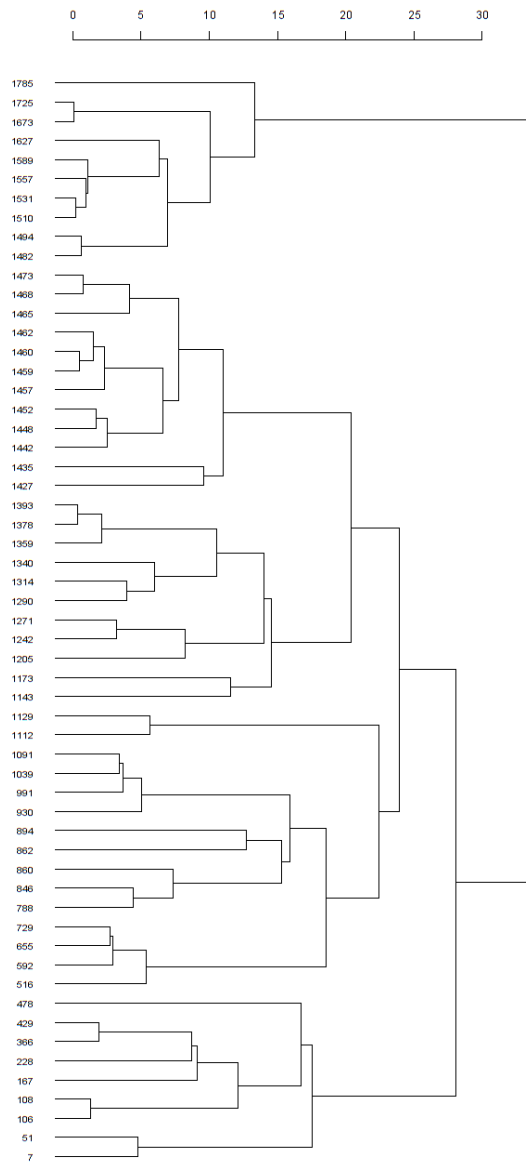


Figure S10. Dendrogram of the CONISS analysis of the palaeoelementome of Lake Caveiro.

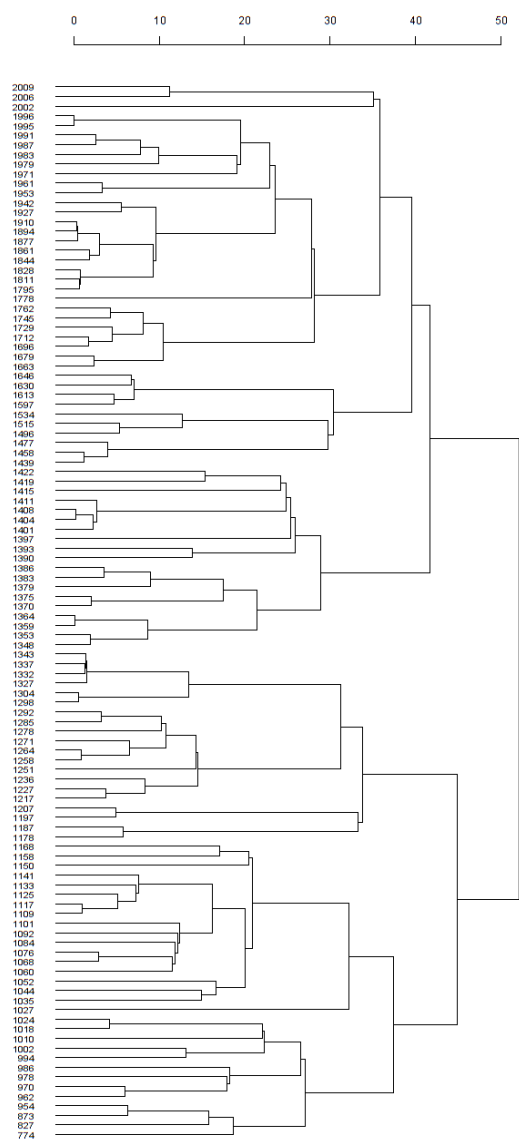


Figure S11. Dendrogram of the CONISS analysis of the palaeoelementome of Lake Funda.

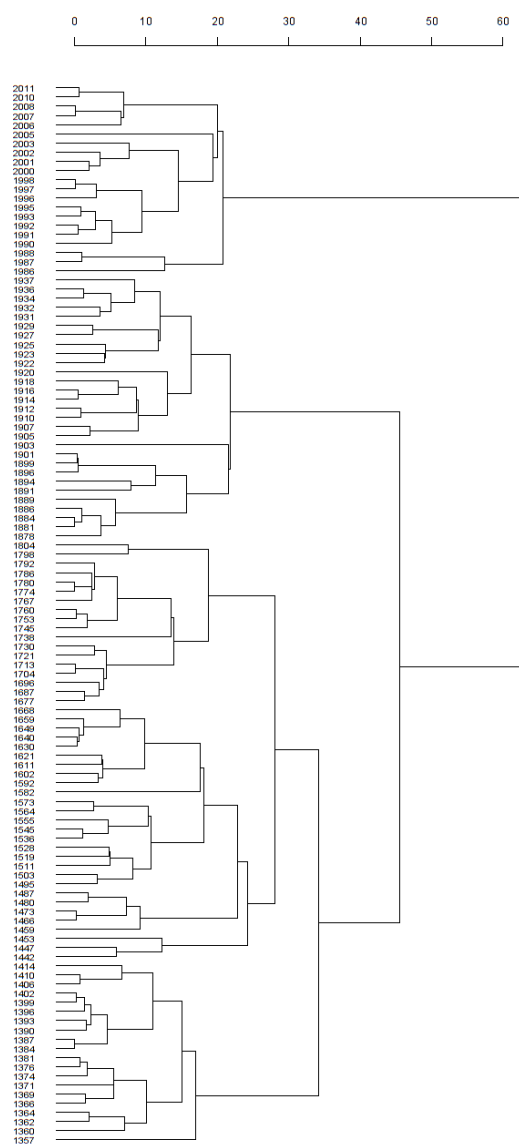


Figure S12. Dendrogram of the CONISS analysis of the palaeoelementome of Lake Empadadas.

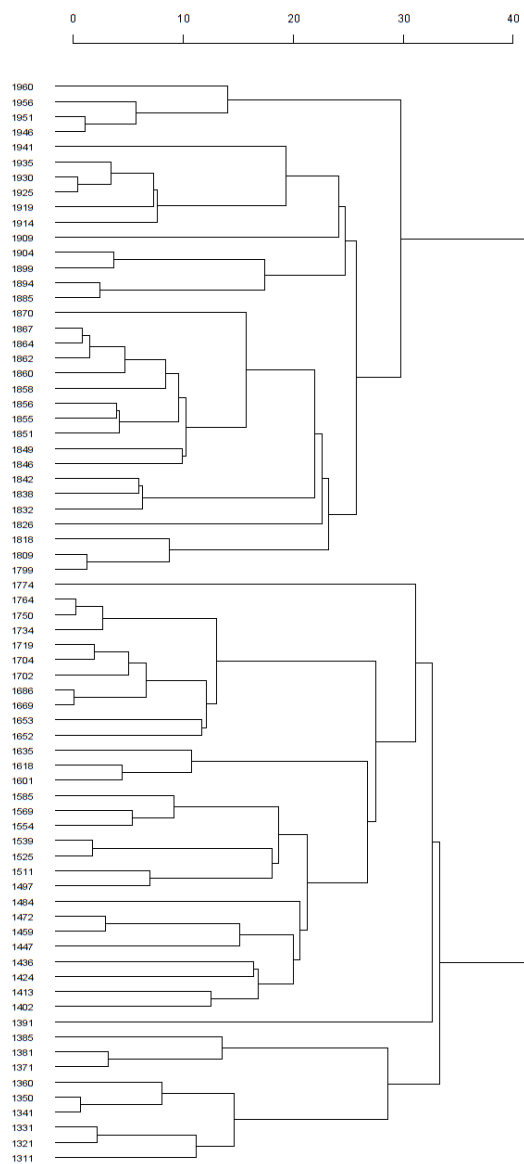


Figure S13. Dendrogram of the CONISS analysis of the palaeoelementome of Lake Azul.



Appendix III:

Supplementary Materials for:

Erosion and geochemical
legacies of human colonisation
on Atlantic islands

Table S1. Site characteristics. Latitude, longitude, elevation and type of record of the sampling sites.

Site (island, archipelago)	Latitude (°)	Longitude (°)	Elevation (m a.s.l.)	Record type
Lake Funda (Flores, Azores)	39.44	-31.19	360	Lake record
Lake Caldeirão (Corvo, Azores)	39.70	-31.10	400	Lake record
Lake Empadadas Norte (São Miguel, Azores)	37.49	-25.75	760	Lake record
Lake Azul (São Miguel, Azores)	37.78	-25.49	260	Lake record
Lake Caveiro (Pico, Azores)	38.43	-28.18	920	Lake record
Cova do Paul (Santo Antão, Cape Verde)	17.1	-25.1	1175	Soil record
Calderinha (São Nicolau, Cabo Verde)	16.6	-24.3	1035	Soil record
Cova Galhina (Brava, Cabo Verde)	14.85	-24.7	810	Soil record
Alcatraces (Santiago, Cabo Verde)	15.03	-23.45	10	Soil record
Ka Nazario (Fogo, Cabo Verde)	14.96	-24.43	1010	Soil record
La Orotava (Tenerife, Canary Islands)	28.35	-16.55	1180	Soil record
Calderilla (Gran Canaria, Canary Islands)	28.1	-15.5	1770	Soil record
Laguna Grande (La Gomera, Canary Islands)	28.15	-17.25	1250	Soil record
Lagoa Amelia (São Tomé, Gulf of Guinea Islands)	0.27	6.6	1443	Soil/ peat record
Jodavannet (Spitsbergen, Svalbard)	79.33	16.0	140	Lake record
Kløverbladvatna (Nordaustlandet, Svalbard)	79.75	21.71	8	Lake record
Nykurvatn (Iceland)	65.63	-15.14	428	Lake record
Torfdalsvatn (Iceland)	66.06	-20.38	40	Lake record
Blackwood Sinkhole (Abaco, Bahamas)	26.79	-77.42	10	Lake record
Belmont Pond (Tortola, British Virgin Islands)	18.25	-64.37	2	Lake record
Hooker's point (East Falkland, Falklands/Malvinas)	-51.42	-57.47	8	Peat record

Table S2. Time span, number of samples, time resolution, sizes of the moving time windows, and step size (years distance between moving windows) for each record. The sample sizes for the rate of sedimentation and Ti-index are the number of samples minus one.

Site (island, archipelago)	Time span (yr)	Number of samples	Time resolution(samples/time)	Moving-window size (yr)	Step size (yr)	Elemental turnover and directionality (N)
Lake Funda (Flores, Azores)	1235	109	0.088	308	31	36
Lake Caldeirão (Corvo, Azores)	2036	65	0.034	509	51	22
Lake Empadadas Norte (São Miguel, Azores)	653	116	0.174	163	16	36
Lake Azul (São Miguel, Azores)	648	73	0.112	162	16	25
Lake Caveiro (Pico, Azores)	2604	77	0.029	651	65	26
Cova do Paul (Santo Antão, Cape Verde)	2129	10	0.0004	532	53	4
Calderinha (São Nicolau, Cabo Verde)	1520	25	0.016	380	38	9
Cova Galhina (Brava, Cabo Verde)	2944	18	0.006	736	77	5
Alcatrazes (Santiago, Cabo Verde)	578	49	0.084	144	14	17
Ka Nazario (Fogo, Cabo Verde)	2971	30	0.010	742	74	10
La Orotava (Tenerife, Canary Islands)	2722	32	0.011	680	68	10
Calderilla (Gran Canaria, Canary Islands)	2650	91	0.034	662	66	28
Laguna Grande (La Gomera, Canary islands)	2648	10	0.003	662	66	4
Lagoa Amelia (São Tomé, Gulf of Guinea Islands)	2446	12	0.004	611	61	4
Jodavannet (Spitsbergen, Svalbard)	2920	69	0.023	730	73	21
Kløverbladvatna (Nordaustlandet, Svalbard)	2173	76	0.034	543	54	26
Nykurvatn (Iceland)	2258	120	0.053	564	56	40
Torfdalsvatn (Iceland)	3034	402	0.132	784	78	134
Blackwood Sinkhole (Abaco, Bahamas)	2983	112	0.037	741	74	38
Belmont Pond (Tortola, British Virgin Islands)	766	267	0.348	191	191	89
Hooker's point (East Falkland, Falklands/Malvinas)	3020	82	0.027	755	76	56

Table S3. Sources of data for human presence on the islands.

Site (island, archipelago)	First arrival (cal. yr BP)	Reference	Arrivals in the European overseas expansion (cal. yr BP)	Reference
Lake Funda (Flores, Azores)	620	Ritter et al. 2022	498	Matos 1989
Lake Caldeirão (Corvo, Azores)	1100	Raposeiro et al. 2021	498	Matos 1989
Lake Empadadas Norte (São Miguel, Azores)	670	Raposeiro et al. 2021	518	Matos 1989
Lake Azul (São Miguel, Azores)	670	Raposeiro et al. 2021	518	Matos 1989
Lake Caveiro (Pico, Azores)	1100	Connor et al. 2012	500	Matos 1989
Cova do Paul (Santo Antão, Cape Verde)	488	Nogué et al. 2021	488	Castilla-Beltrán et al. 2021a
Calderinha (São Nicolau, Cabo Verde)	488	Nogué et al. 2021	488	Castilla-Beltrán et al. 2021a
Cova Galhina (Brava, Cabo Verde)	488	Nogué et al. 2021	488	Castilla-Beltrán et al. 2021a
Alcatraces (Santiago, Cabo Verde)	488	Nogué et al. 2021	488	Castilla-Beltrán et al. 2021a
Ka Nazario (Fogo, Cabo Verde)	488	Nogué et al. 2021	488	Castilla-Beltrán et al. 2021
La Orotava (Tenerife, Canary Islands)	1630	Santana et al. 2024	454	Santana et al. 2024
Calderilla (Gran Canaria, Canary Islands)	1440	Santana et al. 2024	467	Santana et al. 2024
Laguna Grande (La Gomera, Canary islands)	1610	Santana et al. 2024	500	Santana et al. 2024
Lagoa Amelia (São Tomé, Gulf of Guinea Islands)	480	Castilla-Beltrán et al. 2023a	480	Castilla-Beltrán et al. 2023a
Jodavannet (Spitsbergen, Svalbard)	338	Kruse et al. 2016	338	Kruse, 2016
Kløverbladvatna (Nordaustlandet, Svalbard)	338	Kruse et al. 2016	338	Kruse et al. 2016
Nykurvatn (Iceland)	1080	Streeter et al. 2015	688	Streeter et al. 2015
Torfdalsvatn (Iceland)	1080	Streeter et al. 2015	688	Streeter et al. 2015
Blackwood Sinkhole (Abaco, Bahamas)	1120	Fall et al. 2021	450	Fall et al. 2021
Belmont Pond (Tortola, British Virgin Islands)	2250	Mueller et al. 2019	450	Mueller et al. 2019
Hooker's point (East Falkland, Falklands/Malvinas)	186	Ross, 1978	186	Ross, 1978

Table S4. Sources of geochemical data.

Site (island, archipelago)	Chronology	Geochemical data	XRF technique
Lake Funda (Flores, Azores)	Raposeiro et al. 2021	Raposeiro et al. 2021	XRF core scanner
Lake Caldeirão (Corvo, Azores)	Raposeiro et al. 2021	Raposeiro et al. 2021	XRF core scanner
Lake Empadadas Norte (São Miguel, Azores)	Hernandez et al. 2017	Hernandez et al. 2017	XRF core scanner
Lake Azul (São Miguel, Azores)	Raposeiro et al. 2021	Raposeiro et al. 2021	XRF core scanner
Lake Caveiro (Pico, Azores)	Benavente, 2024	Benavente, 2024	XRF core scanner
Cova do Paul (Santo Antão, Cape Verde)	Castilla-Beltrán et al. 2019	Castilla-Beltrán et al. 2019	Portable XRF
Calderinha (São Nicolau, Cabo Verde)	Castilla-Beltrán et al. 2019	Castilla-Beltrán et al. 2019	Portable XRF
Cova Galhina (Brava, Cabo Verde)	Castilla-Beltrán 2021b	Castilla-Beltrán 2021b	Portable XRF
Alcatraces (Santiago, Cabo Verde)	Castilla-Beltrán et al. In preparation	This study	Portable XRF
Ka Nazario (Fogo, Cabo Verde)	Castilla-Beltrán 2023b	Castilla-Beltrán 2023b	Portable XRF
La Orotava (Tenerife, Canary Islands)	Lea de Nascimento	This study	Portable XRF
Calderilla (Gran Canaria, Canary Islands)	Lea de Nascimento	This study	Portable XRF
Laguna Grande (La Gomera, Canary islands)	Nogué et al. 2013	Castilla-Beltrán et al. 2021b	Portable XRF
Lagoa Amelia (São Tomé, Gulf of Guinea Islands)	Castilla-Beltrán 2023a	Castilla-Beltrán 2023a	Portable XRF
Jodavannet (Spitsbergen, Svalbard)	Kjellman et al. 2024	Voldstad et al. 2020, Kjellman et al. 2024, This study	XRF core scanner
Kløverbladvatna (Nordaustlandet, Svalbard)	Kjellman et al. 2024	Schomacker et al. 2019, Kjellman et al. 2024, This study	XRF core scanner
Nykurvatn (Iceland)	Alsos et al. 2021	Alsos et al. 2021, This study	XRF core scanner
Torfdalsvatn (Iceland)	Alsos et al. 2021	Alsos et al. 2021, This study	XRF core scanner
Blackwood Sinkhole (Abaco, Bahamas)	Fall et al. 2021	Fall et al. 2021	XRF core scanner
Belmont Pond (Tortola, British Virgin Islands)	Mueller et al. 2019	Mueller et al. 2019	XRF core scanner
Hooker's point (East Falkland, Falkland Islands)	Panaretos et al. In preparation	This study	XRF core scanner

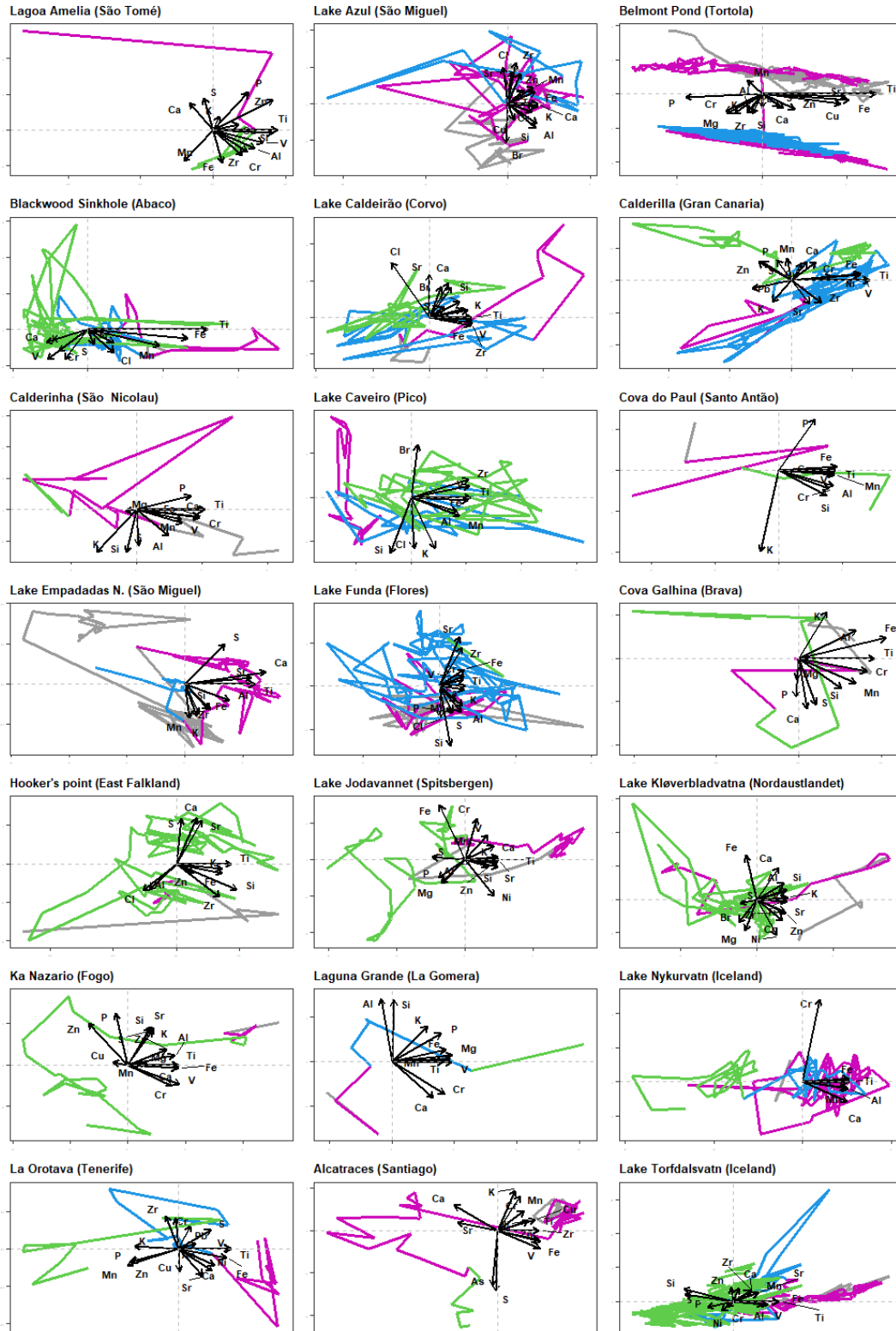


Figure S1. PCA plots for each record, with values rotated to position Ti at 0° to the PC1 axis. The color of the trajectory indicates the waves of human colonisation in the islands: Green indicates prehuman, blue precolonial, purple colonial era and grey postindustrial.

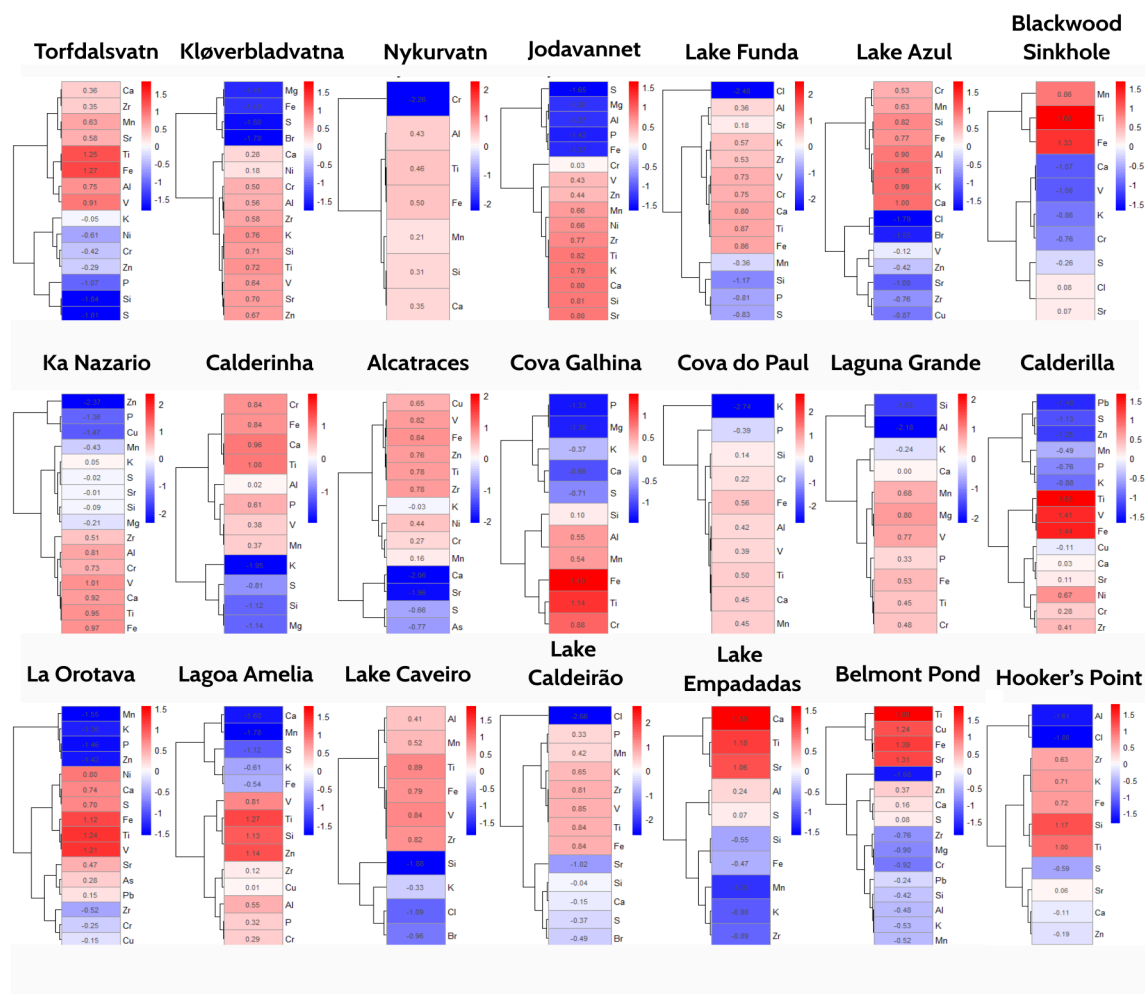


Figure S2. Heatmaps and dendrograms of the correlations between elements in the first principal component of each record data set. Red and blue indicate the PC1 values of the PCA loadings. The numbers on the boxes depict Pearson's correlation coefficients.

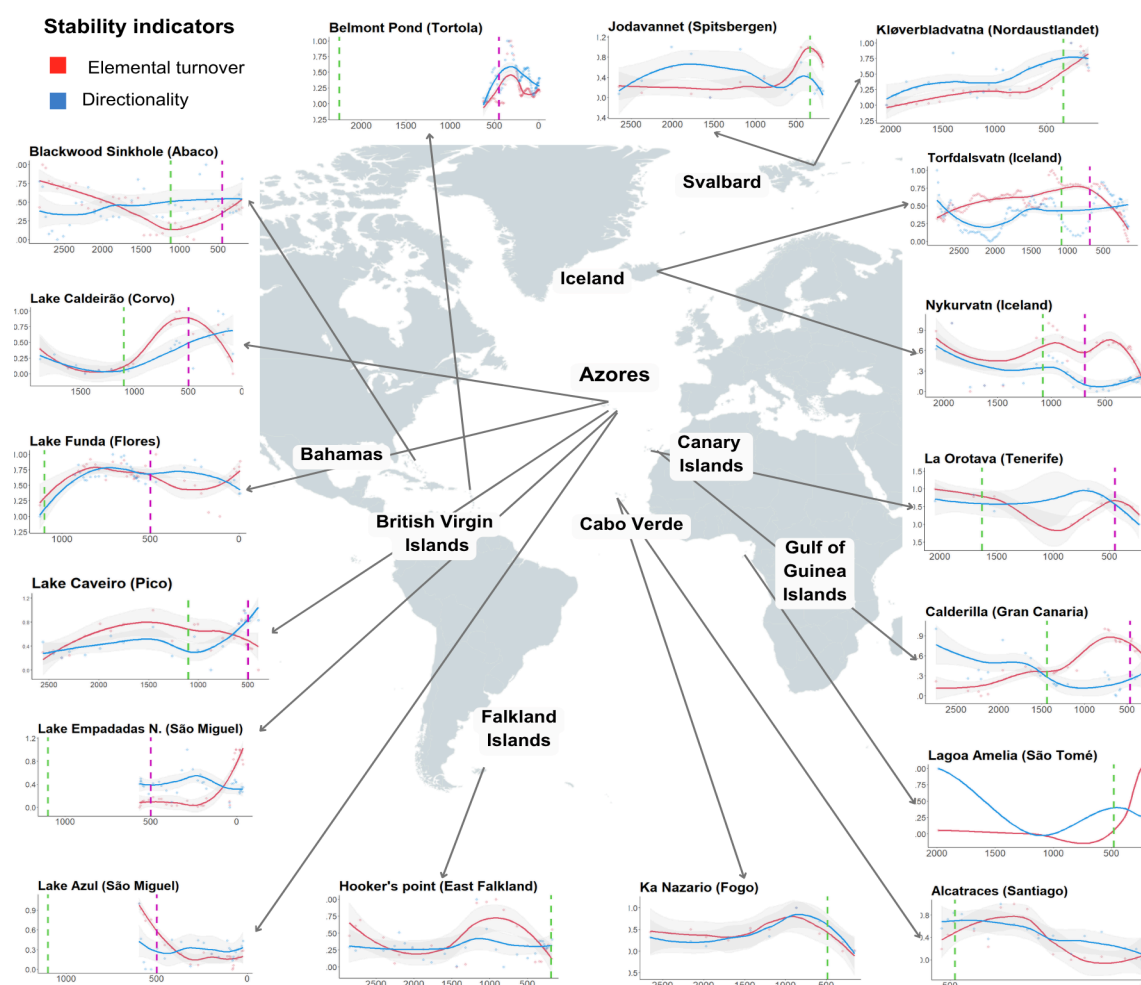


Figure S3. Map of the 17 sedimentary records with temporal values for elemental turnover and directionality. The green dashed vertical lines indicate the arrival of humans on the island. The number of samples for each trend is available in Table S2. The X axes represent cal. years BP while Y axis is the values of elemental turnover and directionality (unitless). The plot only represents the records which were suitable for the calculation of elemental turnover and directionality (see Methods).

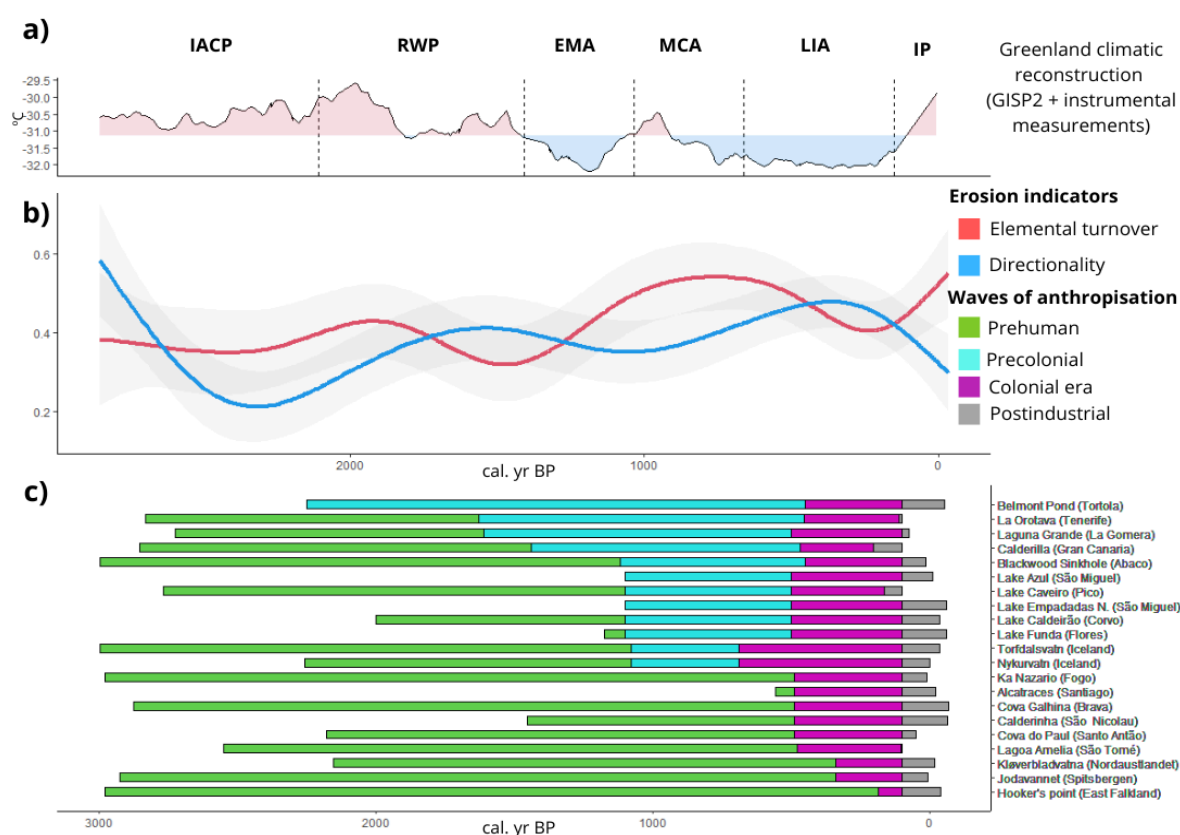


Figure S4. a) Greenland climatic reconstruction (Alley et al. 2004) with different climatic periods: Iron Age Climate Period (IACP), Roman Warm Period (RWP), Early Medieval Age (EMA), Medieval Climate Anomaly (MCA), Little Ice Age (LIA), and Industrial Period (IP). b) Temporal trends as generalised additive mixed models (GAMM) of the elemental turnover and directionality over time for all records, with confidence intervals of 95% in gray. c) Chronologies for each island, with different colours for each wave of anthropisation. The X axis values are cal. yr BP and corresponding to a, b and c plots.

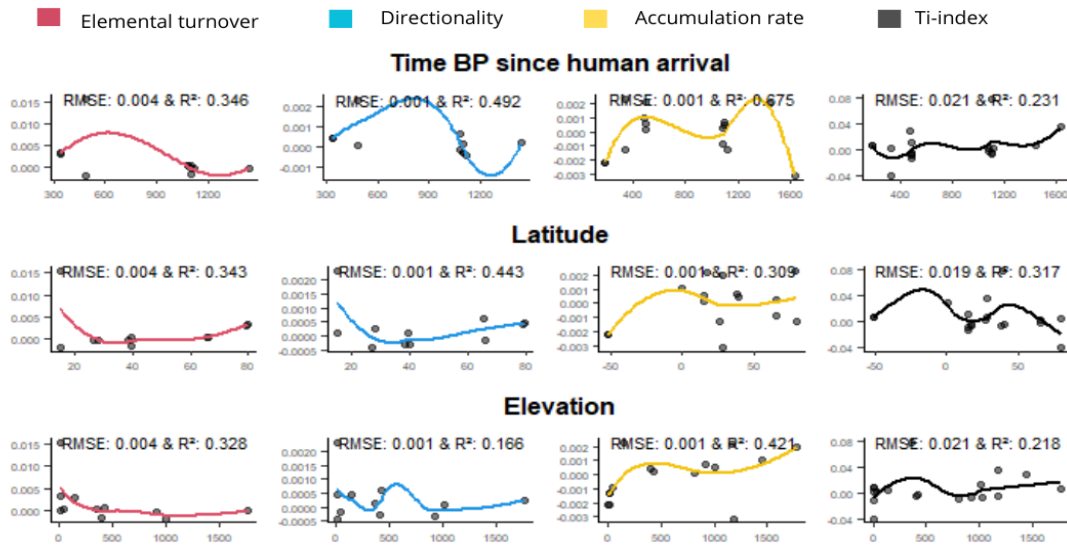


Figure S5. Relationships between the characteristics of the records (years since human arrival, latitude, elevation and record type) and the differences in the rates of change of elemental turnover (red), directionality (blue), rate of sedimentation (yellow), and Ti-index (black) before and after humans arrived. R^2 and RMSE are displayed at the corner of each plot. All Y axes represent the difference in the rate of change before and after human arrival. Only the records that have enough data before and after human arrival were suitable for the analysis of elemental turnover and directionality (Blackwood Sinkhole, Lake Caldeirão, Calderilla, Lake Caveiro, Lake Funda, Jodavannet, Kløverbladvatna, Ka Nazario, Nykurvatn, Alcatraces and Torfdalsvatn); accumulation rate (Lagoa Amelia, Blackwood Sinkhole, Lake Caldeirão, Calderilla, Lake Caveiro, Cova do Paul, Cova Galhina, Hooker's Point, Lake Funda, Jodavannet, Kløverbladvatna, Ka Nazario, Nykurvatn, La Orotava and Torfdalsvatn); and Ti-index (Lagoa Amelia, Blackwood Sinkhole, Lake Caldeirão, Calderilla, Lake Caveiro, Cova do Paul, Cova Galhina, Hooker's Point, Lake Funda, Jodavannet, Kløverbladvatna, Ka Nazario, Nykurvatn, La Orotava, Alcatraces, Lake Funda, Calderinha and Torfdalsvatn)



Appendix IV:

Supplementary Materials for:

Biogeochemical and vegetation
coupling in the Alps: climate change
and livestock effects on alpine
ecosystems across the Holocene

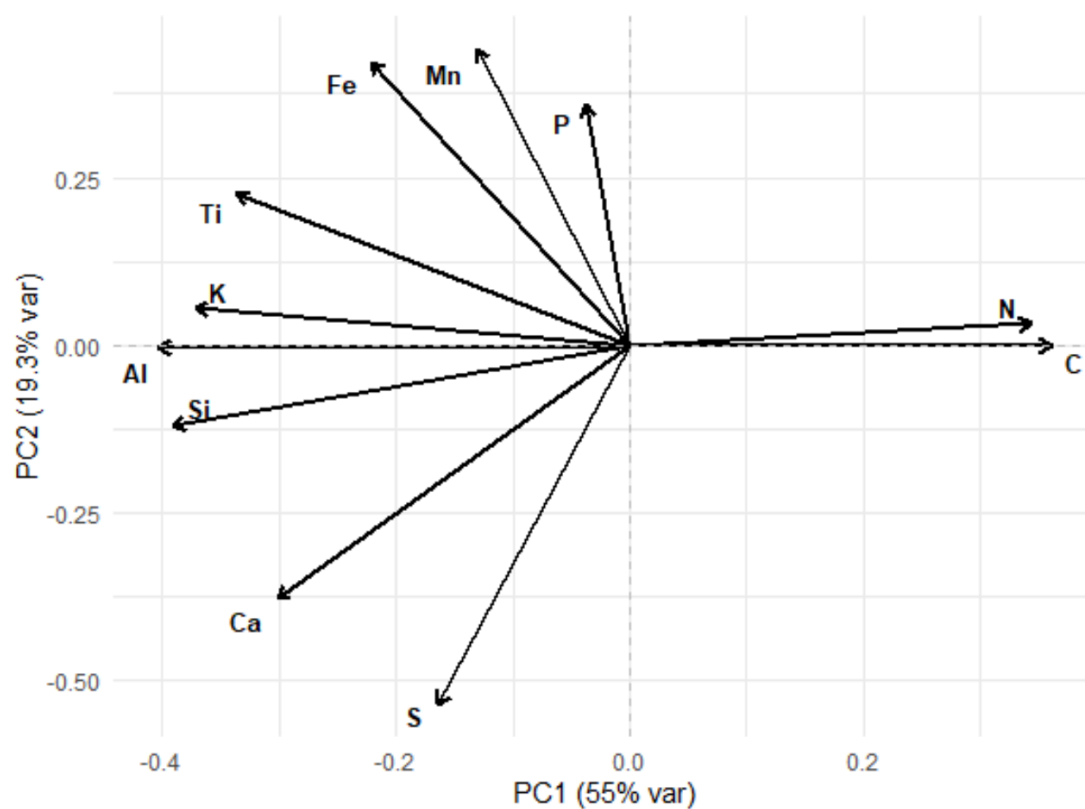


Figure S1. PCA plot loadings for elementome. The PCA elements are displayed so the carbon (C) loading is parallel to the X axis

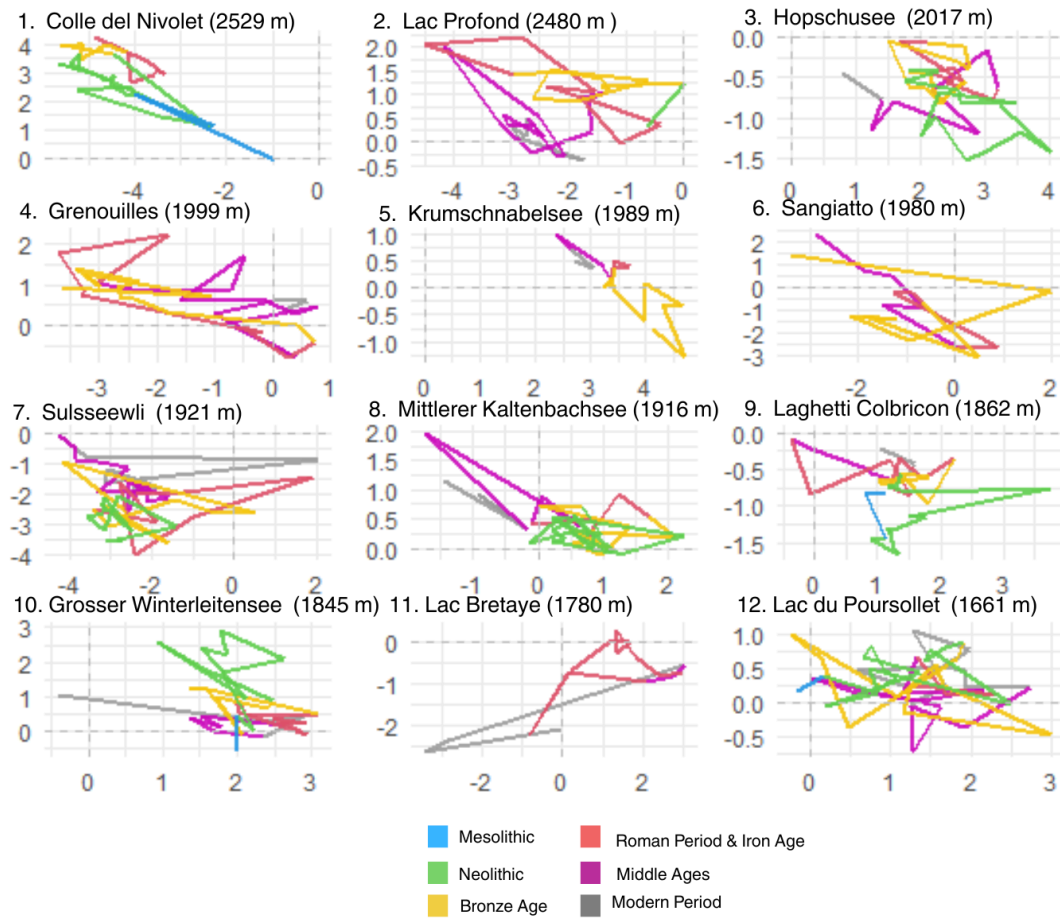


Figure S2. Elementome trajectories for each lake within the multivariate space described in Figure S1. Colors depict different archaeological stages

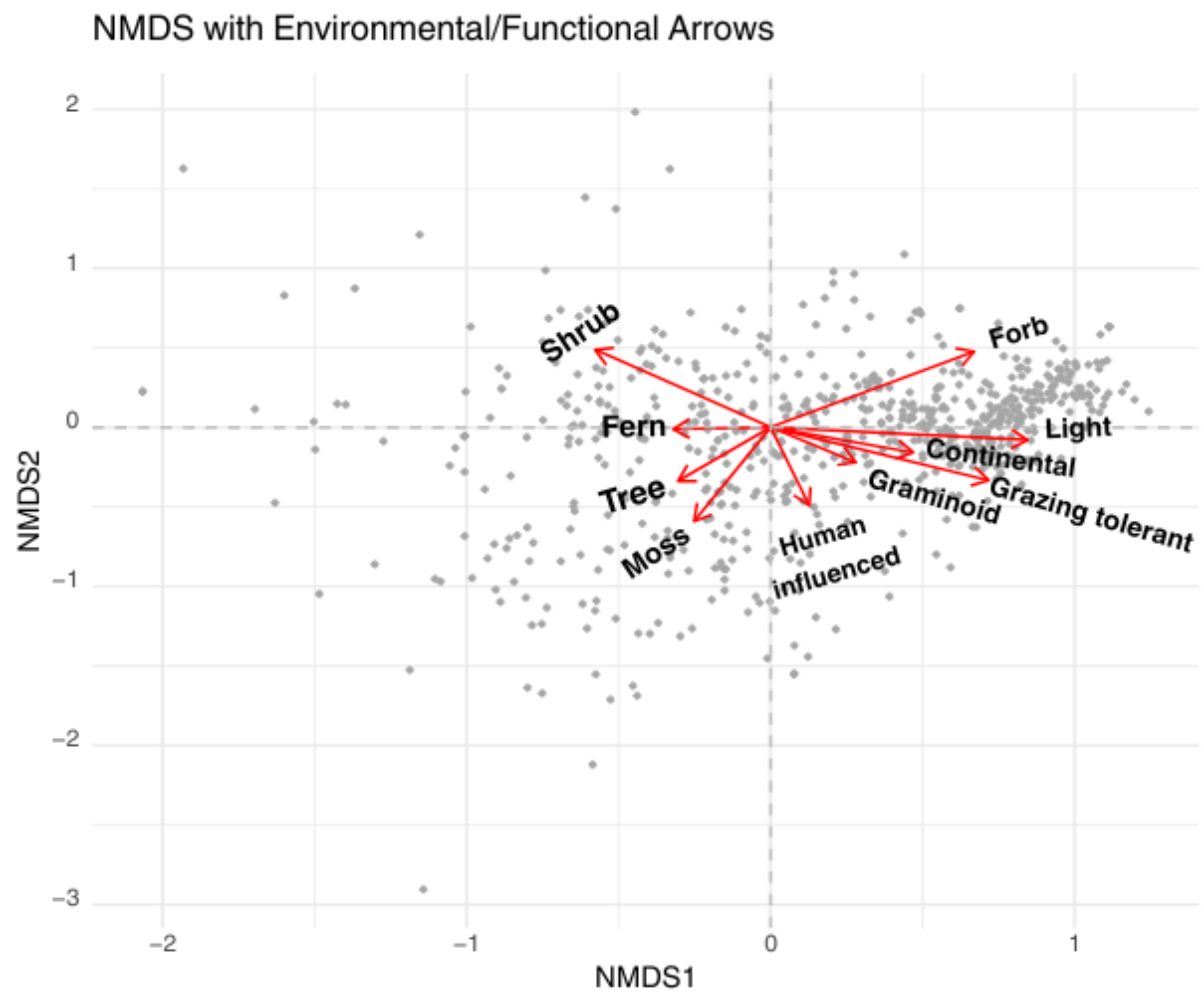


Figure S3. NMDS plot representing the taxa space. The grey dots are the loading for each plat taxa (i.e. the position of each taxa within the taxa space). The red arrows represent environmental traits of the taxa that help the interpretation of the plot

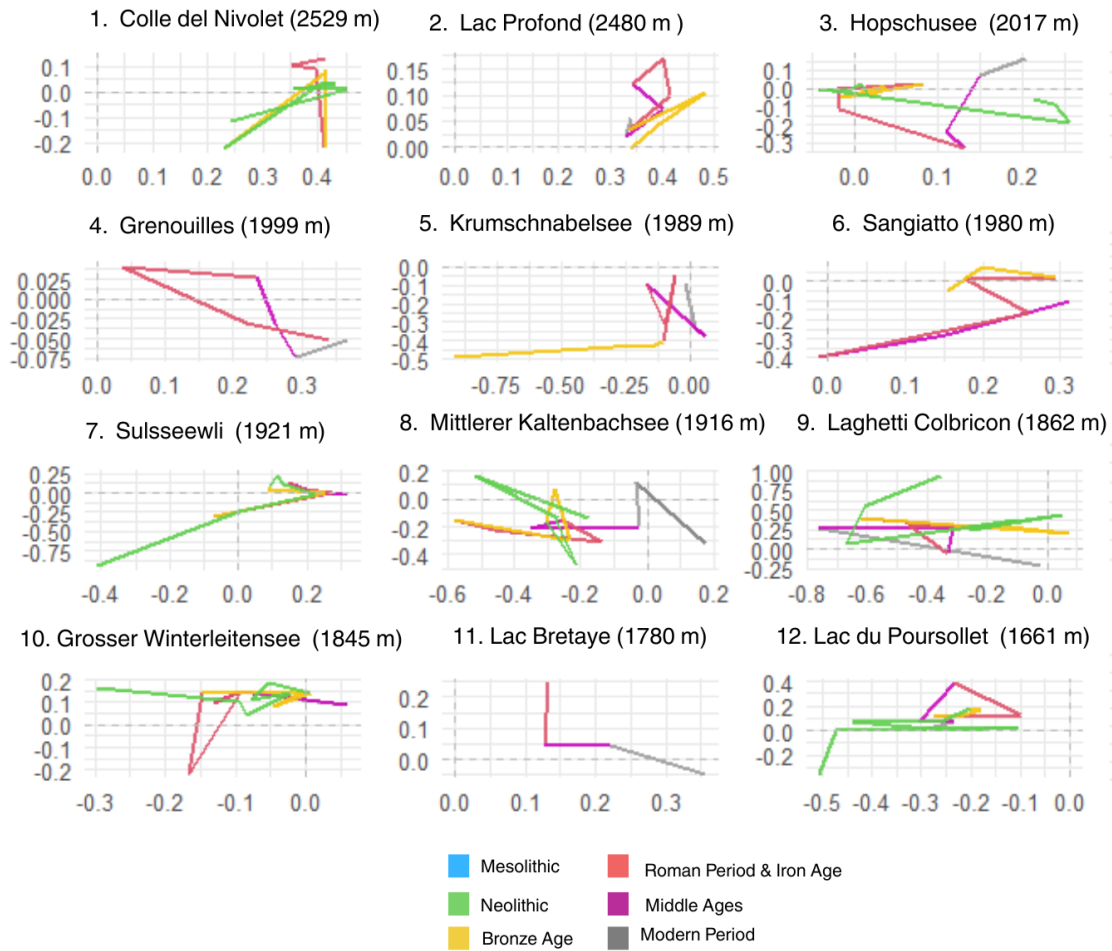


Figure S4. Taxa trajectories for each lake within the multivariate space described in Figure S3. Colors depict different archaeological stages

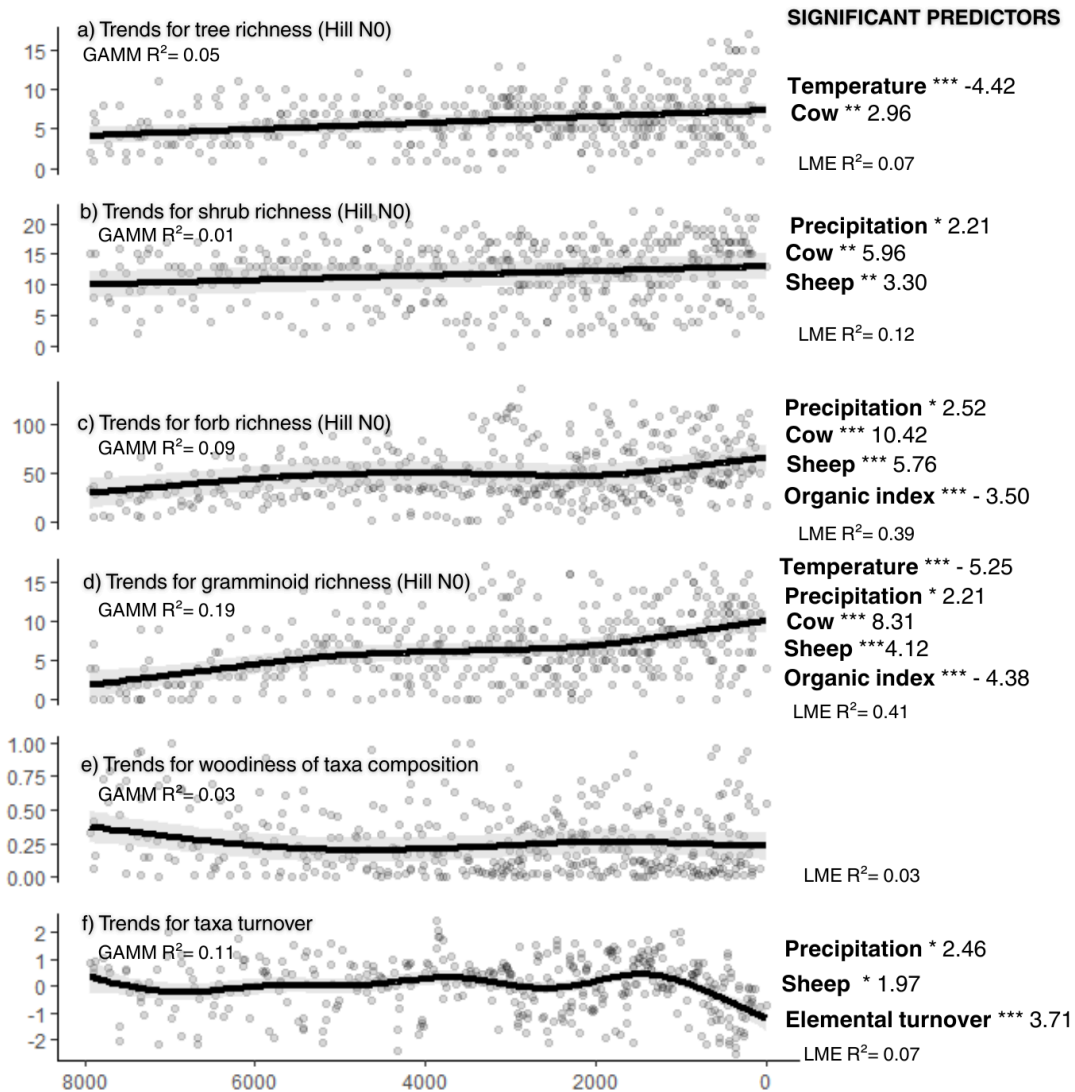


Figure S4. Effects of vegetation, climate and livestock on sediment biogeochemistry. At the left the combined trend across lakes of the variable, using generalised additive mixed models (GAMMs). At the right the standardised linear estimates (linear mixed model with similar structure, LME) of the different predictors included: precipitation (centred), temperature (centred), cow abundance (log transformed), sheep abundance (log transformed), Hill N1, taxa turnover (centred) and woodiness. The coefficients of the LMM models are available in the Supplementary Table annex .

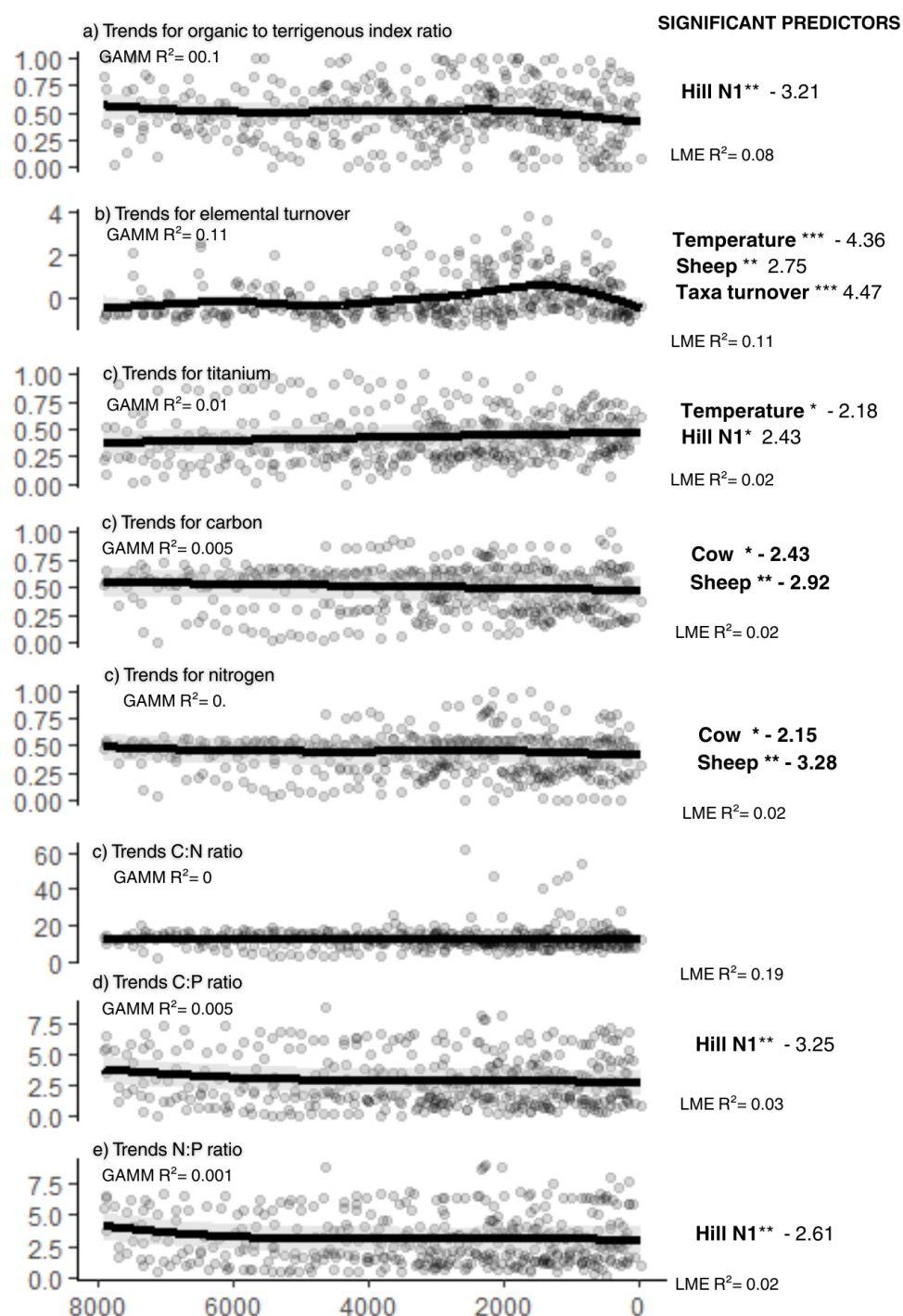
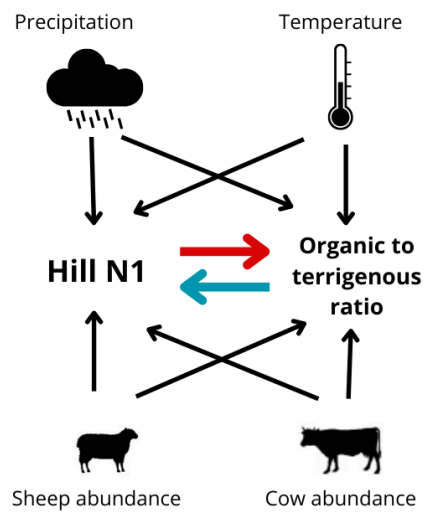


Figure S5. Effects sediment biogeochemistry, climate and livestock on alpine vegetation dynamics. At the left the combined trend across lakes of the variable, using generalised additive mixed models (GAMMs). At the right the standardised linear estimates (linear mixed model with similar structure, LME) of the different predictors included: precipitation (centred), temperature (centred), cow abundance (log transformed), sheep abundance (log transformed), organic to terrigenous ratio and elemental turnover. The coefficients of the LMM models are available in the Supplementary Table annex



$$\Delta AIC = AIC(\text{Model A}) - AIC(\text{Model B})$$

All period $\Delta AIC = -18.279$

Mesolithic & Neolithic $\Delta AIC = -17.274$

Bronze Age $\Delta AIC = -18.271$

Iron Age & Roman Period $\Delta AIC = -18.183$

Middle Ages $\Delta AIC = -18.828$

Modern Era $\Delta AIC = -18.153$

Figure S6. Comparison of models considering the effects of organic to terrigenous ratio vs Hill N1, and vice versa. The difference in the AIC values was compared across all period and also across each archaeological periods

The following terms are shortened in acronyms for model construction. Here is a description of all. This does not include the names of the response variable, which can be guessed by the title of the table.

- *alps_mod_clean* is the database cleared from NA values
- *lake_combination* is the combination of lakes that were present during the Mantel test
- *lake* is the name of the lake
- *c_temp* is the lake-mean centred value of temperature
- *c_prec* is the lake-mean centred value of precipitation
- *log_cow* is the log-transformed cow abundance
- *log_sheep* is the log-transformed sheep abundance
- *hill1_n* is the plant diversity (Hill N1)
- *lign* is the woodiness of the taxa composition
- *c_tturn* is the lake-mean centred value of taxa turnover
- *c_eturn* is the lake-mean centred value of elemental turnover
- *organic_index* is the organic to terrigenous ratio

Table S1. Model structure and coefficients for Mantel correlation between alpine vegetation and sediment biogeochemistry across all periods

Model: lme(mantelboot_r ~ c_temp + c_prec + log_cow + log_sheep, random = ~ 1 | lake_combination, correlation = corAR1(form = ~ age_scaled | lake_combination), data = alps_mod_clean)

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.474	0.015	29.891	385	0.000
c_temp	0.002	0.002	1.177	385	0.239
c_prec	-0.000	0.000	-3.269	385	0.001
log_cow	0.001	0.001	0.543	385	0.587
log_sheep	-0.001	0.001	-2.083	385	0.003

$R^2_m = 0.032$

$R^2_c = 0.761$

$\Phi = 0.06$

Table S2. Model structure and coefficients for organic to terrigenous ratio

Model: lme(fixed = organic_index ~ c_temp + c_prec + log_cow + log_sheep + lign + hilln1_n + c_tturn, random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data = alps_mod_clean, method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.483	0.155	386	3.115	0.002
c_temp	-0.010	0.019	386	-0.504	0.615
c_prec	0.000	0.000	386	-0.877	0.381
log_cow	-0.018	0.013	386	-1.419	0.157
log_sheep	0.002	0.010	386	0.184	0.854
lign	0.014	0.064	386	0.221	0.826
hilln1_n	-0.002	0.001	386	-3.219	0.001
c_tturn	0.018	0.011	386	1.654	0.099

$R^2_m = 0.085$

$R^2_c = 0.323$

$\Phi = 0$

Table S3. Model structure and coefficients for carbon

Model: lme(fixed = carbon ~ c_temp + c_prec + log_cow + log_sheep + lign + hilln1_n + c_tturn, random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data = alps_mod_clean, method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.347	0.080	386	4.365	<0.001
c_temp	0.011	0.006	386	1.807	0.072
c_prec	0.000	0.000	386	-0.210	0.833
log_cow	-0.010	0.004	386	-2.413	0.016
log_sheep	-0.010	0.003	386	-2.922	0.004
lign	0.036	0.021	386	1.678	0.094
hilln1_n	0.000	0.000	386	-1.759	0.079
c_tturn	0.004	0.004	386	1.209	0.228

$R^2_m = 0.028$

$R^2_c = 0.907$

$\Phi = 0$

Table S4. Model structure and coefficients for nitrogen

Model: lme(fixed = nitrogen ~ c_temp + c_prec + log_cow + log_sheep + lign + hilln1_n + c_tturn, random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data = alps_mod_clean, method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.265	0.079	386	3.359	<0.001
c_temp	0.003	0.007	386	0.399	0.690
c_prec	0.000	0.000	386	-1.509	0.132
log_cow	-0.010	0.005	386	-2.157	0.032
log_sheep	-0.012	0.004	386	-3.281	0.001
lign	0.022	0.023	386	0.950	0.343
hilln1_n	0.000	0.000	386	-0.415	0.678
c_tturn	0.001	0.004	386	0.198	0.843

$R^2_m = 0.021$

$R^2_c = 0.881$

$\Phi = 0$

Table S5. Model structure and coefficients for titanium

Model: lme(fixed = titanium ~ c_temp + c_prec + log_cow + log_sheep + lign + hilln1_n + c_tturn, random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data = alps_mod_clean, method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.433	0.092	386	4.729	<0.001
c_temp	-0.020	0.009	386	-2.186	0.029
c_prec	0.000	0.000	386	-0.127	0.899
log_cow	0.008	0.006	386	1.209	0.227
log_sheep	-0.002	0.005	386	-0.345	0.730
lign	0.001	0.031	386	0.024	0.981
hilln1_n	0.001	0.000	386	2.436	0.015
c_tturn	-0.007	0.005	386	-1.351	0.177

$R^2_m = 0.022$

$R^2_c = 0.771$

$\Phi = 0$

Table S6. Model structure and coefficients for C:N

Model: lme(fixed = CN ~ c_temp + c_prec + log_cow + log_sheep + lign + hilln1_n + tturn,
 random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data = alps_mod_clean,
 method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	13.738	4.008	386	3.428	<0.001
c_temp	-0.083	0.468	386	-0.178	0.859
c_prec	0.005	0.005	386	0.867	0.387
log_cow	-0.075	0.318	386	-0.235	0.814
log_sheep	0.224	0.250	386	0.897	0.370
lign	1.854	1.577	386	1.176	0.240
hilln1_n	-0.018	0.014	386	-1.312	0.190
tturn	4.087	4.041	386	1.011	0.312

$R^2_m = 0.019$

$R^2_c = 0.244$

$\Phi = 0$

Table S7. Model structure and coefficients for C:P

Model: lme(fixed = CP ~ c_temp + c_prec + log_cow + log_sheep + lign + hilln1_n + c_tturn, random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data = alps_mod_clean, method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	3.226	0.968	386	3.332	<0.001
c_temp	-0.051	0.102	386	-0.498	0.619
c_prec	0.000	0.001	386	0.023	0.982
log_cow	0.017	0.071	386	0.245	0.806
log_sheep	-0.057	0.055	386	-1.038	0.300
lign	0.132	0.353	386	0.374	0.709
hilln1_n	-0.010	0.003	386	-3.258	0.001
c_tturn	0.104	0.059	386	1.760	0.079

$R^2_m = 0.033$

$R^2_c = 0.694$

$\Phi = 0$

Table S8. Model structure and coefficients for N:P

Model: lme(fixed = NP ~ c_temp + c_prec + log_cow + log_sheep + lign + hilln1_n + c_tturn, random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data = alps_mod_clean, method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	3.478	1.016	386	3.424	<0.001
c_temp	-0.042	0.109	386	-0.389	0.698
c_prec	-0.001	0.001	386	-0.528	0.598
log_cow	0.048	0.075	386	0.637	0.525
log_sheep	-0.075	0.059	386	-1.276	0.203
lign	0.082	0.376	386	0.219	0.827
hilln1_n	-0.008	0.003	386	-2.608	0.009
c_tturn	0.078	0.063	386	1.239	0.216

$R^2_m = 0.023$

$R^2_c = 0.664$

$\Phi = 0$

Table S9. Model structure and coefficients for elemental turnover

Model: lme(fixed = eturn ~ c_temp + c_prec + log_cow + log_sheep + lign + hilln1_n + c_tturn, random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data = alps_mod_clean, method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.115	0.038	386	3.009	0.003
c_temp	-0.022	0.005	386	-4.364	<0.001
c_prec	0.000	0.000	386	0.295	0.768
log_cow	-0.005	0.003	386	-1.378	0.169
log_sheep	0.007	0.003	386	2.755	0.006
lign	-0.006	0.016	386	-0.365	0.716
hilln1_n	0.000	0.000	386	-1.386	0.167
c_tturn	0.013	0.003	386	4.470	<0.001

$R^2_m = 0.118$

$R^2_c = 0.176$

Phi = 0

Table S10. Model structure and coefficients for woodiness

Model: lme(fixed = lign ~ c_temp + c_prec + log_cow + log_sheep + organic_index +
 c_eturn, random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data =
 alps_mod_clean, method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	-0.019	0.089	387	-0.214	0.831
c_temp	-0.003	0.016	387	-0.169	0.866
c_prec	0.000	0.000	387	-1.937	0.054
log_cow	-0.014	0.010	387	-1.415	0.158
log_sheep	-0.015	0.008	387	-1.787	0.075
organic_index	0.064	0.041	387	1.538	0.125
c_eturn	0.003	0.009	387	0.314	0.753

$R^2_m = 0.035$

$R^2_c = 0.379$

$\Phi = 0$

Table S11. Model structure and coefficients for tree richness (Hill 0)

Model: lme(fixed = hilln0_tree ~ c_temp + c_prec + log_cow + log_sheep + organic_index + c_eturn, random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data = alps_mod_clean, method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	9.886	1.180	387	8.376	<0.001
c_temp	-0.969	0.219	387	-4.426	<0.001
c_prec	0.004	0.002	387	1.646	0.101
log_cow	0.388	0.131	387	2.963	0.003
log_sheep	0.026	0.112	387	0.235	0.814
organic_index	-0.654	0.563	387	-1.162	0.246
c_eturn	-0.063	0.129	387	-0.490	0.625

$R^2_m = 0.078$

$R^2_c = 0.349$

$\Phi = 0$

Table S12. Model structure and coefficients for shrub richness (Hill 0)

Model: lme(fixed = hilln0_shrub ~ c_temp + c_prec + log_cow + log_sheep + organic_index + c_eturn, random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data = alps_mod_clean, method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	23.237	1.675	387	13.872	<0.001
c_temp	-0.405	0.257	387	-1.574	0.116
c_prec	0.006	0.003	387	2.206	0.028
log_cow	0.929	0.156	387	5.962	<0.001
log_sheep	0.438	0.133	387	3.300	0.001
organic_index	-0.381	0.667	387	-0.571	0.568
c_eturn	-0.124	0.151	387	-0.819	0.413

$R^2_m = 0.124$

$R^2_c = 0.660$

Phi = 0

Table S13. Model structure and coefficients for forb richness (Hill 0)

Model: lme(fixed = hilln0_forb ~ c_temp + c_prec + log_cow + log_sheep + organic_index + c_eturn, random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data = alps_mod_clean, method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	159.834	7.886	387	20.268	<0.001
c_temp	-1.635	1.367	387	-1.196	0.232
c_prec	0.038	0.015	387	2.529	0.012
log_cow	8.574	0.823	387	10.423	<0.001
log_sheep	4.041	0.701	387	5.761	<0.001
organic_index	-12.362	3.529	387	-3.503	<0.001
c_eturn	-0.943	0.802	387	-1.175	0.241

R²m = 0.391

R²c = 0.654

Phi = 0

Table S14. Model structure and coefficients for graminoid richness (Hill 0)

Model: lme(fixed = hilln0_gram ~ c_temp + c_prec + log_cow + log_sheep + organic_index + c_eturn, random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data = alps_mod_clean, method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	23.479	1.351	387	17.377	<0.001
c_temp	-1.403	0.267	387	-5.254	<0.001
c_prec	0.007	0.003	387	2.216	0.027
log_cow	1.309	0.157	387	8.319	<0.001
log_sheep	0.557	0.135	387	4.128	<0.001
organic_index	-2.951	0.680	387	-4.338	<0.001
c_eturn	-0.196	0.157	387	-1.246	0.213

$R^2_m = 0.406$

$R^2_c = 0.507$

$\Phi = 0$

Table S15. Model structure and coefficients for taxa turnover

Model: lme(fixed = tturn ~ c_temp + c_prec + log_cow + log_sheep + organic_index + c_eturn, random = ~ 1 | lake, correlation = corAR1(form = ~ age | lake), data = alps_mod_clean, method = "REML")

Term	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.307	0.027	387	11.489	<0.001
c_temp	-0.004	0.006	387	-0.718	0.473
c_prec	0.000	0.000	387	2.468	0.014
log_cow	-0.003	0.003	387	-0.839	0.402
log_sheep	0.006	0.003	387	1.971	0.049
organic_index	0.019	0.014	387	1.326	0.186
c_eturn	0.013	0.003	387	3.713	<0.001

$R^2_m = 0.071$

$R^2_c = 0.123$

$\Phi = 0$

Table S16. Model structure and coefficients for the structural equation model of alpine diversity (Hill N1) under climate change, livestock introduction and shifting vegetation and biogeochemical dynamics. Here we present a table for each period.

Model: psem(lme(hilln1_n ~ c_eturn + c_tturn + organic_index + lign + c_temp + c_prec + log_sheep + log_cow, random = ~1 | lake, correlation = corAR1(form = ~ age_jitter | lake), data = alps_mod_clean),

lme(c_tturn ~ n_window + organic_index + lign + c_temp + c_prec + log_sheep + log_cow, random = ~1 | lake, correlation = corAR1(form = ~ age_jitter | lake), data = alps_mod_clean),

lme(c_eturn ~ n_window + organic_index + c_temp + lign + c_prec + log_sheep + log_cow, random = ~1 | lake, correlation = corAR1(form = ~ age_jitter | lake), data = alps_mod_clean),

lme(organic_index ~ c_temp + c_prec + lign + log_sheep + log_cow, random = ~1 | lake, correlation = corAR1(form = ~ age_jitter | lake), data = alps_mod_clean),

lme(lign ~ c_temp + c_prec + log_sheep + log_cow, random = ~1 | lake, correlation = corAR1(form = ~ age_jitter | lake), data = alps_mod_clean))

ALL PERIOD

Response	Predictor	Estimate	Std.Error	df	P.Value	Std.Estimate
hilln1_n	c_eturn	-0.86	1.00	386	0.39	-0.03
hilln1_n	organic_index	-13.89	4.38	386	0.00	-0.11
hilln1_n	lign	-41.86	5.27	386	0.00	-0.31
hilln1_n	c_temp	-4.68	1.70	386	0.01	-0.09
hilln1_n	c_prec	0.04	0.02	386	0.02	0.07
hilln1_n	log_sheep	4.25	0.87	386	0.00	0.20
hilln1_n	log_cow	10.65	1.02	386	0.00	0.44
c_eturn	n_window	0.09	0.02	386	0.00	0.24
c_eturn	organic_index	0.31	0.19	386	0.11	0.08
c_eturn	c_temp	-0.26	0.09	386	0.00	-0.15
c_eturn	lign	0.15	0.21	386	0.48	0.04
c_eturn	c_prec	0.00	0.00	386	0.55	0.03
c_eturn	log_sheep	0.04	0.04	386	0.26	0.07
c_eturn	log_cow	-0.11	0.04	386	0.01	-0.14
organic_index	c_temp	0.00	0.02	388	0.84	-0.01
organic_index	c_prec	0.00	0.00	388	0.29	-0.05
organic_index	lign	0.09	0.06	388	0.12	0.09
organic_index	log_sheep	0.00	0.01	388	0.66	-0.03
organic_index	log_cow	-0.04	0.01	388	0.00	-0.21
lign	c_temp	0.00	0.02	389	0.79	-0.01
lign	c_prec	0.00	0.00	389	0.04	-0.08
lign	log_sheep	-0.01	0.01	389	0.07	-0.10
lign	log_cow	-0.02	0.01	389	0.07	-0.09

$R^2_m = 0.55$

$R^2_c = 0.66$

MESOLITHIC & NEOLITHIC

Response	Predictor	Estimate	Std.Error	df	P.Value	Std.Estimate
hilln1_n	c_eturn	-0.42	1.70	91	0.81	-0.02
hilln1_n	organic_index	0.83	6.68	91	0.90	0.01
hilln1_n	lign	-36.98	6.78	91	0.00	-0.48
hilln1_n	c_temp	-9.05	2.55	91	0.00	-0.24
hilln1_n	c_prec	0.05	0.02	91	0.02	0.14
hilln1_n	log_sheep	-0.05	3.03	91	0.99	0.00
hilln1_n	log_cow	18.59	15.12	91	0.22	0.07
c_eturn	n_window	-0.12	0.07	91	0.07	-0.21
c_eturn	organic_index	0.41	0.33	91	0.22	0.13
c_eturn	c_temp	0.18	0.16	91	0.25	0.13
c_eturn	lign	-0.46	0.29	91	0.11	-0.17
c_eturn	c_prec	0.00	0.00	91	0.17	-0.13
c_eturn	log_sheep	0.18	0.18	91	0.33	0.10
c_eturn	log_cow	-0.74	0.89	91	0.41	-0.08
organic_index	c_temp	0.05	0.04	93	0.21	0.11
organic_index	c_prec	0.00	0.00	93	0.29	-0.08
organic_index	lign	-0.11	0.10	93	0.28	-0.12
organic_index	log_sheep	-0.05	0.04	93	0.30	-0.08
organic_index	log_cow	0.00	0.22	93	0.98	0.00
lign	c_temp	0.09	0.03	94	0.02	0.17
lign	c_prec	0.00	0.00	94	0.00	-0.20
lign	log_sheep	-0.01	0.04	94	0.86	-0.01
lign	log_cow	-0.19	0.22	94	0.37	-0.06

$R^2_m = 0.37$

$R^2_c = 0.69$

BRONZE AGE

Response	Predictor	Estimate	Std.Error	df	P.Value	Std.Estimate
hilln1_n	c_eturn	-1.76	2.17	84	0.42	-0.05
hilln1_n	organic_index	-9.75	9.34	84	0.30	-0.07
hilln1_n	lign	-29.88	10.94	84	0.01	-0.18
hilln1_n	c_temp	-0.75	5.75	84	0.90	-0.01
hilln1_n	c_prec	0.01	0.06	84	0.90	0.01
hilln1_n	log_sheep	7.73	1.98	84	0.00	0.33
hilln1_n	log_cow	7.41	2.53	84	0.00	0.24
c_eturn	n_window	0.14	0.05	84	0.01	0.24
c_eturn	organic_index	-0.34	0.39	84	0.38	-0.09
c_eturn	c_temp	-0.46	0.23	84	0.04	-0.20
c_eturn	lign	-0.35	0.46	84	0.45	-0.08
c_eturn	c_prec	0.00	0.00	84	0.28	0.11
c_eturn	log_sheep	-0.13	0.08	84	0.11	-0.21
c_eturn	log_cow	-0.14	0.10	84	0.16	-0.17
organic_index	c_temp	0.02	0.06	86	0.74	0.03
organic_index	c_prec	0.00	0.00	86	0.84	-0.02
organic_index	lign	0.12	0.12	86	0.34	0.10
organic_index	log_sheep	-0.05	0.02	86	0.03	-0.29
organic_index	log_cow	-0.01	0.03	86	0.77	-0.04
lign	c_temp	-0.05	0.05	87	0.34	-0.10
lign	c_prec	0.00	0.00	87	0.11	0.15
lign	log_sheep	-0.04	0.02	87	0.03	-0.28
lign	log_cow	-0.01	0.02	87	0.63	-0.06

$R^2_m = 0.45$

$R^2_c = 0.69$

IRON & ROMAN PERIOD

Response	Predictor	Estimate	Std.Error	DF	P.Value	Std.Estimate
hilln1_n	c_eturn	1.28	2.06	61	0.54	0.05
hilln1_n	organic_index	-23.44	10.48	61	0.03	-0.19
hilln1_n	lign	-46.33	12.34	61	0.00	-0.32
hilln1_n	c_temp	-10.44	8.37	61	0.22	-0.12
hilln1_n	c_prec	0.03	0.05	61	0.46	0.06
hilln1_n	log_sheep	-0.31	2.11	61	0.88	-0.02
hilln1_n	log_cow	13.78	2.99	61	0.00	0.57
c_eturn	n_window	0.04	0.09	61	0.68	0.05
c_eturn	organic_index	0.89	0.54	61	0.10	0.19
c_eturn	c_temp	0.04	0.41	61	0.92	0.01
c_eturn	lign	-0.65	0.67	61	0.33	-0.12
c_eturn	c_prec	0.00	0.00	61	0.22	0.16
c_eturn	log_sheep	0.07	0.12	61	0.57	0.09
c_eturn	log_cow	-0.20	0.15	61	0.20	-0.21
organic_index	c_temp	-0.07	0.10	63	0.48	-0.10
organic_index	c_prec	0.00	0.00	63	0.68	0.04
organic_index	lign	0.20	0.14	63	0.14	0.17
organic_index	log_sheep	-0.01	0.02	63	0.80	-0.04
organic_index	log_cow	-0.01	0.03	63	0.86	-0.03
lign	c_temp	-0.08	0.08	64	0.31	-0.13
lign	c_prec	0.00	0.00	64	1.00	0.00
lign	log_sheep	-0.02	0.02	64	0.29	-0.17
lign	log_cow	-0.02	0.03	64	0.51	-0.11

$R^2_m = 0.48$

$R^2_c = 0.61$

MIDDLE AGES

Response	Predictor	Estimate	Std.Error	df	P.Value	Std.Estimate
hilln1_n	c_eturn	-0.44	2.74	63	0.87	-0.01
hilln1_n	organic_index	-15.65	10.72	63	0.15	-0.12
hilln1_n	lign	-34.54	15.14	63	0.03	-0.23
hilln1_n	c_temp	3.29	7.05	63	0.64	0.04
hilln1_n	c_prec	0.03	0.05	63	0.51	0.04
hilln1_n	log_sheep	7.60	1.71	63	0.00	0.39
hilln1_n	log_cow	6.66	1.90	63	0.00	0.32
c_eturn	n_window	0.08	0.02	63	0.00	0.31
c_eturn	organic_index	0.26	0.39	63	0.52	0.07
c_eturn	c_temp	-0.57	0.26	63	0.03	-0.25
c_eturn	lign	1.10	0.51	63	0.04	0.27
c_eturn	c_prec	0.00	0.00	63	0.05	-0.19
c_eturn	log_sheep	0.09	0.07	63	0.15	0.18
c_eturn	log_cow	-0.12	0.07	63	0.07	-0.22
organic_index	c_temp	0.12	0.07	65	0.09	0.19
organic_index	c_prec	0.00	0.00	65	0.77	0.03
organic_index	lign	0.15	0.16	65	0.35	0.13
organic_index	log_sheep	0.03	0.02	65	0.09	0.20
organic_index	log_cow	-0.06	0.02	65	0.00	-0.39
lign	c_temp	-0.06	0.05	66	0.26	-0.10
lign	c_prec	0.00	0.00	66	0.20	0.10
lign	log_sheep	-0.01	0.01	66	0.40	-0.08
lign	log_cow	-0.01	0.01	66	0.47	-0.07

$R^2_m = 0.54$

$R^2_c = 0.76$

MODERN ERA

Response	Predictor	Estimate	Std.Error	df	P.Value	Std.Estimate
hilln1_n	c_eturn	2.45	6.70	18	0.72	0.07
hilln1_n	organic_index	-13.51	18.57	18	0.48	-0.13
hilln1_n	lign	-6.26	22.21	18	0.78	-0.06
hilln1_n	c_temp	-1.61	16.42	18	0.92	-0.02
hilln1_n	c_prec	0.05	0.10	18	0.63	0.09
hilln1_n	log_sheep	2.00	4.74	18	0.68	0.09
hilln1_n	log_cow	9.86	3.15	18	0.01	0.57
c_eturn	n_window	0.08	0.05	18	0.13	0.27
c_eturn	organic_index	-0.46	0.53	18	0.40	-0.15
c_eturn	c_temp	0.76	0.44	18	0.10	0.36
c_eturn	lign	0.80	0.54	18	0.15	0.26
c_eturn	c_prec	0.01	0.00	18	0.00	0.56
c_eturn	log_sheep	0.02	0.14	18	0.89	0.03
c_eturn	log_cow	-0.08	0.08	18	0.33	-0.16
organic_index	c_temp	-0.03	0.16	20	0.85	-0.04
organic_index	c_prec	0.00	0.00	20	0.60	-0.10
organic_index	lign	0.10	0.21	20	0.62	0.10
organic_index	log_sheep	0.05	0.05	20	0.32	0.23
organic_index	log_cow	-0.05	0.03	20	0.11	-0.31
lign	c_temp	-0.08	0.15	21	0.62	-0.11
lign	c_prec	0.00	0.00	21	0.92	-0.01
lign	log_sheep	-0.04	0.03	21	0.25	-0.20
lign	log_cow	-0.02	0.03	21	0.38	-0.15

$R^2_m = 0.35$

$R^2_c = 0.46$

References

- Abaye, A. O., Allen, V. G., & Fontenot, J. P. (1997). Grazing Sheep and Cattle Together or Separately: Effect on Soils and Plants. *Agronomy Journal*, 89(3), 380-386.
<https://doi.org/10.2134/agronj1997.00021962008900030003x>
- Abdalla, M., Hastings, A., Chadwick, D. R., Jones, D. L., Evans, C. D., Jones, M. B., Rees, R. M., & Smith, P. (2018). Critical review of the impacts of grazing intensity on soil organic carbon storage and other soil quality indicators in extensively managed grasslands. *Agriculture, Ecosystems & Environment*, 253, 62-81. <https://doi.org/10.1016/j.agee.2017.10.023>
- Adrian, R., O'Reilly, C. M., Zagarese, H., Baines, S. B., Hessen, D. O., Keller, W., Livingstone, D. M., Sommaruga, R., Straile, D., Van Donk, E., Weyhenmeyer, G. A., & Winder, M. (2009). Lakes as sentinels of climate change. *Limnology and Oceanography*, 54(6part2), 2283-2297.
https://doi.org/10.4319/lo.2009.54.6_part_2.2283
- Alley, R. B. (2004). *NOAA/WDS Paleoclimatology – GISP2 – Temperature reconstruction and accumulation data [Data set]*. NOAA National Centers for Environmental Information.
<https://doi.org/10.25921/36sb-3355>.
- Alsos, I. G., Boussange, V., Rijal, D. P., Beaulieu, M., Brown, A. G., Herzs Schuh, U., Svenning, J.-C., & Pellissier, L. (2024). Using ancient sedimentary DNA to forecast ecosystem trajectories under climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 379(1902), 20230017. <https://doi.org/10.1098/rstb.2023.0017>
- Alsos, I. G., Lammers, Y., Kjellman, S. E., Merkel, M. K. F., Bender, E. M., Rouillard, A., Erlendsson, E., Guðmundsdóttir, E. R., Benediktsson, Í. Ö., Farnsworth, W. R., Brynjólfsson, S., Gísladóttir, G., Eddudóttir, S. D., & Schomacker, A. (2021). Ancient sedimentary DNA shows rapid post-glacial colonisation of Iceland followed by relatively stable vegetation until the Norse settlement (Landnám) AD 870. *Quaternary Science Reviews*, 259, 106903.
<https://doi.org/10.1016/j.quascirev.2021.106903>

- Ammann, B. (1986). Litho- and palynostratigraphy at Lobsigensee: Evidences for trophic changes during the Holocene: Studies in the Late-Quaternary of Lobsigensee No 13. *Hydrobiologia*, 143(1), 301-307. <https://doi.org/10.1007/BF00026674>
- Arlov, T. B. (1989). *A short history of Svalbard*. Norsk Polarinstitut.
- Arosio, T., Leuenberger, M., Nicolussi, K., Esper, J., Krusic, P. J., Bebhuk, T., Tegel, W., Hafner, A., Kirdyanov, A., Schlüchter, C., Reinig, F., Muschitiello, F., & Büntgen, U. (2025). Tree-ring stable isotopes from the European Alps reveal long-term summer drying over the Holocene. *Science Advances*, 11(14), eadr4161. <https://doi.org/10.1126/sciadv.adr4161>
- Astolfi, M. L., Massimi, L., Rapa, M., Plà, R. R., Jasan, R. C., Tudino, M. B., Canepari, S., & Conti, M. E. (2023). A multi-analytical approach to studying the chemical composition of typical carbon sink samples. *Scientific Reports*, 13(1), 7971. <https://doi.org/10.1038/s41598-023-35180-x>
- Bajard, M., Poulénard, J., Sabatier, P., Develle, A.-L., Giguët-Covex, C., Jacob, J., Crouzet, C., David, F., Pignol, C., & Arnaud, F. (2017). Progressive and regressive soil evolution phases in the Anthropocene. *CATENA*, 150, 39-52. <https://doi.org/10.1016/j.catena.2016.11.001>
- Balesdent, J., Basile-Doelsch, I., Chadoeuf, J., Cornu, S., Derrien, D., Fekiacova, Z., & Hatté, C. (2018). Atmosphere–soil carbon transfer as a function of soil depth. *Nature*, 559(7715), 599-602. <https://doi.org/10.1038/s41586-018-0328-3>
- Ballantyne, A. P., Brahney, J., Fernandez, D., Lawrence, C. L., Saros, J., & Neff, J. C. (2011). Biogeochemical response of alpine lakes to a recent increase in dust deposition in the Southwestern, US. *Biogeosciences*, 8(9), 2689-2706. <https://doi.org/10.5194/bg-8-2689-2011>
- Ballesteros-Cánovas, J. A., Stoffel, M., St George, S., & Hirschboeck, K. (2015). A review of flood records from tree rings. *Progress in Physical Geography: Earth and Environment*, 39(6), 794-816. <https://doi.org/10.1177/0309133315608758>
- Bao, K., Zhang, Y., Zaccone, C., & Meadows, M. E. (2021). Human impact on C/N/P accumulation in lake sediments from northeast China during the last 150 years. *Environmental Pollution*, 271, 116345. <https://doi.org/10.1016/j.envpol.2020.116345>
- Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., & Ferrer, E. A. (2011). Has the

- Earth's sixth mass extinction already arrived? *Nature*, 471(7336), 51-57.
<https://doi.org/10.1038/nature09678>
- Baud, A., Jenny, J.-P., Francus, P., & Gregory-Eaves, I. (2021). Global acceleration of lake sediment accumulation rates associated with recent human population growth and land-use changes. *Journal of Paleolimnology*, 66(4), 453-467. <https://doi.org/10.1007/s10933-021-00217-6>
- Benavente, M. (2024). *The biogeochemical imprint of the Azores Archipelago lacustrine sedimentary infill. A linkage between the climatic effects of the North Atlantic atmospheric circulation and the tectono-volcanic landscape of the triple junction during the late Holocene* [(Doctoral dissertation).]. Universitat de Barcelona.
- Benoit, G., & Rozan, T. F. (2001). 210Pb and 137Cs dating methods in lakes: A retrospective study. *Journal of Paleolimnology*, 25(4), 455-465. <https://doi.org/10.1023/A:1011179318352>
- Bertrand, S., Tjallingii, R., Kylander, M. E., Wilhelm, B., Roberts, S. J., Arnaud, F., Brown, E., & Bindler, R. (2024). Inorganic geochemistry of lake sediments: A review of analytical techniques and guidelines for data interpretation. *Earth-Science Reviews*, 249, 104639. <https://doi.org/10.1016/j.earscirev.2023.104639>
- Bethell, P. H., Goad, L. J., Evershed, R. P., & Ottaway, J. (1994). The Study of Molecular Markers of Human Activity: The Use of Coprostanol in the Soil as an Indicator of Human Faecal Material. *Journal of Archaeological Science*, 21(5), 619-632. <https://doi.org/10.1006/jasc.1994.1061>
- Bidwell, A. L., Callahan, S. T., Tobin, P. C., Nelson, B. K., & DeLuca, T. H. (2019). Quantifying the elemental composition of mosses in western Washington USA. *Science of The Total Environment*, 693, 133404. <https://doi.org/10.1016/j.scitotenv.2019.07.210>
- Binda, G., Di Iorio, A., & Monticelli, D. (2021). The what, how, why, and when of dendrochemistry: (Paleo)environmental information from the chemical analysis of tree rings. *Science of The Total Environment*, 758, 143672. <https://doi.org/10.1016/j.scitotenv.2020.143672>
- Bintliff, J., & Degryse, P. (2022). A review of soil geochemistry in archaeology. *Journal of Archaeological Science: Reports*, 43, 103419. <https://doi.org/10.1016/j.jasrep.2022.103419>
- Birks, H. J. B. (2008). Paleoecology. En *Encyclopedia of Ecology* (pp. 2623-2634). Elsevier. <https://doi.org/10.1016/B978-008045405-4.00525-5>

- Birks, H. J. B. (2019). Contributions of Quaternary botany to modern ecology and biogeography. *Plant Ecology & Diversity*, 12(3), 189-385. <https://doi.org/10.1080/17550874.2019.1646831>
- Bishop, T. (2017, enero 25). *Itrax data manipulation in R*. Tom Bishop: Lab Notes.
<https://thomasbishop.uk/itrax-data-manipulation-in-r/>
- Blaus, A., Reitalu, T., Amon, L., Vassiljev, J., Alliksaar, T., & Veski, S. (2020). From bog to fen: Palaeoecological reconstruction of the development of a calcareous spring fen on Saaremaa, Estonia. *Vegetation History and Archaeobotany*, 29(3), 373-391.
<https://doi.org/10.1007/s00334-019-00748-z>
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.-W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., & Vries, W. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications*, 20(1), 30-59.
<https://doi.org/10.1890/08-1140.1>
- Boës, X., Rydberg, J., Martinez-Cortizas, A., Bindler, R., & Renberg, I. (2011). Evaluation of conservative lithogenic elements (Ti, Zr, Al, and Rb) to study anthropogenic element enrichments in lake sediments. *Journal of Paleolimnology*, 46(1), 75-87.
<https://doi.org/10.1007/s10933-011-9515-z>
- Booth, R. K., & Jackson, S. T. (2003). A high-resolution record of late-Holocene moisture variability from a Michigan raised bog, USA. *The Holocene*, 13(6), 863-876.
<https://doi.org/10.1191/0959683603hl669rp>
- Borderieux, J., Gégout, J.-C., & Serra-Diaz, J. M. (2024). Extinction drives recent thermophilization but does not trigger homogenization in forest understorey. *Nature Ecology & Evolution*, 8(4), 695-704. <https://doi.org/10.1038/s41559-024-02362-3>
- Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., Adler, P. B., Alberti, J., Anderson, T. M., Bakker, J. D., Biederman, L., Blumenthal, D., Brown, C. S., Brudvig, L. A., Buckley, Y. M., Cadotte, M., Chu, C., Cleland, E. E., Crawley, M. J., ... Yang, L. H. (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, 508(7497), 517-520. <https://doi.org/10.1038/nature13144>

- Bornmann, L. (2025, marzo 18). Metrics sonification as a new way to convey bibliometric data. *Leiden Madtrics*. <https://doi.org/10.59350/h057p-evj38>
- Borrelli, P., Robinson, D. A., Fleischer, L. R., Lugato, E., Ballabio, C., Alewell, C., Meusburger, K., Modugno, S., Schütt, B., Ferro, V., Bagarello, V., Oost, K. V., Montanarella, L., & Panagos, P. (2017). An assessment of the global impact of 21st century land use change on soil erosion. *Nature Communications*, 8(1), 2013. <https://doi.org/10.1038/s41467-017-02142-7>
- Bottjer, D. J. (2016). *Paleoecology: Past, present, and future*. John Wiley & Sons Ltd.
- Boyle, J., Chiverrell, R., Plater, A., Thrasher, I., Bradshaw, E., Birks, H., & Birks, J. (2013). Soil mineral depletion drives early Holocene lake acidification. *Geology*, 41(4), 415-418. <https://doi.org/10.1130/G33907.1>
- Boyle, J. F. (1991). Acidity and organic carbon in lake water: Variability and estimation of means. *Journal of Paleolimnology*, 6(2), 95-101. <https://doi.org/10.1007/BF00153733>
- Boyle, J. F. (2001). Inorganic geochemical methods in palaeolimnology. En W. M. Last & J. P. Smol (Eds.), *Tracking environmental change using lake sediments: Volume 2: Physical and geochemical methods* (pp. 83-141). Springer. https://doi.org/10.1007/0-306-47670-3_5
- Boyle, J. F. (2002). Inorganic Geochemical Methods in Palaeolimnology. En W. M. Last & J. P. Smol (Eds.), *Tracking Environmental Change Using Lake Sediments* (Vol. 2, pp. 83-141). Kluwer Academic Publishers. https://doi.org/10.1007/0-306-47670-3_5
- Boyle, J. F. (2007). Loss of apatite caused irreversible early-Holocene lake acidification. *The Holocene*, 17(4), 543-547. <https://doi.org/10.1177/0959683607077046>
- Boyle, J., Moyle, M., Søndergaard, M., & Jeppesen, E. (2023). Using sediment geochemical records to infer past lake-water total phosphorus concentrations at a site with high internal P loading, Lake Søbygaard, Denmark. *Journal of Paleolimnology*, 69(4), 345-357. <https://doi.org/10.1007/s10933-022-00276-3>
- Brice, M., Cazelles, K., Legendre, P., & Fortin, M. (2019). Disturbances amplify tree community responses to climate change in the temperate–boreal ecotone. *Global Ecology and Biogeography*, 28(11), 1668-1681. <https://doi.org/10.1111/geb.12971>
- Brodie, C. R., Leng, M. J., Casford, J. S. L., Kendrick, C. P., Lloyd, J. M., Yongqiang, Z., & Bird, M. I. (2011). Evidence for bias in C and N concentrations and $\delta^{13}\text{C}$ composition of terrestrial and

- aquatic organic materials due to pre-analysis acid preparation methods. *Chemical Geology*, 282(3-4), 67-83. <https://doi.org/10.1016/j.chemgeo.2011.01.007>
- Brown, A. G., Lucas, M., Alsos, I. G., Fromm, B., & Hudson, S. (2025). The sedaDNA revolution and archaeology: Progress, challenges, and a research agenda. *Journal of Archaeological Science*, 174, 106132. <https://doi.org/10.1016/j.jas.2024.106132>
- Bruna, P. (2024). *Embolismo por soleá (seguiriy y muerte)*. Universidad de Granada.
- Bullard, J. E., Baddock, M., Bradwell, T., Crusius, J., Darlington, E., Gaiero, D., Gassó, S., Gisladottir, G., Hodgkins, R., McCulloch, R., McKenna-Neuman, C., Mockford, T., Stewart, H., & Thorsteinsson, T. (2016). High-latitude dust in the Earth system. *Reviews of Geophysics*, 54(2), 447-485. <https://doi.org/10.1002/2016RG000518>
- Büntgen, U., Urban, O., Krusic, P. J., Rybníček, M., Kolář, T., Kyncl, T., Ač, A., Koňasová, E., Čáslavský, J., Esper, J., Wagner, S., Saurer, M., Tegel, W., Dobrovolný, P., Cherubini, P., Reinig, F., & Trnka, M. (2021). Recent European drought extremes beyond Common Era background variability. *Nature Geoscience*, 14(4), 190-196. <https://doi.org/10.1038/s41561-021-00698-0>
- Camp, E. F., Nitschke, M. R., Clases, D., Gonzalez De Vega, R., Reich, H. G., Goyen, S., & Suggett, D. J. (2022). Micronutrient content drives elementome variability amongst the Symbiodiniaceae. *BMC Plant Biology*, 22(1), 184. <https://doi.org/10.1186/s12870-022-03512-0>
- Campbell, M., McDonough, L., Treble, P. C., Baker, A., Kosarac, N., Coleborn, K., Wynn, P. M., & Schmitt, A. K. (2023). A Review of Speleothems as Archives for Paleofire Proxies, With Australian Case Studies. *Reviews of Geophysics*, 61(2), e2022RG000790. <https://doi.org/10.1029/2022RG000790>
- Canty, A., & Ripley, B. (1999). *boot: Bootstrap Functions* (p. 1.3-32) [Dataset]. <https://doi.org/10.32614/CRAN.package.boot>
- Cardinale, B. J., Wright, J. P., Cadotte, M. W., Carroll, I. T., Hector, A., Srivastava, D. S., Loreau, M., & Weis, J. J. (2007). Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences*, 104(46), 18123-18128. <https://doi.org/10.1073/pnas.0709069104>

- Castilla-Beltrán, A., De Nascimento, L., Fernández-Palacios, J.-M., Whittaker, R. J., Willis, K. J., Edwards, M., & Nogué, S. (2021). Anthropogenic transitions from forested to human-dominated landscapes in southern Macaronesia. *Proceedings of the National Academy of Sciences*, 118(40), e2022215118. <https://doi.org/10.1073/pnas.2022215118>
- Castilla-Beltrán, A., Hooghiemstra, H., Hoogland, M. L. P., Pagán-Jiménez, J., Van Geel, B., Field, M. H., Prins, M., Donders, T., Herrera Malatesta, E., Ulloa Hung, J., McMichael, C. H., Gosling, W. D., & Hofman, C. L. (2018). Columbus' footprint in Hispaniola: A paleoenvironmental record of indigenous and colonial impacts on the landscape of the central Cibao Valley, northern Dominican Republic. *Anthropocene*, 22, 66-80. <https://doi.org/10.1016/j.ancene.2018.05.003>
- Castilla-Beltrán, Á., Lima, R. F., Benítez Bosco, L., Castillo Armas, R. D., Strandberg, N., Stévar, T., Nascimento, L., Fernández-Palacios, J. M., & Nogué, S. (2023). 14,000 years of climatic and anthropogenic change in the Afromontane forest of São Tomé Island, Gulf of Guinea. *Quaternary Science Reviews*, 322, 108381. <https://doi.org/10.1016/j.quascirev.2023.108381>
- Castilla-Beltrán, Á., Monteath, A., Jensen, B. J. L., Nascimento, L., Fernández-Palacios, J. M., Strandberg, N., Edwards, M., & Nogué, S. (2023). Taming Fogo Island: Late-Holocene volcanism, natural fires and land use as recorded in a scoria-cone sediment sequence in Cabo Verde. *The Holocene*, 33(4), 371-381. <https://doi.org/10.1177/09596836221145442>
- Castilla-Beltrán, A., Nascimento, L., & Fernández-Palacios, J. M. (2021). Anthropogenic transitions from forested to human-dominated landscapes in southern Macaronesia. *Proceedings of the National Academy of Sciences*, 118(11), 1-8. <https://doi.org/10.1073/pnas.2022215118>
- Castilla-Beltrán, A., Nascimento, L., Fernández-Palacios, J. M., Fonville, T., Whittaker, R. J., Edwards, M., & Nogué, S. (2019). Late Holocene environmental change and the anthropization of the highlands of Santo Antão Island, Cabo Verde. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 524, 101-117.
- Catalan, J., Monteoliva, A. P., Vega, J. C., Domínguez, A., Negro, A. I., Alonso, R., Valero Garcés, B., Batalla, M., García-Gómez, H., Leira, M., Nuño, C., Pahissa, J., Peg, M., Pla-Rabés, S., Roblas, N., Vargas, J. L., & Toro, M. (2024). Reduced precipitation can induce ecosystem

- regime shifts in lakes by increasing internal nutrient recycling. *Scientific Reports*, 14, 12408.
<https://doi.org/10.1038/s41598-024-62810-9>
- Catalan, J., Pla-Rabés, S., & Wolfe, A. P. (2013). Global change revealed by palaeolimnological records from remote lakes: A review. *Journal of Paleolimnology*, 49, 513-535.
<https://doi.org/10.1007/s10933-013-9681-2>
- Cernusak, L. A., & Ubierna, N. (2022). Carbon Isotope Effects in Relation to CO₂ Assimilation by Tree Canopies. En R. T. W. Siegwolf, J. R. Brooks, J. Roden, & M. Saurer (Eds.), *Stable Isotopes in Tree Rings* (Vol. 8, pp. 291-310). Springer International Publishing.
https://doi.org/10.1007/978-3-030-92698-4_9
- Chakraborty, A. (2024). Rethinking the Anthropocene: Not a time-transgressive event but a sudden rupture on the geologic time scale. *Anthropocene*, 48, 100454.
<https://doi.org/10.1016/j.ancene.2024.100454>
- Chen, M., & Graedel, T. E. (2016). A half-century of global phosphorus flows, stocks, production, consumption, recycling, and environmental impacts. *Global Environmental Change*, 36, 139-152. <https://doi.org/10.1016/j.gloenvcha.2015.12.005>
- Chen, Q., Blowes, S. A., Harpole, W. S., Ladouceur, E., Borer, E. T., MacDougall, A., Martina, J. P., Bakker, J. D., Tognetti, P. M., Seabloom, E. W., Daleo, P., Power, S., Roscher, C., Adler, P. B., Donohue, I., Wheeler, G., Stevens, C., Veen, G. F. C., Risch, A. C., ... Chase, J. M. (2025). Local nutrient addition drives plant diversity losses but not biotic homogenization in global grasslands. *Nature Communications*, 16(1), 4903.
<https://doi.org/10.1038/s41467-025-59166-7>
- Chen, S., Yao, Q., Chen, X., Liu, J., Chen, D., Ou, T., Liu, J., Dong, Z., Zheng, Z., & Fang, K. (2021). Tree-ring recorded variations of 10 heavy metal elements over the past 168 years in southeastern China. *Elementa: Science of the Anthropocene*, 9(1), 00075.
<https://doi.org/10.1525/elementa.2020.20.00075>
- Chichagova, O. A., & Cherkinsky, A. E. (1993). Problems in Radiocarbon Dating of Soils. *Radiocarbon*, 35(3), 351-362. <https://doi.org/10.1017/S0033822200060355>
- Chilaka, C. A., Aparicio-Muriana, M. D. M., Petchkongkaew, A., Quinn, B., Birse, N., & Elliott, C. T. (2025). A combined elementomics, metabolomics, and chemometrics approach as tools to

- identify the geographic origins of black pepper. *Food Chemistry*, 492, 145420.
<https://doi.org/10.1016/j.foodchem.2025.145420>
- Chirakkal, A., Stienal, C. C., Birk, J. J., Újvári, G., & Wright, D. K. (2025). Biomarker evidence on Early Paleolithic human-environment interactions from loess records in Tajikistan, Central Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 663, 112786.
<https://doi.org/10.1016/j.palaeo.2025.112786>
- Cintra, B. B. L., Gloor, E., Baker, J. C. A., Boom, A., Schöngart, J., Clerici, S., Pattnayak, K., & Brien, R. J. W. (2025). Tree ring isotopes reveal an intensification of the hydrological cycle in the Amazon. *Communications Earth & Environment*, 6(1), 453.
<https://doi.org/10.1038/s43247-025-02408-9>
- Cipro, C. V. Z., Cherel, Y., Bocher, P., Caurant, F., Miramand, P., & Bustamante, P. (2018). Trace elements in invertebrates and fish from Kerguelen waters, southern Indian Ocean. *Polar Biology*, 41(1), 175-191. <https://doi.org/10.1007/s00300-017-2180-6>
- Clackett, S. P., Porter, T. J., & Lehnher, I. (2018). 400-Year Record of Atmospheric Mercury from Tree-Rings in Northwestern Canada. *Environmental Science & Technology*, 52(17), 9625-9633. <https://doi.org/10.1021/acs.est.8b01824>
- Cleveland, W. S., Grosse, E., & Shyu, W. M. (1988). Regression by local fitting: Methods, properties, and computational algorithms. *Journal of Econometrics*, 37(1), 87-114.
[https://doi.org/10.1016/0304-4076\(88\)90077-2](https://doi.org/10.1016/0304-4076(88)90077-2)
- Cohen, A. (2003). The chemical environment of lakes. En I. (Ed. (Ed.)), *Paleolimnology: The History and Evolution of Lake Systems*. Oxford Academics.
- Columbu, A., Chiarini, V., Spötl, C., Benazzi, S., Hellstrom, J., Cheng, H., & De Waele, J. (2020). Speleothem record attests to stable environmental conditions during Neanderthal–modern human turnover in southern Italy. *Nature Ecology & Evolution*, 4(9), 1188-1195.
<https://doi.org/10.1038/s41559-020-1243-1>
- Connor, S. E., Leeuwen, J., Rittenour, T. M., Knapp, P., Ammann, B., & Björck, S. (2012). The ecological impact of oceanic island colonization—A palaeoecological perspective from the Azores. *Journal of Biogeography*, 39, 1007-1023.
<https://doi.org/10.1111/j.1365-2699.2011.02638.x>

- Crosby, A. W. (2004). *Ecological imperialism: The biological expansion of Europe, 900–1900* (2nd ed.). Cambridge University Press. <https://doi.org/10.1017/CBO9780511805554>
- Croudace, I. W., & Rothwell, R. G. (Eds.). (2015). *Micro-XRF Studies of Sediment Cores: Applications of a non-destructive tool for the environmental sciences* (Vol. 17). Springer Netherlands. <https://doi.org/10.1007/978-94-017-9849-5>
- Crutzen, P. J., & Stoermer, E. F. (2017). “The ‘Anthropocene’” (2000). En L. Robin, S. Sörlin, & P. Warde (Eds.), *The Future of Nature* (pp. 479-490). Yale University Press. <https://doi.org/10.12987/9780300188479-041>
- Cui, H., Sun, W., & Delgado-Baquerizo, M. (2021). Cascading effects of N fertilization activate biologically driven mechanisms promoting P availability in a semi-arid grassland ecosystem. *Functional Ecology*, 35, 1001-1011. <https://doi.org/10.1111/1365-2435.13773>
- Da Silva, K. A., Snyder, R. A., Packalen, M. S., McLaughlin, J. W., Peteet, D. M., & Finkelstein, S. A. (2022). Mineral inputs, paleoecological change, and Holocene carbon accumulation at a boreal peatland in the Hudson Bay Lowlands, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 596, 110996. <https://doi.org/10.1016/j.palaeo.2022.110996>
- Daleo, P., Alberti, J., Chaneton, E. J., Iribarne, O., Tognetti, P. M., Bakker, J. D., Borer, E. T., Bruschetti, M., MacDougall, A. S., Pascual, J., Sankaran, M., Seabloom, E. W., Wang, S., Bagchi, S., Brudvig, L. A., Catford, J. A., Dickman, C. R., Dickson, T. L., Donohue, I., ... Hautier, Y. (2023). Environmental heterogeneity modulates the effect of plant diversity on the spatial variability of grassland biomass. *Nature Communications*, 14(1), 1809. <https://doi.org/10.1038/s41467-023-37395-y>
- Data Sonification Archive. (s. f.). *Data Sonification Archive*. <https://sonification.design/>
- Davies, A. L. (2019). Dung fungi as an indicator of large herbivore dynamics in peatlands. *Review of Palaeobotany and Palynology*, 271, 104108. <https://doi.org/10.1016/j.revpalbo.2019.104108>
- Dayé, C., & De Campo, A. (2006). Sounds sequential: Sonification in the social sciences. *Interdisciplinary Science Reviews*, 31(4), 349-364. <https://doi.org/10.1179/030801806X143286>

- Dayhoff, M. O., & Eck, R. V. (1969). Paleobiochemistry. En G. Eglinton & M. T. J. Murphy (Eds.), *Organic Geochemistry* (pp. 196-212). Springer Berlin Heidelberg.
https://doi.org/10.1007/978-3-642-87734-6_8
- De Cáceres, M., Coll, L., Legendre, P., Allen, R. B., Wiser, S. K., Fortin, M., Condit, R., & Hubbell, S. (2019). Trajectory analysis in community ecology. *Ecological Monographs*, 89(2), e01350.
<https://doi.org/10.1002/ecm.1350>
- De Cáceres, M., & Djeghri, N. (2025, septiembre). *Introduction to Ecological Trajectory Analysis (ETA)*. <https://emf-creaf.github.io/ecotraj/articles/IntroductionETA.html>
- De Jonge, C., Dubois, N., Ladd, S. N., Deng, L., Gajendra, N., Haghipour, N., Schubert, C. J., & Lever, M. (2025). Holocene environmental change in Rotsee and its impact on sedimentary carbon storage. *Journal of Paleolimnology*, 73(4), 311-327.
<https://doi.org/10.1007/s10933-025-00361-3>
- de la Casa, J., Bautista, L., & Múgica, J. (2025, September). *soundtraj: Sonification of multivariate trajectories*. <https://linalab.com/Projects/Multivariate+spaces+sonification>
- de la Casa, J., Nogué, S., De Cáceres, M., Pla-Rabés, S., Sardans, J., Benavente, M., Giralt, S., Hernandez, A., Raposeiro, P. M., & Peñuelas, J. (2025). Unveiling two millennia of ecosystem changes in the Azores through elementome trajectory analysis. *Ecological Indicators*, 176, 113630. <https://doi.org/10.1016/j.ecolind.2025.113630>
- de la Casa, J., Sardans, J., Galindo, M., & Peñuelas, J. (2025). Stoichiometry of litter decomposition under the effects of climate change and nutrient enrichment: A meta-analysis. *Plant and Soil*, 506(1-2), 709-726. <https://doi.org/10.1007/s11104-024-06718-3>
- De Micco, V., Balzano, A., Čufar, K., Aronne, G., Gričar, J., Merela, M., & Battipaglia, G. (2016). Timing of False Ring Formation in *Pinus halepensis* and *Arbutus unedo* in Southern Italy: Outlook from an Analysis of Xylogenesis and Tree-Ring Chronologies. *Frontiers in Plant Science*, 7. <https://doi.org/10.3389/fpls.2016.00705>
- de Nascimento, L., Nogué, S., Naranjo-Cigala, A., Criado, C., McGlone, M., Fernández-Palacios, E., & Fernández-Palacios, J. M. (2020). Human impact and ecological changes during prehistoric settlement on the Canary Islands. *Quaternary Science Reviews*, 239, 106332.
<https://doi.org/10.1016/j.quascirev.2020.106332>

- Deng, L., Shangguan, Z., Bell, S. M., Soromotin, A. V., Peng, C., An, S., Wu, X., Xu, X., Wang, K., Li, J., Tang, Z., Yan, W., Zhang, F., Li, J., Wu, J., & Kuzyakov, Y. (2023). Carbon in Chinese grasslands: Meta-analysis and theory of grazing effects. *Carbon Research*, 2(1), 19. <https://doi.org/10.1007/s44246-023-00051-7>
- Diniz, É. S., Rodríguez-Penedo, E., Grau-Andrés, R., Vayreda, J., & Fernández-Martínez, M. (2025). Optimal set of leaf and aboveground tree elements for predicting forest functioning. *Biogeosciences*, 22(8), 2115-2132. <https://doi.org/10.5194/bg-22-2115-2025>
- Dirnböck, T., Essl, F., & Rabitsch, W. (2011). Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Global Change Biology*, 17(2), 990-996. <https://doi.org/10.1111/j.1365-2486.2010.02266.x>
- Douglas, P. M. J., Stratigopoulos, E., Park, S., & Keenan, B. (2022). Spatial differentiation of sediment organic matter isotopic composition and inferred sources in a temperate forest lake catchment. *Chemical Geology*, 603, 120887. <https://doi.org/10.1016/j.chemgeo.2022.120887>
- Dray, S., Péliissier, R., Couteron, P., Fortin, M.-J., Legendre, P., Peres-Neto, P. R., Bellier, E., Bivand, R., Blanchet, F. G., De Cáceres, M., Dufour, A.-B., Heegaard, E., Jombart, T., Munoz, F., Oksanen, J., Thioulouse, J., & Wagner, H. H. (2012). Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs*, 82(3), 257-275. <https://doi.org/10.1890/11-1183.1>
- Dubois, N., & Jacob, J. (2016). Molecular Biomarkers of Anthropic Impacts in Natural Archives: A Review. *Frontiers in Ecology and Evolution*, 4. <https://doi.org/10.3389/fevo.2016.00092>
- Dubois, N., Saulnier-Talbot, É., Mills, K., Gell, P., Battarbee, R., Bennion, H., Chawchai, S., Dong, X., Francus, P., Flower, R., Gomes, D. F., Gregory-Eaves, I., Humane, S., Kattel, G., Jenny, J., Langdon, P., Massaferrro, J., McGowan, S., Mikomägi, A., ... Valero-Garcés, B. (2018). First human impacts and responses of aquatic systems: A review of palaeolimnological records from around the world. *The Anthropocene Review*, 5(1), 28-68. <https://doi.org/10.1177/2053019617740365>
- Durand, M., Rose, C., Dupouey, J.-L., Legout, A., & Ponton, S. (2020). Do tree rings record changes in soil fertility? Results from a *Quercus petraea* fertilization trial. *Science of The Total Environment*, 712, 136148. <https://doi.org/10.1016/j.scitotenv.2019.136148>

- Dzombak, R. (2021). *Geochemical Variability in Fossil Soils and Implications for Past Biogeochemical Cycling, Climates, and Atmospheres* [University of Michigan]. <https://doi.org/10.7302/3066>
- Ehnvall, B., Ratcliffe, J. L., Olid, C., Smeds, J., Bishop, K., Klaminder, J., Li, C., Mörtz, C.-M., Nilsson, M. B., & Öquist, M. G. (2025). Carbon accumulation in recently deposited peat is reduced by increased nutrient supply. *Nature Communications*, 16(1), 4271. <https://doi.org/10.1038/s41467-025-59387-w>
- Einsele, G., Yan, J., & Hinderer, M. (2001). Atmospheric carbon burial in modern lake basins and its significance for the global carbon budget. *Global and Planetary Change*, 30(3), 167-195. [https://doi.org/10.1016/S0921-8181\(01\)00105-9](https://doi.org/10.1016/S0921-8181(01)00105-9)
- Ellis, E. C., Gauthier, N., Klein Goldewijk, K., Bliege Bird, R., Boivin, N., Díaz, S., Fuller, D. Q., Gill, J. L., Kaplan, J. O., Kingston, N., Locke, H., McMichael, C. N. H., Ranco, D., Rick, T. C., Shaw, M. R., Stephens, L., Svenning, J.-C., Watson, J. E. M., & Watson, J. E. M. (2021). People have shaped most of terrestrial nature for at least 12,000 years. *Proceedings of the National Academy of Sciences*, 118(17), 2023483118. <https://doi.org/10.1073/pnas.2023483118>
- Esper, J., Büntgen, U., Luterbacher, J., & Krusic, P. J. (2013). Testing the hypothesis of post-volcanic missing rings in temperature sensitive dendrochronological data. *Dendrochronologia*, 31(3), 216-222. <https://doi.org/10.1016/j.dendro.2012.11.002>
- Evans, C., Sørensen, M. L. S., Allen, M. J., Appleby, J., Casimiro, T. M., French, C., Inskip, S., Lima, J., Newman, R., Richter, K., & Scaife, R. (2017). Finding Alcatrazes and early Luso-African settlement on Santiago Island, Cape Verde. *Antiquity*, 91(358), 1-9. <https://doi.org/10.15184/aqy.2017.104>
- Evans, C., Sørensen, M.-L., Castilla-Beltrán, A., Nogue Bosch, S., Casimiro, T. M., Detry, C., Hamilton-Dyer, S., & Silva Lima, J. (2025). Excavating Alcatrazes, Santiago Island, Cape Verde: Early colonial impacts on land, people and material culture. *Antiquity*, 00(00), 1-9. <https://doi.org/10.15184/aqy.2025.10149>
- Fall, P. L., Hengstum, P. J., Lavold-Foote, L., Donnelly, J. P., Albury, N. A., & Tamalavage, A. E. (2021). Human arrival and landscape dynamics in the northern Bahamas. *Proceedings of the National Academy of Sciences*, 118(10), 2015764118. <https://doi.org/10.1073/pnas.2015764118>

- F.A.O. & I.T.P.S. (2015). Status of the world's soil resources (SWSR) – Main report. En *Food and Agriculture Organization of the United Nations (FAO) & Intergovernmental Technical Panel on Soils (ITPS)*. <https://www.fao.org/3/i5199e/i5199e.pdf>
- Farnsworth, W. R. (2025). Explosive volcanic history of Snæfellsjökull W. *Iceland: Geochemistry, Chronology and Distribution. Quaternary Science Reviews*.
- Fay, P. A., Prober, S. M., Harpole, W. S., Knops, J. M. H., Bakker, J. D., Borer, E. T., Lind, E. M., MacDougall, A. S., Seabloom, E. W., Wragg, P. D., Adler, P. B., Blumenthal, D. M., Buckley, Y. M., Chu, C., Cleland, E. E., Collins, S. L., Davies, K. F., Du, G., Feng, X., ... Yang, L. H. (2015). Grassland productivity limited by multiple nutrients. *Nature Plants*, 1(7), 15080. <https://doi.org/10.1038/nplants.2015.80>
- Fernández-Martínez, M. (2022). From atoms to ecosystems: Elementome diversity meets ecosystem functioning. *New Phytologist*, 234(1), 35-42. <https://doi.org/10.1111/nph.17864>
- Fernández-Martínez, M., Janssens, I. A., Obersteiner, M., Manning, P., Andrade, F. M., Rodríguez-Penedo, E., & Peñuelas, J. (2025). Temporal complexity of terrestrial ecosystem functioning and its drivers. *Nature Communications*, 16(1), 7725. <https://doi.org/10.1038/s41467-025-63246-z>
- Fernández-Martínez, M., Preece, C., Corbera, J., Cano, O., Garcia-Porta, J., Sardans, J., Janssens, I. A., Sabater, F., & Peñuelas, J. (2021). Bryophyte C:N:P stoichiometry, biogeochemical niches and elementome plasticity driven by environment and coexistence. *Ecology Letters*, 24(7), 1375-1386. <https://doi.org/10.1111/ele.13752>
- Fernández-Martínez, M., Vicca, S., Janssens, I. A., Sardans, J., Luyssaert, S., Campioli, M., Chapin III, F. S., Ciais, P., Malhi, Y., Obersteiner, M., Papale, D., Piao, S. L., Reichstein, M., Rodà, F., & Peñuelas, J. (2014). Nutrient availability as the key regulator of global forest carbon balance. *Nature Climate Change*, 4(6), 471-476. <https://doi.org/10.1038/nclimate2177>
- Fernández-Palacios, J. M., Kreft, H., Irl, S. D. H., Norder, S., Ah-Peng, C., Borges, P. A. V., Burns, K. C., Nascimento, L., Meyer, J.-Y., Montes, E., & Drake, D. R. (2021). Scientists' warning – The outstanding biodiversity of islands is in peril. *Global Ecology and Conservation*, 31, 01847. <https://doi.org/10.1016/j.gecco.2021.e01847>

- Ferrín, M., Asensio, D., Gargallo-Garriga, A., Grau, O., Llusà, J., Màrquez, L., Murienne, J., Ogaya, R., Orivel, J., Sardans, J., Janssens, I. A., Peñuelas, J., & Peguero, G. (2025). Micronutrients are drivers of abundance, richness, and composition of soil insect communities in tropical rainforests. *Ecosphere*, 16(5), e70200. <https://doi.org/10.1002/ecs2.70200>
- Fischer, M. L., Markowska, M., Bachofer, F., Foerster, V. E., Asrat, A., Zielhofer, C., Trauth, M. H., & Junginger, A. (2020). Determining the Pace and Magnitude of Lake Level Changes in Southern Ethiopia Over the Last 20,000 Years Using Lake Balance Modeling and SEBAL. *Frontiers in Earth Science*, 8, 197. <https://doi.org/10.3389/feart.2020.00197>
- Fitzhugh, W. W., & Ward, E. I. (Eds.). (2000). *Vikings*. Smithsonian Institution Press.
- Fitzpatrick, S. M. (2015). The Pre-Columbian Caribbean: Colonisation, population dispersal, and island adaptations. *PaleoAmerica*, 1(4), 305-331. <https://doi.org/10.1179/20555557115Y.000000001>
- Flantua, S. G. A., Payne, D., Borregaard, M. K., Beierkuhnlein, C., Steinbauer, M. J., Dullinger, S., Essl, F., Irl, S. D. H., Kienle, D., Kreft, H., Lenzner, B., Norder, S. J., Rijdsdijk, K. F., Rumpf, S. B., Weigelt, P., & Field, R. (2020). Snapshot isolation and isolation history challenge the analogy between mountains and islands used to understand endemism. *Global Ecology and Biogeography*, 29(10), 1651-1673. <https://doi.org/10.1111/geb.13155>
- Flowers, J. H., & Hauer, T. A. (1995). Musical versus visual graphs: Cross-modal equivalence in perception of time series data. *Human Factors*, 37(3), 553-569. <https://doi.org/10.1518/001872095779049264>
- Foley, S. F., Gronenborn, D., Andreae, M. O., Kadereit, J. W., Esper, J., Scholz, D., Pöschl, U., Jacob, D. E., Schöne, B. R., Schreg, R., Vött, A., Jordan, D., Lelieveld, J., Weller, C. G., Alt, K. W., Gaudzinski-Windheuser, S., Bruhn, K.-C., Tost, H., Sirocko, F., & Crutzen, P. J. (2013). The Palaeoanthropocene – The beginnings of anthropogenic environmental change. *Anthropocene*, 3, 83-88. <https://doi.org/10.1016/j.ancene.2013.11.002>
- Fowler, D., Coyle, M., Skiba, U., Sutton, M. A., Cape, J. N., Reis, S., Sheppard, L. J., Jenkins, A., Grizzetti, B., Galloway, J. N., Vitousek, P., Leach, A., Bouwman, A. F., Butterbach-Bahl, K., Dentener, F., Stevenson, D., Amann, M., & Voss, M. (2013). The global nitrogen cycle in the

- twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1621), 20130164. <https://doi.org/10.1098/rstb.2013.0164>
- Friedrich, M., Remmele, S., Kromer, B., Hofmann, J., Spurk, M., Felix Kaiser, K., Orzel, C., & Küppers, M. (2004). The 12,460-Year Hohenheim Oak and Pine Tree-Ring Chronology from Central Europe—A Unique Annual Record for Radiocarbon Calibration and Paleoenvironment Reconstructions. *Radiocarbon*, 46(3), 1111-1122. <https://doi.org/10.1017/S003382220003304X>
- Frutuoso, G. (1981). *Livro Quarto das Saudades da Terra*. Instituto Cultural de Ponta Delgada.
- Galloway, J. N., Leach, A. M., Bleeker, A., & Erisman, J. W. (2013). A chronology of human understanding of the nitrogen cycle . *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1621), 20130120. <https://doi.org/10.1098/rstb.2013.0120>
- Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda, M., Cai, Z., Freney, J. R., Martinelli, L. A., Seitzinger, S. P., & Sutton, M. A. (2008). Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. *Science*, 320(5878), 889-892. <https://doi.org/10.1126/science.1136674>
- Gao, X., Thomas, B. W., Beck, R., Thompson, D. J., Zhao, M., Willms, W. D., & Hao, X. (2018). Long-Term Grazing Alters Soil Trace Gas Fluxes from Grasslands in the Foothills of the Rocky Mountains, Canada. *Land Degradation & Development*, 29(2), 292-302. <https://doi.org/10.1002/ldr.2664>
- Garcés-Pastor, S., Coissac, E., Lavergne, S., Schwörer, C., Theurillat, J.-P., Heintzman, P. D., Wangenstein, O. S., Tinner, W., Rey, F., Heer, M., Rützer, A., Walsh, K., Lammers, Y., Brown, A. G., Goslar, T., Rijal, D. P., Karger, D. N., Pellissier, L., The PhyloAlps Consortium, ... Alsos, I. G. (2022). High resolution ancient sedimentary DNA shows that alpine plant diversity is associated with human land use and climate change. *Nature Communications*, 13(1), 6559. <https://doi.org/10.1038/s41467-022-34010-4>
- Garcés-Pastor, S., Fletcher, W. J., & Ryan, P. A. (2023). Ecological impacts of the industrial revolution in a lowland raised peat bog near Manchester, NW England. *Ecology and Evolution*, 13(2), e9807. <https://doi.org/10.1002/ece3.9807>

- Garcés-Pastor, S., Heintzman, P. D., Zetter, S., Lammers, Y., Yoccoz, N. G., Theurillat, J.-P., Schwörer, C., Tribsch, A., Walsh, K., Vannière, B., Wangenstein, O. S., Heiri, O., Coissac, E., Lavergne, S., Van Vugt, L., Rey, F., Giguët-Covex, C., Ficetola, G. F., Karger, D. N., ... Alsos, I. G. (2025). Wild and domesticated animal abundance is associated with greater late-Holocene alpine plant diversity. *Nature Communications*, 16(1), 3924. <https://doi.org/10.1038/s41467-025-59028-2>
- García-Oteyza, J., Giralt, S., & Pla-Rabés, S. (2024). A ~5000 year multiproxy record of summer climate in NE Greenland. *Science of The Total Environment*, 906, 167713. <https://doi.org/10.1016/j.scitotenv.2023.167713>
- García-Regalado, A., Herrera, A., & Almeda, R. (2024). Microplastic and mesoplastic pollution in surface waters and beaches of the Canary Islands: A review. *Marine Pollution Bulletin*, 201, 116230. <https://doi.org/10.1016/j.marpolbul.2024.116230>
- Geirsdóttir, Á., Miller, G. H., Thordarson, T., & Ólafsdóttir, K. B. (2009). A 2000 year record of climate variations reconstructed from Haukadalsvatn, West Iceland. *Journal of Paleolimnology*, 41(1), 95-115. <https://doi.org/10.1007/s10933-008-9253-z>
- Giguët-Covex, C., Bajard, M., & Chen, W. (2023). Long-term trajectories of mountain agro-ecosystems in the North-Western Alps. *Regional Environmental Change*, 23, Article 20. <https://doi.org/10.1007/s10113-023-02030-5>
- Giguët-Covex, C., Pansu, J., Arnaud, F., Rey, P.-J., Griggo, C., Gielly, L., Domaizon, I., Coissac, E., David, F., Choler, P., Poulenard, J., & Taberlet, P. (2014). Long livestock farming history and human landscape shaping revealed by lake sediment DNA. *Nature Communications*, 5(1), 3211. <https://doi.org/10.1038/ncomms4211>
- Gill, R. (2014). *Modern Analytical Geochemistry* (0 ed.). Routledge. <https://doi.org/10.4324/9781315844381>
- Giralt, S., Moreno, A., & Bao, R. (2007). A statistical approach to disentangle environmental forcings in a lacustrine record: The Lago Chungará case (Chilean Altiplano). *Journal of Paleolimnology*, 38(2), 247-260. <https://doi.org/10.1007/s10933-006-9079-3>
- Giralt, S., Moreno, A., Bao, R., Sáez, A., Prego, R., Valero-Garcés, B. L., Pueyo, J. J., González-Sampériz, P., & Taberner, C. (2008). A statistical approach to disentangle

- environmental forcings in a lacustrine record: The Lago Chungará case (Chilean Altiplano). *Journal of Paleolimnology*, 40(1), 195-215. <https://doi.org/10.1007/s10933-007-9151-9>
- Giralt, S., Rico-Herrero, M. T., Vega, J. C., & Valero-Garcés, B. L. (2011). Quantitative climate reconstruction linking meteorological, limnological and XRF core scanner datasets: The Lake Sanabria case study, NW Spain. *Journal of Paleolimnology*, 46(3), 487-502. <https://doi.org/10.1007/s10933-011-9509-x>
- Giralt, S., Rico-Herrero, T., & Vega, C. (2011). Quantitative climate reconstruction linking meteorological, limnological, and XRF core scanner datasets: The Lake Sanabria case study, NW Spain. *Journal of Paleolimnology*, 46(3), 487-502. <https://doi.org/10.1007/s10933-011-9509-x>
- Glibert, P. M. (2016). Margalef revisited: A new phytoplankton mandala incorporating twelve dimensions, including nutritional physiology. *Harmful Algae*, 55, 25-30. <https://doi.org/10.1016/j.hal.2016.01.008>
- Govers, G., Merckx, R., Wesemael, B., & Oost, K. (2017). Soil conservation in the 21st century: Why we need smart agricultural intensification. *SOIL*, 3(1), 45-59. <https://doi.org/10.5194/soil-3-45-2017>
- Grace, J. B., Anderson, T. M., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., Hautier, Y., Hillebrand, H., Lind, E. M., Pärtel, M., Bakker, J. D., Buckley, Y. M., Crawley, M. J., Damschen, E. I., Davies, K. F., Fay, P. A., Firn, J., Gruner, D. S., Hector, A., ... Smith, M. D. (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, 529(7586), 390-393. <https://doi.org/10.1038/nature16524>
- Granmo, M. N., Reavie, E. D., Post, S. P., & Zanko, L. M. (2020). Anthropocene geochemistry of metals in sediment cores from the Laurentian Great Lakes. *PeerJ*, 8, 9034. <https://doi.org/10.7717/peerj.9034>
- Graven, H., Keeling, R. F., & Rogelj, J. (2020). Changes to Carbon Isotopes in Atmospheric CO₂ Over the Industrial Era and Into the Future. *Global Biogeochemical Cycles*, 34(11), e2019GB006170. <https://doi.org/10.1029/2019GB006170>
- Gregory-Eaves, I., & Smol, J. P. (2024). Paleolimnology: Approaches and Applications. En *Wetzel's Limnology* (pp. 1015-1043). Elsevier. <https://doi.org/10.1016/B978-0-12-822701-5.00030-6>

- Grim, E. C. (1987). CONISS, a FORTRAN-77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers & Geosciences*, 13, 13-35.
- Gruber, N., & Galloway, J. N. (2008). An Earth-system perspective of the global nitrogen cycle. *Nature*, 451, 293-296. <https://doi.org/10.1038/nature06592>
- Gu, B., Schelske, C. L., & Brenner, M. (1996). Relationship between sediment and plankton isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and primary productivity in Florida lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(4), 875-883. <https://doi.org/10.1139/f95-248>
- Guo, X., Song, H., Wu, P., Liu, L., Li, M., Xie, L., Jespersen, E., Ye, S., & Guo, W. (2025). Intraspecific elementome variation of the clonal grass *Phragmites australis* reflects environmental variation more than genetic and epigenetic variation. *Journal of Plant Ecology*, 18(4), rtaf070. <https://doi.org/10.1093/jpe/rtaf070>
- Haas, M., Baumann, F., Castella, D., Haghipour, N., Reusch, A., Strasser, M., Eglinton, T. I., & Dubois, N. (2019). Roman-driven cultural eutrophication of Lake Murten, Switzerland. *Earth and Planetary Science Letters*, 505, 110-117. <https://doi.org/10.1016/j.epsl.2018.10.027>
- Hagemeyer, J., & Weinand, T. (1996). Radial distributions of Pb in stems of young Norway spruce trees grown in Pb-contaminated soil. *Tree Physiology*, 16(6), 591-594. <https://doi.org/10.1093/treephys/16.6.591>
- Hallett, Lauren; Avolio, Meghan; Carroll, Ian; Jones, Sydney K.; MacDonald, Andrew A.; Flynn, Dan F. B.; Slaughter, Peter; Ripplinger, Julie; Collins, Scott L.; Gries, Corinna; Jones, Matthew B. (2018). *codyn: Community Dynamics Metrics R package (version 2)* [Software]. KNB Data Repository. <https://doi.org/10.5063/F1N877Z6>
- Hamley, K. M., Gill, J. L., Krasinski, K. E., Groff, D. V., Hall, B. L., Sandweiss, D. H., Southon, J. R., Brickle, P., & Lowell, T. V. (2021). Evidence of prehistoric human activity in the Falkland Islands. *Science Advances*, 7(44), 3803. <https://doi.org/10.1126/sciadv.abh3803>
- Haraway, D. J. (2016). *Staying with the trouble: Making kin in the Chthulucene*. Duke University Press.
- Harpole, W. S., Sullivan, L. L., Lind, E. M., Firn, J., Adler, P. B., Borer, E. T., Chase, J., Fay, P. A., Hautier, Y., Hillebrand, H., MacDougall, A. S., Seabloom, E. W., Williams, R., Bakker, J. D., Cadotte, M. W., Chaneton, E. J., Chu, C., Cleland, E. E., D'Antonio, C., ... Wragg, P. D.

- (2016). Addition of multiple limiting resources reduces grassland diversity. *Nature*, 537(7618), 93-96. <https://doi.org/10.1038/nature19324>
- Harrison, J. A., Maranger, R. J., Alexander, R. B., Giblin, A. E., Jacinthe, P.-A., Mayorga, E., Seitzinger, S. P., Sobota, D. J., & Wollheim, W. M. (2009). The regional and global significance of nitrogen removal in lakes and reservoirs. *Biogeochemistry*, 93(1), 145-157. <https://doi.org/10.1007/s10533-008-9272-x>
- Hayashi, M., & Kamp, G. (2007). Water Level Changes in Ponds and Lakes: The Hydrological Processes. En E. Johnson & K. Miyanishi (Eds.), *Plant Disturbance Ecology*. Academic Press. <https://doi.org/10.1016/B978-012088778-1/50012-1>
- He, P., Ni, Y., Sardans, J., Ma, C., Liu, H., Wang, R., Peñuelas, J., Han, X., Jiang, Y., & Li, M.-H. (2025). Evolutionary history shapes plant elementome and biogeochemical niches in a forest-steppe ecotone. *Plant and Soil*. <https://doi.org/10.1007/s11104-025-07353-2>
- Herczeg, A. L., Smith, A. K., & Dighton, J. C. (2001). A 120 year record of changes in nitrogen and carbon cycling in Lake Alexandrina, South Australia: C:N, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in sediments. *Applied Geochemistry*, 16(1), 73-84. [https://doi.org/10.1016/S0883-2927\(00\)00016-0](https://doi.org/10.1016/S0883-2927(00)00016-0)
- Hernández, A., Bao, R., Giralt, S., Sáez, A., Leng, M. J., Barker, P. A., & Sloane, H. J. (2013). Climate, catchment runoff and limnological drivers of carbon and oxygen isotope composition of diatom frustules from the central Andean Altiplano during the Lateglacial and Early Holocene. *Quaternary Science Reviews*, 66, 64-73. <https://doi.org/10.1002/jqs.1173>
- Hernández, A., Sáez, A., Bao, R., & Others. (2017). The influences of the AMO and NAO on the sedimentary infill in an Azores Archipelago lake since ca. 1350 CE. *Global and Planetary Change*, 154, 61-74. <https://doi.org/10.1016/j.gloplacha.2017.05.007>
- Hevia, A., Sánchez-Salguero, R., Camarero, J. J., Buras, A., Sangüesa-Barreda, G., Galván, J. D., & Gutiérrez, E. (2018). Towards a better understanding of long-term wood-chemistry variations in old-growth forests: A case study on ancient *Pinus uncinata* trees from the Pyrenees. *Science of The Total Environment*, 625, 220-232. <https://doi.org/10.1016/j.scitotenv.2017.12.229>
- Hobbie, E. A., Chen, J., Hanson, P. J., Iversen, C. M., McFarlane, K. J., Thorp, N. R., & Hofmockel, K. S. (2017). Long-term carbon and nitrogen dynamics at SPRUCE revealed through stable

- isotopes in peat profiles. *Biogeosciences*, 14(9), 2481-2494.
<https://doi.org/10.5194/bg-14-2481-2017>
- Hong, Y., Chen, J., Lü, X., Li, D., Sheteiwy, M. S., Maestre, F. T., Smith, P., Ochoa-Hueso, R., Sinsabaugh, R. L., & Chen, H. (2025). Decoupling of plant nitrogen and phosphorus under global change over the last two decades. *Journal of Ecology*, 113(8), 2120-2130.
<https://doi.org/10.1111/1365-2745.70081>
- Hooper, D. U., & Vitousek, P. M. (1998). EFFECTS OF PLANT COMPOSITION AND DIVERSITY ON NUTRIENT CYCLING. *Ecological Monographs*, 68(1), 121-149.
[https://doi.org/10.1890/0012-9615\(1998\)068%255B0121:EOPCAD%255D2.0.CO;2](https://doi.org/10.1890/0012-9615(1998)068%255B0121:EOPCAD%255D2.0.CO;2)
- Hörhold, M., Münch, T., Weißbach, S., Kipfstuhl, S., Freitag, J., Sasgen, I., Lohmann, G., Vinther, B., & Laepple, T. (2023). Modern temperatures in central–north Greenland warmest in past millennium. *Nature*, 613(7944), 503-507. <https://doi.org/10.1038/s41586-022-05517-z>
- Hou, E., Luo, Y., Kuang, Y., Chen, C., Lu, X., Jiang, L., Luo, X., & Wen, D. (2020). Global meta-analysis shows pervasive phosphorus limitation of aboveground plant production in natural terrestrial ecosystems. *Nature Communications*, 11(1), 637.
<https://doi.org/10.1038/s41467-020-14492-w>
- Hu, M., Chen, Y., Sardans, J., Peñuelas, J., Chen, H. Y. H., Chu, C., & Ma, Z. (2025). Legacy effects control root elemental composition and stoichiometry in subtropical forests: Empirical support for the biogeochemical niche hypothesis. *Journal of Ecology*, 113(6), 1461-1474.
<https://doi.org/10.1111/1365-2745.70031>
- Hu, Y.-Y., Wei, H.-W., Zhang, Z.-W., Hou, S.-L., Yang, J.-J., Wang, J.-F., & Lü, X.-T. (2020). Changes of plant community composition instead of soil nutrient status drive the legacy effects of historical nitrogen deposition on plant community N:P stoichiometry. *Plant and Soil*, 453(1-2), 503-513. <https://doi.org/10.1007/s11104-020-04631-z>
- Hughes, P. D. M., Mauquoy, D., Barber, K. E., & Langdon, P. G. (2000). Mire-development pathways and palaeoclimatic records from a full Holocene peat archive at Walton Moss, Cumbria, England. *The Holocene*, 10(4), 465-479. <https://doi.org/10.1191/095968300675142023>

- Hunt, A. M. W., & Speakman, R. J. (2015). Portable XRF analysis of archaeological sediments and ceramics. *Journal of Archaeological Science*, 53, 626-638.
<https://doi.org/10.1016/j.jas.2014.11.031>
- Inagawa, T., Riutta, T., Majalap-Lee, N., Nilus, R., Josue, J., & Malhi, Y. (2023). Radial and vertical variation of wood nutrients in Bornean tropical forest trees. *Biotropica*, 55(5), 1019-1032.
<https://doi.org/10.1111/btp.13250>
- Janes-Bassett, V., Bassett, R., Rowe, E. C., Tipping, E., Yumashev, D., & Davies, J. (2021). Changes in carbon storage since the pre-industrial era: A national scale analysis. *Anthropocene*, 34, 100289. <https://doi.org/10.1016/j.ancene.2021.100289>
- Jenny, J.-P., Koirala, S., Gregory-Eaves, I., Francus, P., Niemann, C., Ahrens, B., Brovkin, V., Baud, A., Ojala, A. E. K., Normandeau, A., Zolitschka, B., & Carvalhais, N. (2019). Human and climate global-scale imprint on sediment transfer during the Holocene. *Proceedings of the National Academy of Sciences*, 116(46), 22972-22976.
<https://doi.org/10.1073/pnas.1908179116>
- Ji, P., Chen, J., Chen, R., Liu, J., Yu, C., & Chen, F. (2024). Nitrogen and phosphorus trends in lake sediments of China may diverge. *Nature Communications*, 15(1), 2644.
<https://doi.org/10.1038/s41467-024-46968-4>
- Jiang, S., Zhou, X., Hu, D., Liu, X., Chen, A., & Zhang, G. (2024). Changes in total sulfur of lake sediments from central-eastern China linked to volcanic aerosol and human activity. *Science of The Total Environment*, 957, 177628. <https://doi.org/10.1016/j.scitotenv.2024.177628>
- Jiménez-Navarro, C., Mesman, J., Pierson, D., Trolle, D., Nielsen, A., & Senent-Aparicio, J. (2023). Application of an integrated catchment-lake model approach for simulating effects of climate change on lake inputs and biogeochemistry. *Science of The Total Environment*.
<https://doi.org/10.1016/j.scitotenv.2023.163946>
- Jobbágy, E. G., & Jackson, R. B. (2004). THE UPLIFT OF SOIL NUTRIENTS BY PLANTS: BIOGEOCHEMICAL CONSEQUENCES ACROSS SCALES. *Ecology*, 85(9), 2380-2389.
<https://doi.org/10.1890/03-0245>

- Joosten, H., & Clarke, D. (with International Peat Society & International Mire Conservation Group). (2002). *Wise use of mires and peatlands: Background and principles including a framework for decision-making*. International Peat Society ; International Mire Conservation Group.
- Karger, D. N., Nobis, M. P., Normand, S., Graham, C. H., & Zimmermann, N. E. (2023). CHELSA-TraCE21k – high-resolution (1 km) downscaled transient temperature and precipitation data since the Last Glacial Maximum. *Climate of the Past*, 19(2), 439-456. <https://doi.org/10.5194/cp-19-439-2023>
- Karlsson, J., Segerström, U., Berg, A., Mattielli, N., & Bindler, R. (2015). Tracing modern environmental conditions to their roots in early mining, metallurgy, and settlement in Gladhammar, southeast Sweden: Vegetation and pollution history outside the traditional Bergslagen mining region. *The Holocene*, 25(6), 944-955. <https://doi.org/10.1177/0959683615574586>
- Kastowski, M., Hinderer, M., & Vecsei, A. (2011). Long-term carbon burial in European lakes: Analysis and estimate: CARBON BURIAL IN EUROPEAN LAKES. *Global Biogeochemical Cycles*, 25(3), n/a-n/a. <https://doi.org/10.1029/2010GB003874>
- Kirdyanov, A. V., Krusic, P. J., Shishov, V. V., Vaganov, E. A., Fertikov, A. I., Myglan, V. S., Barinov, V. V., Browse, J., Esper, J., Ilyin, V. A., Knorre, A. A., Korets, M. A., Kukarskikh, V. V., Mashukov, D. A., Onuchin, A. A., Piermattei, A., Pimenov, A. V., Prokushkin, A. S., Ryzhkova, V. A., ... Büntgen, U. (2020). Ecological and conceptual consequences of Arctic pollution. *Ecology Letters*, 23(12), 1827-1837. <https://doi.org/10.1111/ele.13611>
- Kjellman, S. E., Thomas, E. K., Farnsworth, W. R., Cowling, O. C., Allaart, L., Brynjólfsson, S., & Schomacker, A. (2024). Seasonal precipitation variability on Svalbard inferred from Holocene sedimentary leaf wax $\delta^2\text{H}$. *Boreas*, 53(3), 1-20. <https://doi.org/10.1111/bor.12661>
- Kline, R. B. (2023). *Principles and practice of structural equation modeling* (Fifth edition). The Guilford Press.
- Kobashi, T., Kawamura, K., Severinghaus, J. P., Barnola, J.-M., Nakaegawa, T., Vinther, B. M., Johnsen, S. J., & Box, J. E. (2011). High variability of Greenland surface temperature over the past 4000 years estimated from trapped air in an ice core. *Geophysical Research Letters*, 38(21), 21501. <https://doi.org/10.1029/2011GL049444>

- Kohler, M., Niederberger, J., Wichser, A., Bierbaß, P., Rötzer, T., Spiecker, H., & Bauhus, J. (2019). Using tree rings to reconstruct changes in soil P availability – Results from forest fertilization trials. *Dendrochronologia*, 54, 11-19. <https://doi.org/10.1016/j.dendro.2019.01.001>
- Kramer, G. (Ed.). (1994). *Auditory display: Sonification, audification, and auditory interfaces*. International Conference on Auditory Display, Reading, Mass. Addison-Wesley.
- Krüger, N., Finn, D. R., & Don, A. (2024). Soil depth gradients of organic carbon-13 – A review on drivers and processes. *Plant and Soil*, 495(1-2), 113-136. <https://doi.org/10.1007/s11104-023-06328-5>
- Kruse, F. (2016). Is Svalbard a pristine ecosystem? Reconstructing 420 years of human presence in an Arctic archipelago. *Polar Record*, 52(5), 518-534. <https://doi.org/10.1017/S0032247416000309>
- Kulkarni, C., Finsinger, W., Anand, P., & Others. (2021). Synergistic impacts of anthropogenic fires and aridity on plant diversity in the Western Ghats: Implications for management of ancient social-ecological systems. *Journal of Environmental Management*, 283. <https://doi.org/10.1016/j.jenvman.2021.111957>
- Kuosmanen, N., Čada, V., Halsall, K., Chiverrell, R. C., Schafstall, N., Kuneš, P., Boyle, J. F., Knížek, M., Appleby, P. G., Svoboda, M., & Clear, J. L. (2020). Integration of dendrochronological and palaeoecological disturbance reconstructions in temperate mountain forests. *Forest Ecology and Management*, 475, 118413. <https://doi.org/10.1016/j.foreco.2020.118413>
- Kuwae, M., Yokoyama, Y., Tims, S., Froehlich, M., Fifield, L. K., Aze, T., Tsugeki, N., Doi, H., & Saito, Y. (2024). Toward defining the Anthropocene onset using a rapid increase in anthropogenic fingerprints in global geological archives. *Proceedings of the National Academy of Sciences*, 121(41), e2313098121. <https://doi.org/10.1073/pnas.2313098121>
- Lacourse, T., & Gajewski, K. (2020). Current practices in building and reporting age-depth models. *Quaternary Research*, 96, 28-38. <https://doi.org/10.1017/qua.2020.47>
- Ladwig, R., Heinrich, L., Singer, G., & Hupfer, M. (2017). Sediment core data reconstruct the management history and usage of a heavily modified urban lake in Berlin, Germany. *Environmental Science and Pollution Research*, 24(32), 25166-25178. <https://doi.org/10.1007/s11356-017-0191-z>

- Laird, N. M., & Ware, J. H. (1982). Random-Effects Models for Longitudinal Data. *Biometrics*, 38(4), 963. <https://doi.org/10.2307/2529876>
- Lapointe, F., Bradley, R. S., Francus, P., Balascio, N. L., Abbott, M. B., Stoner, J. S., St-Onge, G., Coninck, A., & Labarre, T. (2020). Annually resolved Atlantic sea surface temperature variability over the past 2,900 y. *Proceedings of the National Academy of Sciences*, 117(44), 27171-27178. <https://doi.org/10.1073/pnas.2014166117>
- Lapointe, F., Retelle, M., Bradley, R. S., Farnsworth, W. R., Støren, E., Cook, T., & Rosario, J. (2023). Multi-proxy evidence of unprecedented hydroclimatic change in a high Arctic proglacial lake: Linnévatnet, Svalbard. *Arctic, Antarctic, and Alpine Research*, 55(1), 2223403. <https://doi.org/10.1080/15230430.2023.2223403>
- Larsson, A., Segerström, U., Laudon, H., & Nilsson, M. B. (2017). Holocene carbon and nitrogen accumulation rates in a boreal oligotrophic fen. *The Holocene*, 27(6), 811-821. <https://doi.org/10.1177/0959683616675936>
- Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, 16(5), 545-556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Leeuwen, J., Schäfer, H., Knaap, W. O., & Others. (2005). Native or introduced? Fossil pollen and spores may say. An example from the Azores Islands. *Neobiota*, 6, 27-34.
- Legendre, P., & Cáceres, M. (2013). Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. *Ecology Letters*, 16, 951-963. <https://doi.org/10.1111/ele.12141>
- Legendre, P., & Legendre, L. (2012). *Numerical Ecology* (3rd ed.). Elsevier.
- Lenzi, S., & Ciuccarelli, P. (2020). Intentionality and design in the data sonification of social issues. *Big Data & Society*, 7(2), 2053951720944603. <https://doi.org/10.1177/2053951720944603>
- Levesque, M., Andreu-Hayles, L., Smith, W. K., Williams, A. P., Hobi, M. L., Allred, B. W., & Pederson, N. (2019). Tree-ring isotopes capture interannual vegetation productivity dynamics at the biome scale. *Nature Communications*, 10(1), 742. <https://doi.org/10.1038/s41467-019-08634-y>

- Li, H., Santos, F., Butler, K., & Herndon, E. (2021). A Critical Review on the Multiple Roles of Manganese in Stabilizing and Destabilizing Soil Organic Matter. *Environmental Science & Technology*, 55(18), 12136-12152. <https://doi.org/10.1021/acs.est.1c00299>
- Li, J., Du, J., Zhong, S., Ci, E., & Wei, C. (2021). Changes in the profile properties and chemical weathering characteristics of cultivated soils affected by anthropic activities. *Scientific Reports*, 11(1), 20822. <https://doi.org/10.1038/s41598-021-00302-w>
- Li, J., Yang, S., Smith, P., Li, J., Gu, X., Huo, H., Wei, Y., Zhao, L., Yu, M., & Ding, J. (2025). Peak accumulation of soil organic carbon in the early Holocene. *Science Bulletin*, 70(16), 2691-2700. <https://doi.org/10.1016/j.scib.2025.05.046>
- Li, J., Zhang, Y., & Katsev, S. (2018). Phosphorus recycling in deeply oxygenated sediments in Lake Superior controlled by organic matter mineralization. *Limnology and Oceanography*, 63(3), 1372-1385. <https://doi.org/10.1002/lno.10778>
- Li, X., Zhang, J., Rousk, K., Zhang, Y., Jiao, Y., Yan, P., & He, N. (2025). Leaf multi-dimensional stoichiometry as a robust predictor of productivity on the Tibetan Plateau. *Journal of Integrative Plant Biology*, 67(9), 2416-2429. <https://doi.org/10.1111/jipb.13960>
- Li, Y., Li, J., Are, K. S., Huang, Z., Yu, H., & Zhang, Q. (2019). Livestock grazing significantly accelerates soil erosion more than climate change in Qinghai-Tibet Plateau: Evidenced from ¹³⁷Cs and ²¹⁰Pbex measurements. *Agriculture, Ecosystems & Environment*, 285, 106643. <https://doi.org/10.1016/j.agee.2019.106643>
- Li, Y., Tian, D., Yang, H., & Niu, S. (2018). Size-dependent nutrient limitation of tree growth from subtropical to cold temperate forests. *Functional Ecology*, 32, 95-105. <https://doi.org/10.1111/1365-2435.12975>
- Lin, H. (2011). Three Principles of Soil Change and Pedogenesis in Time and Space. *Soil Science Society of America Journal*, 75(6), 2049-2070. <https://doi.org/10.2136/sssaj2011.0130>
- Lindborg, P., Lenzi, S., & Chen, M. (2023). Climate data sonification and visualization: An analysis of topics, aesthetics, and characteristics in 32 recent projects. *Frontiers in Psychology*, 13, 1020102. <https://doi.org/10.3389/fpsyg.2022.1020102>
- Ling, J., Dungait, J. A. J., Delgado-Baquerizo, M., Cui, Z., Zhou, R., Zhang, W., Gao, Q., Chen, Y., Yue, S., Kuzyakov, Y., Zhang, F., Chen, X., & Tian, J. (2025). Soil organic carbon thresholds

- control fertilizer effects on carbon accrual in croplands worldwide. *Nature Communications*, 16(1), 3009. <https://doi.org/10.1038/s41467-025-57981-6>
- Liu, J., Wang, H., Mou, J., Penuelas, J., Delgado-Baquerizo, M., Martiny, A. C., Zhou, G., Hutchins, D. A., Inomura, K., Lomas, M. W., Fakhraee, M., Pellegrini, A., Kohler, T. J., Deutsch, C. A., Planavsky, N., Lapointe, B., Zhang, Y., Li, Y., Zhou, J., ... Chen, J. (2025). Global-scale shifts in marine ecological stoichiometry over the past 50 years. *Nature Geoscience*, 18(8), 769-778. <https://doi.org/10.1038/s41561-025-01735-y>
- Liu, S., Kruse, S., Scherler, D., Ree, R. H., Zimmermann, H. H., Stoof-Leichsenring, K. R., Epp, L. S., Mischke, S., & Herzsuh, U. (2021). Sedimentary ancient DNA reveals a threat of warming-induced alpine habitat loss to Tibetan Plateau plant diversity. *Nature Communications*, 12(1), 2995. <https://doi.org/10.1038/s41467-021-22986-4>
- Liu, X., Sheng, H., Wang, Z., Ma, Z., Huang, X., & Li, L. (2020). Does Grazing Exclusion Improve Soil Carbon and Nitrogen Stocks in Alpine Grasslands on the Qinghai-Tibetan Plateau? A Meta-Analysis. *Sustainability*, 12(3), 977. <https://doi.org/10.3390/su12030977>
- Load Numbers. (s. f.). *Load Numbers*. <https://www.loudnumbers.net/>
- Loreau, M., Mouquet, N., & Holt, R. D. (2003). Meta-ecosystems: A theoretical framework for spatial ecosystem ecology. *Ecology Letters*, 6, 673-679. <https://doi.org/10.1046/j.1461-0248.2003.00483.x>
- Lourenco, M., Fitchett, J. M., & Woodborne, S. (2023). Peat definitions: A critical review. *Progress in Physical Geography: Earth and Environment*, 47(4), 506-520. <https://doi.org/10.1177/03091333221118353>
- Luo, M., Moorhead, D. L., Ochoa-Hueso, R., Mueller, C. W., Ying, S. C., & Chen, J. (2022). Nitrogen loading enhances phosphorus limitation in terrestrial ecosystems with implications for soil carbon cycling. *Functional Ecology*, 36(11), 2845-2858. <https://doi.org/10.1111/1365-2435.14178>
- Ma, B., Stirling, E., Liu, Y., Zhao, K., Zhou, J., Singh, B. K., Tang, C., Dahlgren, R. A., & Xu, J. (2021). Soil Biogeochemical Cycle Couplings Inferred from a Function-Taxon Network. *Research*, 2021, 2021/7102769. <https://doi.org/10.34133/2021/7102769>

- Makri, S., Wienhues, G., Bigalke, M., & Others. (2021). Variations of sedimentary Fe and Mn fractions under changing lake mixing regimes, oxygenation, and land surface processes during Late-glacial and Holocene times. *Science of the Total Environment*, 755, 143418. <https://doi.org/10.1016/j.scitotenv.2020.143418>
- Mann, C. C. (2012). *1493: How Europe's discovery of the Americas revolutionized trade, ecology and life on Earth*. Granta.
- Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, 27(2), 209-220.
- Margalef, R. (1978). *Life-forms of phytoplankton as survival alternatives in an unstable environment*. 1(4), 493-509.
- Martin, P., Boes, X., Goddeeris, B., & Fagel, N. (2005). A qualitative assessment of the influence of bioturbation in Lake Baikal sediments. *Global and Planetary Change*, 46(1-4), 87-99. <https://doi.org/10.1016/j.gloplacha.2004.11.012>
- Martinez, A. E. J., Garcia, M. J. B., De Assis Marques, F., Figueira, R. C. L., De Lima Ferreira, P. A., & Froehner, S. (2024). Examining the source and composition of organic matter through saturated hydrocarbons, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ in a subtropical water reservoir. *Science of The Total Environment*, 944, 173909. <https://doi.org/10.1016/j.scitotenv.2024.173909>
- Matthews, J., Marsh-Matthews, E., Cashner, C., & Gelwick, F. (2013). Disturbance and trajectory of change in a stream fish community over four decades. *Oecologia*, 173(3), 955-969. <https://doi.org/10.1007/s00442-013-2646-3>
- Mattsson, T., Kortelainen, P., Raike, A., Lepisto, A., & Thomas, D. N. (2015). Spatial and temporal variability of organic C and N concentrations and export from 30 boreal rivers induced by land use and climate. *Science of the Total Environment*, 508, 145-154. <https://doi.org/10.1016/j.scitotenv.2014.11.091>
- McCarthy, F. M., Patterson, R. T., Walsh, C., Lafond, K. M., Cumming, B. F., Cundy, A. B., Hain, K., Gaca, P., Steier, P., Boom, A., Hamilton, P. B., Pisaric, M. F., Head, M. J., Boyce, J. I., Rose, N. L., & Turner, S. D. (2025). High-resolution analysis of the varved succession at Crawford lake across the base of the proposed Crawfordian stage and Anthropocene series. *The Anthropocene Review*, 12(2), 243-272. <https://doi.org/10.1177/20530196251315454>

- McDermott, F. (2004). Palaeo-climate reconstruction from stable isotope variations in speleothems: A review. *Quaternary Science Reviews*, 23(7-8), 901-918.
<https://doi.org/10.1016/j.quascirev.2003.06.021>
- McGowan, S., Lacey, J. H., Engels, S., Boyle, J., Briddon, C., Leng, M. J., Moorhouse, H. L., Panizzo, V., & Shafiq, M. (2025). Land use, hydroclimate and damming influence organic carbon sedimentation in a flood pulse wetland, Malaysia. *Journal of Quaternary Science*, 40(4), 657-670. <https://doi.org/10.1002/jqs.3672>
- McLauchlan, K. K., Higuera, P. E., Gavin, D. G., Perakis, S. S., Mack, M. C., Alexander, H., Battles, J., Biondi, F., Buma, B., Colombaroli, D., Enders, S. K., Engstrom, D. R., Hu, F. S., Marlon, J. R., Marshall, J., McGlone, M., Morris, J. L., Nave, L. E., Shuman, B., ... Williams, J. J. (2014). Reconstructing disturbances and their biogeochemical consequences over multiple timescales. *BioScience*, 64(2), 105-116. <https://doi.org/10.1093/biosci/bit017>
- McLauchlan, K. K., Williams, J. J., Craine, J. M., & Jeffers, E. S. (2013). Changes in global nitrogen cycling during the Holocene epoch. *Nature*, 495, 352-355.
<https://doi.org/10.1038/nature11916>
- Milnes, A. R., & Fitzpatrick, R. W. (2018). Titanium and Zirconium Minerals. En J. B. Dixon & S. B. Weed (Eds.), *SSSA Book Series* (pp. 1131-1205). Soil Science Society of America.
<https://doi.org/10.2136/sssabookser1.2ed.c23>
- Mittelbach, B. V. A., Brunmayr, A. S., White, M. E., Rhyner, T. M. Y., Haghipour, N., Blattmann, T. M., Wessels, M., Dubois, N., & Eglinton, T. I. (2025). Pre-aged organic matter dominates organic carbon burial in a major perialpine lake system. *Limnology and Oceanography*, 70(4), 911-924. <https://doi.org/10.1002/lno.12815>
- Møller, A. P. (2019). Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. *Ecology and Evolution*, 9(11), 6581-6587. <https://doi.org/10.1002/ece3.5236>
- Montgomery, D. R. (2007). Soil erosion and agricultural sustainability. *Proceedings of the National Academy of Sciences*, 104(33), 13268-13272. <https://doi.org/10.1073/pnas.0611508104>
- Montgomery, D. R. (2012). *Dirt: The erosion of civilizations*. University of California Press.

- Monticelli, D., Di Iorio, A., Ciceri, E., Castelletti, A., & Dossi, C. (2009). Tree ring microanalysis by LA–ICP–MS for environmental monitoring: Validation or refutation? Two case histories. *Microchimica Acta*, 164(1-2), 139-148. <https://doi.org/10.1007/s00604-008-0049-7>
- Moreira, J. M. (1987). Alguns aspectos de intervenção humana na evolução da paisagem da ilha de S. En Miguel (Açores). *Serviço Nacional de Parques, Reservas e Conservação da Natureza*.
- Moyle, M., Boyle, J., Bennion, H., & Chiverrell, R. (2024). TP or Not TP? Successful Comparison of Two Independent Methods Validates Total Phosphorus Inference for Long-Term Eutrophication Studies. *Environmental Science & Technology*, 58(17), 7425-7432. <https://doi.org/10.1021/acs.est.4c01816>
- Mueller, J. R., Power, M. J., & Long, C. J. (2019). Climate and human influence on late Holocene fire regimes in the British Virgin Islands. *Quaternary Research*, 91(2), 679-690. <https://doi.org/10.1017/qua.2018.123>
- Murtagh, F., & Legendre, P. (2014). Ward's Hierarchical Agglomerative Clustering Method: Which Algorithms Implement Ward's Criterion? *Journal of Classification*, 31, 274-295. <https://doi.org/10.1007/s00357-014-9161-z>
- Nicolussi, K., Kaufmann, M., Patzelt, G., Plicht Van Der, J., & Thurner, A. (2005). Holocene tree-line variability in the Kauner Valley, Central Eastern Alps, indicated by dendrochronological analysis of living trees and subfossil logs. *Vegetation History and Archaeobotany*, 14(3), 221-234. <https://doi.org/10.1007/s00334-005-0013-y>
- Nogué, S., Morueta-Holme, N., Fernández-Palacios, J. M., Alsos, I. G., Brown, A., Roberts, P., & Peñuelas, J. (2025). Human transformation of past terrestrial ecosystems. *Nature Reviews Biodiversity*. <https://doi.org/10.1038/s44358-025-00081-6>
- Nogué, S., Nascimento, L., Fernández-Palacios, J. M., Whittaker, R. J., & Willis, K. J. (2013). The ancient forests of La Gomera, Canary Islands, and their sensitivity to environmental change. *Journal of Ecology*, 101(2), 368-377. <https://doi.org/10.1111/1365-2745.12051>
- Nogué, S., Nascimento, L., Froyd, C. A., Wilmshurst, J. M., Boer, E. J., Coffey, E. E. D., Whittaker, R. J., Fernández-Palacios, J. M., & Willis, K. J. (2017). Island biodiversity conservation needs palaeoecology. *Nature Ecology & Evolution*, 1, 0181. <https://doi.org/10.1038/s41559-017-0181>

- Nogué, S., Nascimento, L., Graham, L., & Others. (2022). The spatiotemporal distribution of pollen traits related to dispersal and desiccation tolerance in Canarian laurel forest. *Journal of Vegetation Science*, 33, 1-10. <https://doi.org/10.1111/jvs.13147>
- Nogué, S., Santos, A. M. C., Birks, H. J. B., Björck, S., Castilla-Beltrán, A., Connor, S., Boer, E. J., Nascimento, L., Felde, V. A., Fernández-Palacios, J. M., Froyd, C. A., Haberle, S. G., Hooghiemstra, H., Ljung, K., Norder, S. J., Peñuelas, J., Prebble, M., Stevenson, J., Whittaker, R. J., ... Steinbauer, M. J. (2024). The human dimension of biodiversity changes on islands. *Scientific Reports*. <https://doi.org/10.1038/s41598-024-62810-9>
- Nogué, S., Santos, A. M. C., Birks, H. J. B., Björck, S., Castilla-Beltrán, A., Connor, S., De Boer, E. J., De Nascimento, L., Felde, V. A., Fernández-Palacios, J. M., Froyd, C. A., Haberle, S. G., Hooghiemstra, H., Ljung, K., Norder, S. J., Peñuelas, J., Prebble, M., Stevenson, J., Whittaker, R. J., ... Steinbauer, M. J. (2021). The human dimension of biodiversity changes on islands. *Science*, 372(6541), 488-491. <https://doi.org/10.1126/science.abd6706>
- Nolan, C., Overpeck, J. T., Allen, J. R. M., Anderson, P. M., Betancourt, J. L., Binney, H. A., Brewer, S., Bush, M. B., Chase, B. M., Cheddadi, R., Djamali, M., Dodson, J., Edwards, M. E., Gosling, W. D., Haberle, S., Hotchkiss, S. C., Huntley, B., Ivory, S. J., & Jackson, S. T. (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science*, 361(6405), 920-923. <https://doi.org/10.1126/science.aan5360>
- Observatorio Pirenaico de Cambio Climático. (s. f.). *La Sinfonía de Marboré*. <https://opcc-ctp.org/es/noticia/sinfonia-marbore>
- Ochoa-Hueso, R., Delgado-Baquerizo, M., Risch, A. C., Schrama, M., Morriën, E., Barmentlo, S. H., Geisen, S., Hannula, S. E., Resch, M. C., Snoek, B. L., & Van Der Putten, W. H. (2021). Ecosystem coupling: A unifying framework to understand the functioning and recovery of ecosystems. *One Earth*, 4(7), 951-966. <https://doi.org/10.1016/j.oneear.2021.06.011>
- Ochoa-Hueso, R., Plaza, C., Moreno-Jiménez, E., & Delgado-Baquerizo, M. (2021). Soil element coupling is driven by ecological context and atomic mass. *Ecology Letters*, 24(2), 319-326. <https://doi.org/10.1111/ele.13648>
- Oksanen, J., Simpson, G., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H. H., Barbour, M. G., Bedward, M.,

- Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Cáceres, M., Durand, S., ... Furneaux, W. J. (2024). *Vegan: Community Ecology Package. R package version 2.6-5*.
- Olde Venterink, H. (2011). Does phosphorus limitation promote species-rich plant communities? *Plant and Soil*, 345(1-2), 1-9. <https://doi.org/10.1007/s11104-011-0796-9>
- Orr, T. J., & Roberts, E. M. (2024). A review and field guide for the standardized description and sampling of paleosols. *Earth-Science Reviews*, 253, 104788. <https://doi.org/10.1016/j.earscirev.2024.104788>
- Oulehle, F., Tahovská, K., Ač, A., Kolář, T., Rybníček, M., Čermák, P., Štěpánek, P., Trnka, M., Urban, O., & Hruška, J. (2022). Changes in forest nitrogen cycling across deposition gradient revealed by $\delta^{15}\text{N}$ in tree rings. *Environmental Pollution*, 304, 119104. <https://doi.org/10.1016/j.envpol.2022.119104>
- Owens, P. N., Deeks, L. K., Wood, G. A., Betson, M. J., Lord, E. I., & Davison, P. S. (2008). Variations in the depth distribution of phosphorus in soil profiles and implications for model-based catchment-scale predictions of phosphorus delivery to surface waters. *Journal of Hydrology*, 350(3-4), 317-328. <https://doi.org/10.1016/j.jhydrol.2007.10.043>
- Oxmann, J. F., Pham, Q. H., & Lara, R. J. (2008). Quantification of individual phosphorus species in sediment: A sequential conversion and extraction method. *European Journal of Soil Science*, 59(6), 1177-1190. <https://doi.org/10.1111/j.1365-2389.2008.01062.x>
- Pacheco, I., Acevedo, P., Prado, E., Mihalca, A. D., & De La Fuente, J. (2020). Targeting the Exoskeleton Elementome to Track Tick Geographic Origins. *Frontiers in Physiology*, 11, 572758. <https://doi.org/10.3389/fphys.2020.572758>
- Painter, T. J. (1991). Lindow man, tollund man and other peat-bog bodies: The preservative and antimicrobial action of Sphagnum, a reactive glycuronoglycan with tanning and sequestering properties. *Carbohydrate Polymers*, 15(2), 123-142. [https://doi.org/10.1016/0144-8617\(91\)90028-B](https://doi.org/10.1016/0144-8617(91)90028-B)
- Parducci, L., Bennett, K. D., Ficetola, G. F., Alsos, I. G., Suyama, Y., Wood, J. R., & Pedersen, M. W. (2017). Ancient plant DNA in lake sediments. *New Phytologist*, 214, 924-942. <https://doi.org/10.1111/nph.14412>

- Parenti, C., & Moore, J. W. (Eds.). (2016). *Anthropocene or capitalocene? Nature, history, and the crisis of capitalism*. PM Press.
- Park, H.-J., Baek, N., Lim, S.-S., Jeong, Y.-J., Seo, B.-S., Kwak, J.-H., Lee, S.-M., Yun, S.-I., Kim, H.-Y., Arshad, M. A., & Choi, W.-J. (2023). Coupling of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to understand soil organic matter sources and C and N cycling under different land-uses and management: A review and data analysis. *Biology and Fertility of Soils*, 59(5), 487-499.
<https://doi.org/10.1007/s00374-022-01668-3>
- Park, J.-H., Meusburger, K., Jang, I., Kang, H., & Alewell, C. (2014). Erosion-induced changes in soil biogeochemical and microbiological properties in Swiss Alpine grasslands. *Soil Biology and Biochemistry*, 69, 382-392. <https://doi.org/10.1016/j.soilbio.2013.11.021>
- Parks, S. A., Guiterman, C. H., Margolis, E. Q., Lonergan, M., Whitman, E., Abatzoglou, J. T., Falk, D. A., Johnston, J. D., Daniels, L. D., Lafon, C. W., Loehman, R. A., Kipfmueller, K. F., Naficy, C. E., Parisien, M.-A., Portier, J., Stambaugh, M. C., Williams, A. P., Wion, A. P., & Yocom, L. L. (2025). A fire deficit persists across diverse North American forests despite recent increases in area burned. *Nature Communications*, 16(1), 1493.
<https://doi.org/10.1038/s41467-025-56333-8>
- Pattyn, F. (2025, marzo 18). *The sound of ice: Using radar data and sonification in music composition*.
<https://doi.org/10.5194/egusphere-egu25-10270>
- Pearson, C., Manning, S. W., Coleman, M., & Jarvis, K. (2005). Can tree-ring chemistry reveal absolute dates for past volcanic eruptions? *Journal of Archaeological Science*, 32(8), 1265-1274. <https://doi.org/10.1016/j.jas.2005.03.007>
- Penrose, B. (1952). *Travel and discovery in the Renaissance, 1420–1620*. Cambridge University Press.
- Peñuelas, J. (2021). *GC52B-01: Increasing Biospheric Imbalances Between Nitrogen and Phosphorus. A New Driver of Global Change with Multiple Consequences for the Environment, Food Security and Human Health*. AGU Fall Meeting, New Orleans, USA.
- Peñuelas, J., Fernández-Martínez, M., Ciais, P., & Others. (2019). The bioelements, the elementome, and the biogeochemical niche. *Ecology*, 100, 1-15. <https://doi.org/10.1002/ecy.2652>.

- Peñuelas, J., Janssens, I. A., Ciais, P., & Others. (2020). Anthropogenic global shifts in biospheric N and P concentrations and ratios and their impacts on biodiversity, ecosystem productivity, food security, and human health. *Global Change Biology*, 26, 1962-1985.
<https://doi.org/10.1111/gcb.14981>.
- Peñuelas, J., & Nogué, S. (2023). Catastrophic climate change and the collapse of human societies. *National Science Review*, 10(6), nwad082. <https://doi.org/10.1093/nsr/nwad082>
- Pereira, C. L., Raposeiro, P. M., Costa, A. C., & Others. (2014). Biogeography and lake morphometry drive diatom and chironomid assemblages' composition in lacustrine surface sediments of oceanic islands. *Hydrobiologia*, 730, 93-112. <https://doi.org/10.1007/s10750-014-1824-6>.
- Pérez-Martínez, C., Rühland, K. M., Smol, J. P., Jones, V. J., & Conde-Porcuna, J. M. (2020). Long-term ecological changes in Mediterranean mountain lakes linked to recent climate change and Saharan dust deposition revealed by diatom analyses. *Science of The Total Environment*, 727, 138519. <https://doi.org/10.1016/j.scitotenv.2020.138519>
- Persson, L., Carney Almroth, B. M., Collins, C. D., Cornell, S., Wit, C. A., Diamond, M. L., Fantke, P., Hassellöv, M., MacLeod, M., Ryberg, M. W., Søgaard Jørgensen, P., Villarrubia-Gómez, P., Wang, Z., & Hauschild, M. Z. (2022). Outside the safe operating space of the planetary boundary for novel entities. *Environmental Science & Technology*, 56(3), 1510-1521.
<https://doi.org/10.1021/acs.est.1c04158>
- Pilcher, J. R., Baillie, M. G. L., Schmidt, B., & Becker, B. (1984). A 7,272-year tree-ring chronology for western Europe. *Nature*, 312(5990), 150-152. <https://doi.org/10.1038/312150a0>
- Pilla, R. M., Williamson, C. E., Adamovich, B. V., Adrian, R., Anneville, O., Chandra, S., Colom-Montero, W., Devlin, S. P., Dix, M. A., Dokulil, M. T., Gaiser, E. E., Girdner, S. F., Hambright, K. D., Hamilton, D. P., Havens, K., Hessen, D. O., Higgins, S. N., Huttula, T. H., Huuskonen, H., ... Zadereev, E. (2020). Deeper waters are changing less consistently than surface waters in a global analysis of 102 lakes. *Scientific Reports*, 10(1), 20514.
<https://doi.org/10.1038/s41598-020-76873-x>
- Pimentel, D., & Harvey, C. (1999). Ecological effects of erosion. En *Ecosystems of the World* (pp. 123-136).

- Pinchak, W. E., Smith, M. A., Hart, R. H., & Waggoner, J. W. (1991). Beef Cattle Distribution Patterns on Foothill Range. *Journal of Range Management*, 44(3), 267.
<https://doi.org/10.2307/4002956>
- Pinheiro, J., & Douglas, M. B. (2000). *Mixed-Effects Models in S and S-PLUS*. Springer-Verlag.
<https://doi.org/10.1007/b98882>
- Pla-Rabés, S., & Catalan, J. (2018). Diatom species variation between lake habitats: Implications for interpretation of paleolimnological records. *Journal of Paleolimnology*, 60(2), 169-187.
<https://doi.org/10.1007/s10933-018-0017-0>
- Pla-Rabés, S., Matias, M. G., Gonçalves, V., Loureiro, D. V., Marques, H., Bao, R., Buchaca, T., Hernández, A., Giralt, S., Sáez, A., Simpson, G. L., Nogué, S., & Raposeiro, P. M. (2024). Global warming triggers abrupt regime shifts in island lake ecosystems in the Azores Archipelago. *Communications Earth & Environment*, 5.
<https://doi.org/10.1038/s43247-024-01744-6>
- Power, M. J., Marlon, J., Ortiz, N., Bartlein, P. J., Harrison, S. P., Mayle, F. E., Ballouche, A., Bradshaw, R. H. W., Carcaillet, C., Cordova, C., Mooney, S., Moreno, P. I., Prentice, I. C., Thonicke, K., Tinner, W., Whitlock, C., Zhang, Y., Zhao, Y., Ali, A. A., ... Zhang, J. H. (2008). Changes in fire regimes since the Last Glacial Maximum: An assessment based on a global synthesis and analysis of charcoal data. *Climate Dynamics*, 30(7-8), 887-907.
<https://doi.org/10.1007/s00382-007-0334-x>
- Prentice, I. C., & Raynaud, D. (2001). Paleobiogeochemistry. En *Global Biogeochemical Cycles in the Climate System* (pp. 87-94). Elsevier. <https://doi.org/10.1016/B978-012631260-7/50009-1>
- Processing Foundation. (2025). *Processing*. [Software]. <https://processing.org/>
- Provete, C. S., Dalfior, B. M., Mantovaneli, R., Carneiro, M. T. W. D., & Brandão, G. P. (2024). Comparison of the Performance of ICP-MS, CV-ICP-OES, and TDA AAS in Determining Mercury in Marine Sediment Samples. *ACS Omega*, 9(50), 49229-49238.
<https://doi.org/10.1021/acsomega.4c06144>
- Putfarken, D., Dengler, J., Lehmann, S., & Härdtle, W. (2008). Site use of grazing cattle and sheep in a large-scale pasture landscape: A GPS/GIS assessment. *Applied Animal Behaviour Science*, 111(1-2), 54-67. <https://doi.org/10.1016/j.applanim.2007.05.012>

- Qin, B., Zhou, J., Elser, J. J., Gardner, W. S., Deng, J., & Brookes, J. D. (2020). Water Depth Underpins the Relative Roles and Fates of Nitrogen and Phosphorus in Lakes. *Environmental Science & Technology*, 54(6), 3191-3198. <https://doi.org/10.1021/acs.est.9b05858>
- Quinton, J. N., Govers, G., Oost, K., & Bardgett, R. D. (2010). The impact of agricultural soil erosion on biogeochemical cycling. *Nature Geoscience*, 3(5), 311-314. <https://doi.org/10.1038/ngeo838>
- Rahman, M., Chaity, I. J., Hossain, Md. I. S., & Siddique, M. A. M. (2024). Surface water pollution by some heavy metals in a remote island, Hatiya, northern Bay of Bengal. *Journal of Trace Elements and Minerals*, 8, 100150. <https://doi.org/10.1016/j.jtemin.2024.100150>
- Raposeiro, P. M., Hernández, A., Pla-Rabés, S., & Others. (2021). Climate change facilitated the early colonization of the Azores Archipelago during medieval times. *Proceedings of the National Academy of Sciences of the United States of America*, 118, 1-7. <https://doi.org/10.1073/pnas.2108236118>.
- Raposeiro, P. M., Ritter, C., Abbott, M., Hernández, A., Pimentel, A., Lasher, E., Plóciennik, M., Berljajoli, V., Kotrys, B., Pontevedra-Pombal, X., Souto, M., Giralt, S., & Gonçalves, V. (2024). Late Holocene climate dynamics in the Azores Archipelago. *Quaternary Science Reviews*, 331, 108617. <https://doi.org/10.1016/j.quascirev.2023.108617>.
- Raposeiro, P. M., Rubio, M. J., González, A., & Others. (2017). Impact of the historical introduction of exotic fishes on the chironomid community of Lake Azul (Azores Islands). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 466, 77-88. <https://doi.org/10.1016/j.palaeo.2016.11.015>.
- Rapuc, W., Giguët-Covex, C., Bouchez, J., Sabatier, P., Gaillardet, J., Jacq, K., Genuite, K., Poulénard, J., Messenger, E., & Arnaud, F. (2024). Human-triggered magnification of erosion rates in European Alps since the Bronze Age. *Nature Communications*, 15(1), 1246. <https://doi.org/10.1038/s41467-024-45123-3>
- Rashid, I., Mir, S. H., Zurro, D., Dar, R. A., & Reshi, Z. A. (2019). Phytoliths as proxies of the past. *Earth-Science Reviews*, 194, 234-250. <https://doi.org/10.1016/j.earscirev.2019.05.005>
- Ravazzi, C., Mariani, M., Criado, C., Garozzo, L., Naranjo-Cigala, A., Pérez-Torrado, F. J., Pini, R., Rodríguez-González, A., Nogué, S., Whittaker, R. J., Fernández-Palacios, J. M., & Nascimento, L. (2021). The influence of natural fire and cultural practices on island

- ecosystems: Insights from a 4,800-year record from Gran Canaria, Canary Islands. *Journal of Biogeography*, 48(2), 276-290. <https://doi.org/10.1111/jbi.13995>
- Reimer, P. J., Austin, W. E. N., Bard, E., & Others. (2020). The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP. *Radiocarbon*, 62(4), 725-757. <https://doi.org/10.1017/RDC.2020.41>.
- Ren, S., Terrer, C., Li, J., Cao, Y., Yang, S., & Liu, D. (2024). Historical impacts of grazing on carbon stocks and climate mitigation opportunities. *Nature Climate Change*, 14(4), 380-386. <https://doi.org/10.1038/s41558-024-01957-9>
- Rengel, Z. (2007). Cycling of Micronutrients in Terrestrial Ecosystems. En P. Marschner & Z. Rengel (Eds.), *Nutrient Cycling in Terrestrial Ecosystems* (Vol. 10, pp. 93-121). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-68027-7_4
- Richardson, K., Steffen, W., Lucht, W., Bendtsen, J., Cornell, S. E., Donges, J. F., Drüke, M., Fetzer, I., Bala, G., Von Bloh, W., Feulner, G., Fiedler, S., Gerten, D., Gleeson, T., Hofmann, M., Huiskamp, W., Kummu, M., Mohan, C., Nogués-Bravo, D., ... Rockström, J. (2023). Earth beyond six of nine planetary boundaries. *Science Advances*, 9(37), eadh2458. <https://doi.org/10.1126/sciadv.adh2458>
- Richter, N., Russell, J. M., Amaral-Zettler, L., & Others. (2022). Long-term hydroclimate variability in the sub-tropical North Atlantic and anthropogenic impacts on lake ecosystems: A case study from Flores Island, the Azores. *Quaternary Science Reviews*, 285, 107525. <https://doi.org/10.1016/j.quascirev.2022.107525>.
- Ríos, N., Frias, J. P. G. L., Rodríguez, Y., Carriço, R., Garcia, S. M., Juliano, M., & Pham, C. K. (2018). Spatio-temporal variability of beached macro-litter on remote islands of the North Atlantic. *Marine Pollution Bulletin*, 133, 304-311. <https://doi.org/10.1016/j.marpolbul.2018.05.038>
- Ritter, C., Gonçalves, V., Pla-Rabés, S., & Others. (2022). The vanishing and the establishment of a new ecosystem on an oceanic island – Anthropogenic impacts with no return ticket. *Science of the Total Environment*, 830, 154828. <https://doi.org/10.1016/j.scitotenv.2022.154828>.
- Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F. S., Lambin, E. F., Lenton, T. M., Scheffer, M., Folke, C., Schellnhuber, H. J., Nykvist, B., De Wit, C. A., Hughes, T., Van Der

- Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P. K., Costanza, R., Svedin, U., ... Foley, J. A. (2009). A safe operating space for humanity. *Nature*, 461(7263), 472-475.
<https://doi.org/10.1038/461472a>
- Rodríguez-Hernández, Á., Díaz-Díaz, R., Zumbado, M., & Others. (2022). Impact of chemical elements released by the volcanic eruption of La Palma (Canary Islands, Spain) on banana agriculture and European consumers. *Chemosphere*, 293, 133508.
<https://doi.org/10.1016/j.chemosphere.2021.133508>.
- Roig, F. A., Le-Quesne, C., Boninsegna, J. A., Briffa, K. R., Lara, A., Grudd, H., Jones, P. D., & Villagrán, C. (2001). Climate variability 50,000 years ago in mid-latitude Chile as reconstructed from tree rings. *Nature*, 410(6828), 567-570. <https://doi.org/10.1038/35069040>
- Rothwell, R. G. (2006). New techniques in sediment core analysis. *Geological Society, London, Special Publications*, 267(1).
- Ruddiman, W. F. (2003). The Anthropogenic Greenhouse Era Began Thousands of Years Ago. *Climatic Change*, 61(3), 261-293. <https://doi.org/10.1023/B:CLIM.00000004577.17928.fa>
- Ruddiman, W. F. (2018). Three flaws in defining a formal 'Anthropocene'. *Progress in Physical Geography: Earth and Environment*, 42(4), 451-461.
<https://doi.org/10.1177/0309133318783142>
- Rull, V., Lara, A., Rubio-Inglés, M. J., & Others. (2017). Vegetation and landscape dynamics under natural and anthropogenic forcing on the Azores Islands: A 700-year pollen record from São Miguel Island. *Quaternary Science Reviews*, 159, 155-168.
<https://doi.org/10.1016/j.quascirev.2017.01.021>.
- Russell, J. C., Meyer, J.-Y., Holmes, N. D., & Pagad, S. (2017). Invasive alien species on islands: Impacts, distribution, interactions and management. *Environmental Conservation*, 44(4), 359-370. <https://doi.org/10.1017/S0376892917000297>
- Russo, M., Gernon, T. M., Santaguida, A., & Hincks, T. K. (2024). Improving Earth science communication and accessibility with data sonification. *Nature Reviews Earth & Environment*, 5(1), 1-3. <https://doi.org/10.1038/s43017-023-00512-y>

- Sadler, P. M., & Jerolmack, D. J. (2015). Scaling laws for aggradation, denudation and progradation rates: The case for time-scale invariance at sediment sources and sinks. *Geological Society, London, Special Publications*, 404(1), 69-88. <https://doi.org/10.1144/SP404.7>
- Sánchez-López, G., Hernández, A., Pla-Rabés, S., & Others. (2016). Climate reconstruction for the last two millennia in central Iberia: The role of East Atlantic (EA), North Atlantic Oscillation (NAO), and their interplay over the Iberian Peninsula. *Quaternary Science Reviews*, 149, 135-150. <https://doi.org/10.1016/j.quascirev.2016.07.021>.
- Sánchez-Pinillos, M., Kéfi, S., Cáceres, M., & Dakos, V. (2023). Ecological dynamic regimes: Identification, characterization, and comparison. *Ecological Monographs*, 93, 1-31. <https://doi.org/10.1002/ecm.1589>.
- Sánchez-Salguero, R., Camarero, J. J., Hevia, A., Sangüesa-Barreda, G., Galván, J. D., & Gutiérrez, E. (2019). Testing annual tree-ring chemistry by X-ray fluorescence for dendroclimatic studies in high-elevation forests from the Spanish Pyrenees. *Quaternary International*, 514, 130-140. <https://doi.org/10.1016/j.quaint.2018.09.007>
- Santana, J., Del Pino, M., Morales, J., Fregel, R., Hagenblad, J., Morquecho, A., & Gilson, S. P. (2024). The chronology of the human colonisation of the Canary Islands. *Proceedings of the National Academy of Sciences*, 121(28), 2302924121. <https://doi.org/10.1073/pnas.2302924121>
- Santisteban, J. I., Mediavilla, R., López-Pamo, E., Dabrio, C. J., Zapata, M. B. R., García, M. J. G., Castaño, S., & Martínez-Alfaro, P. E. (2004). Loss on ignition: A qualitative or quantitative method for organic matter and carbonate mineral content in sediments? *Journal of Paleolimnology*, 32(3), 287-299. <https://doi.org/10.1023/B:JOPL.0000042999.30131.5b>.
- Sardans, J., & Penuelas, J. (2024). Atomic ecology: Coupling atoms and ecology. *Science Bulletin*, 69(1), 11-16. <https://doi.org/10.1016/j.scib.2023.11.037>
- Sardans, J., & Peñuelas, J. (2015). Potassium: A neglected nutrient in global change. *Global Ecology and Biogeography*, 24(3), 261-275. <https://doi.org/10.1111/geb.12259>
- Sardans, J., & Peñuelas, J. (2024). Atomic ecology: Coupling atoms and ecology. *Science Bulletin*, 69, 11-16. <https://doi.org/10.1016/j.scib.2023.11.037>.

- Sardans, J., Rivas-Ubach, A., & Peñuelas, J. (2012). The C:N stoichiometry of organisms and ecosystems in a changing world: A review and perspectives. *Perspectives in Plant Ecology, Evolution and Systematics*, 14, 33-47. <https://doi.org/10.1016/j.ppees.2011.08.002>.
- Sardans, J., Vallicrosa, H., Zuccarini, P., & Others. (2021). Empirical support for the biogeochemical niche hypothesis in forest trees. *Nature Ecology & Evolution*, 5, 184-194. <https://doi.org/10.1038/s41559-020-01348-1>.
- Sarkar, S., Ahmed, T., Swami, K., Judd, C. D., Bari, A., Dutkiewicz, V. A., & Husain, L. (2015). History of atmospheric deposition of trace elements in lake sediments, ~1880 to 2007. *Journal of Geophysical Research: Atmospheres*, 120(11), 5658-5669. <https://doi.org/10.1002/2015JD023202>
- Sayedi, S. S., Abbott, B. W., Vannière, B., & Others. (2024). Assessing changes in global fire regimes. *Fire Ecology*, 20. <https://doi.org/10.1186/s42408-023-00237-9>.
- Scaife, R. G., Long, A. J., Monteath, A. J., Hughes, P. D. M., Bentley, M. J., & Stone, P. (2019). The Falkland Islands' palaeoecological response to millennial-scale climate perturbations during the Pleistocene–Holocene transition: Implications for future vegetation stability in the southern ocean islands. *Journal of Quaternary Science*, 34(8), 609-620. <https://doi.org/10.1002/jqs.3150>
- Schillereff, D. N., Boyle, J. F., Toberman, H., Adams, J. L., Bryant, C. L., Chiverrell, R. C., Helliwell, R. C., Keenan, P., Lilly, A., & Tipping, E. (2016). Long-term macronutrient stoichiometry of UK ombrotrophic peatlands. *Science of The Total Environment*, 572, 1561-1572. <https://doi.org/10.1016/j.scitotenv.2016.03.180>
- Schneider, L., Allen, K., Walker, M., Morgan, C., & Haberle, S. (2019). Using Tree Rings to Track Atmospheric Mercury Pollution in Australia: The Legacy of Mining in Tasmania. *Environmental Science & Technology*, 53(10), 5697-5706. <https://doi.org/10.1021/acs.est.8b06712>
- Schomacker, A., Farnsworth, W. R., Ingólfsson, Ó., Allaart, L., Håkansson, L., Retelle, M., Siggaard-Andersen, M.-L., Korsgaard, N. J., Rouillard, A., & Kjellman, S. E. (2019). Postglacial relative sea level change and glacier activity in the early and late Holocene: Wahlenbergfjorden, Nordaustlandet, Svalbard. *Scientific Reports*, 9, 6799. <https://doi.org/10.1038/S31598-019-43342-z>

- Sear, D. A., Allen, M. S., Hassall, J. D., Maloney, A. E., Langdon, P. G., Morrison, A. E., Henderson, A. C. G., Mackay, H., Croudace, I. W., Clarke, C., Sachs, J. P., Macdonald, G., Chiverrell, R. C., Leng, M. J., Cisneros-Dozal, L. M., Fonville, T., & Pearson, E. (2020). Human settlement of East Polynesia earlier, incremental, and coincident with prolonged South Pacific drought. *Proceedings of the National Academy of Sciences*, 117(16), 8813-8819.
<https://doi.org/10.1073/pnas.1920975117>pnas.org
- Sellers, H., Williams, M., Berrio, J. C., De Sabbata, S., Rose, N. L., Turner, S. D., Yang, H., Bennion, H., Sayer, C. D., Roberts, N., Wrisdale, A., & Aquino-Lopez, M. A. (2025). A mid-20th century stratigraphical Anthropocene is recognisable in the birth-area of the industrial revolution. *The Anthropocene Review*, 12(2), 176-200. <https://doi.org/10.1177/20530196241306407>
- Sheppard, P. R. (2010). Dendroclimatology: Extracting climate from trees. *WIREs Climate Change*, 1(3), 343-352. <https://doi.org/10.1002/wcc.42>
- Silveira, P., & Dentinho, T. (2010). Spatial interaction model of land use: An application to Corvo Island from the 16th, 19th and 20th centuries. *Computers, Environment and Urban Systems*, 34(2), 91-103. <https://doi.org/10.1016/j.compenvurbsys.2009.10.003>
- Sitters, J., Kimuyu, D. M., Young, T. P., Claeys, P., & Olde Venterink, H. (2020). Negative effects of cattle on soil carbon and nutrient pools reversed by megaherbivores. *Nature Sustainability*, 3(5), 360-366. <https://doi.org/10.1038/s41893-020-0490-0>
- Skov, T., Buchaca, T., Amsinck, S. L., & Others. (2010). Using invertebrate remains and pigments in the sediment to infer changes in trophic structure after fish introduction in Lake Fogo: A crater lake in the Azores. *Hydrobiologia*, 654, 13-25. <https://doi.org/10.1007/s10750-010-0325-5>.
- Smółka-Danielowska, D., & Jabłońska, M. (2021). Chemical and mineral composition of ashes from wood biomass combustion in domestic wood-fired furnaces. *International Journal of Environmental Science and Technology*, 18(10), 3041-3054.
<https://doi.org/10.1007/s13762-021-03506-9>.
- Speranza, C., Giralt, S., Lupo, L., & Others. (2019). Paleoenvironmental reconstruction of the semi-arid Chaco region of Argentina based on multiproxy lake records over the last six hundred years. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 524, 85-100.
<https://doi.org/10.1016/j.palaeo.2019.03.037>.

- Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O., & Ludwig, C. (2015). The trajectory of the Anthropocene: The Great Acceleration. *The Anthropocene Review*, 2(1), 81-98.
<https://doi.org/10.1177/2053019614564785>
- Steffen, W., Richardson, K., Rockström, J., Cornell, S. E., Fetzer, I., Bennett, E. M., Biggs, R., Carpenter, S. R., Vries, W., Wit, C. A., Folke, C., Gerten, D., Heinke, J., Mace, G. M., Persson, L. M., Ramanathan, V., Reyers, B., & Sörlin, S. (2015). Planetary boundaries: Guiding human development on a changing planet. *Science*, 347(6223), 1259855.
<https://doi.org/10.1126/science.1259855>
- Stein, R. A., Sheldon, N. D., Allen, S. E., Smith, M. E., Dzombak, R. M., & Jicha, B. R. (2021). Climate and ecology in the Rocky Mountain interior after the early Eocene Climatic Optimum. *Climate of the Past*, 17(6), 2515-2536. <https://doi.org/10.5194/cp-17-2515-2021>
- Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., Bjorkman, A. D., Breiner, F. T., Burg, S., Czortek, P., Dawes, M. A., Delimat, A., Dullinger, S., Erschbamer, B., Felde, V. A., ... Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, 556(7700), 231-234. <https://doi.org/10.1038/s41586-018-0005-6>
- Sterner, R. W., & Elser, J. J. (2002). *Ecological stoichiometry: The biology of elements from molecules to the biosphere*. Princeton University Press.
- Stoppani, A. (1873). *Corso di Geologia* (Vol. 3). G. Bernardoni e G. Brigola.
- Strandberg, N. A., Steinbauer, M. J., Walentowitz, A., Gosling, W. D., Fall, P. L., Prebble, M., Stevenson, J., Wilmshurst, J. M., Sear, D. A., Langdon, P. G., Edwards, M. E., & Nogué, S. (2024a). Floristic homogenization of South Pacific islands commenced with human arrival. *Nature Ecology & Evolution*, 8(3), 511-518. <https://doi.org/10.1038/S31559-023-02306-3>
- Strandberg, N. A., Steinbauer, M. J., Walentowitz, A., Gosling, W. D., Fall, P. L., Prebble, M., Stevenson, J., Wilmshurst, J. M., Sear, D. A., Langdon, P. G., Edwards, M. E., & Nogué, S. (2024b). Increases in large-scale plant similarity driven by ancient human impacts. *Nature Ecology & Evolution*, 8(3), 370-371. <https://doi.org/10.1038/S31559-024-02321-y>

- Streeter, R. T., Dugmore, A., Lawson, I. T., Erlendsson, E., & Edwards, K. (2015). The onset of the palaeoanthropocene in Iceland: Changes in complex natural systems. *The Holocene*, 25(10), 1662-1675. <https://doi.org/10.1177/0959683615594468>
- Sturbois, A., Cáceres, M., Bifulchi, & Others. (2023). Ecological quality assessment: A framework to report ecosystems quality and their dynamics from reference conditions. *Ecosphere*, 14(12). <https://doi.org/10.1002/ecs2.4726>.
- Sturbois, A., Cáceres, M., Sánchez-Pinillos, M., & Others. (2023). Extending community trajectory analysis: New metrics and representation. *Ecological Modelling*, 440, 109400. <https://doi.org/10.1016/j.ecolmodel.2020.109400>.
- Sturbois, A., Cucherousset, J., Cáceres, M., & Others. (2021). Stable Isotope Trajectory Analysis (SITA): A new approach to quantify and visualize dynamics in stable isotope studies. *Ecological Monographs*, 92(2), 1501. <https://doi.org/10.1002/ecm.1501>.
- Su, J., Xu, F., & Zhang, Y. (2023). Grassland biodiversity and ecosystem functions benefit more from cattle than sheep in mixed grazing: A meta-analysis. *Journal of Environmental Management*, 337, 117769. <https://doi.org/10.1016/j.jenvman.2023.117769>
- Sun, Y., Wang, C., Chen, H. Y. H., & Others. (2021). *Asymmetric responses of terrestrial C:N*.
- Sundquist, E. (1993). The global carbon dioxide budget. *Science*, 259, 934-941. <https://doi.org/10.1126/science.259.5097.934>.
- Svensk, M., Pittarello, M., Mariotte, P., Nota, G., Schneider, M. K., Frund, D., Dubois, S., Allan, E., & Probo, M. (2023). Nitrogen translocation by Highland cattle grazing in *Alnus viridis*-encroached pastures. *Nutrient Cycling in Agroecosystems*, 126(1), 127-141. <https://doi.org/10.1007/s10705-023-10282-0>
- Swindles, G. T., Plunkett, G., & Roe, H. M. (2007). A delayed climatic response to solar forcing at 2800 cal. BP: Multiproxy evidence from three Irish peatlands. *The Holocene*, 17(2), 177-182. <https://doi.org/10.1177/0959683607075830>
- Tamalavage, A. E., Hengstum, P. J., Louchouart, P., Molodtsov, S., Kaiser, K., Donnelly, J. P., Albury, N. A., & Fall, P. L. (2018). Organic matter sources and lateral sedimentation in a Bahamian karst basin (sinkhole) over the late Holocene: Influence of local vegetation and climate.

- Palaeogeography, Palaeoclimatology, Palaeoecology*, 506, 70-83.
<https://doi.org/10.1016/j.palaeo.2018.06.014>
- Team, R. C. (2023). *R: A language and environment for statistical computing*. Foundation for Statistical Computing.
- Tershy, B. R., Shen, K.-W., Newton, K. M., Holmes, N. D., & Croll, D. A. (2015). The importance of islands for the protection of biological and linguistic diversity. *BioScience*, 65(6), 592-597.
<https://doi.org/10.1093/biosci/biv031>
- Tiberti, R., Rogora, M., Tartari, G., & Callieri, C. (2014). Ecological impact of transhumance on the trophic state of alpine lakes in Gran Paradiso National Park. *Knowledge and Management of Aquatic Ecosystems*, 415, 05. <https://doi.org/10.1051/kmae/2014030>
- Tipping, E., Boyle, J. F., Schillereff, D. N., Spears, B. M., & Phillips, G. (2016). Macronutrient processing by temperate lakes: A dynamic model for long-term, large-scale application. *Science of The Total Environment*, 572, 1573-1585.
<https://doi.org/10.1016/j.scitotenv.2015.09.129>
- Tipping, E., Davies, J. A. C., Henrys, P. A., Kirk, G. J. D., Lilly, A., Dragosits, U., Carnell, E. J., Dore, A. J., Sutton, M. A., & Tomlinson, S. J. (2017). Long-term increases in soil carbon due to ecosystem fertilization by atmospheric nitrogen deposition demonstrated by regional-scale modelling and observations. *Scientific Reports*, 7(1), 1890.
<https://doi.org/10.1038/s41598-017-02002-w>
- Tomlinson, G., Siegwolf, R. T. W., Buchmann, N., Schleppi, P., Waldner, P., & Weber, P. (2014). The mobility of nitrogen across tree-rings of Norway spruce (*Picea abies* L.) and the effect of extraction method on tree-ring $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. *Rapid Communications in Mass Spectrometry*, 28(11), 1258-1264. <https://doi.org/10.1002/rcm.6897>
- Toro-Valdivieso, C., Jugdaohsingh, R., Powell, J. J., Hoffman, J. I., Forcada, J., Moore, C., & Blacklaws, B. (2023). Heavy metal contamination in pristine environments: Lessons from the Juan Fernandez fur seal (*Arctocephalus philippii philippii*). *Royal Society Open Science*, 10(3), 221237. <https://doi.org/10.1098/rsos.221237>

- Torres, I. C., Inglett, P. W., Brenner, M., Kenney, W. F., & Ramesh Reddy, K. (2012). Stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values of sediment organic matter in subtropical lakes of different trophic status. *Journal of Paleolimnology*, 47(4), 693-706. <https://doi.org/10.1007/s10933-012-9593-6>
- Toumi, C., Cáceres, M., Grall, J., & Others. (2023). Long-term coastal macrobenthic community trajectory analysis reveals habitat-dependent stability patterns. *Ecography*, 1-15. <https://doi.org/10.1111/ecog.06489>.
- Tu, L., Gilli, A., Lotter, A. F., Vogel, H., Moyle, M., Boyle, J. F., & Grosjean, M. (2020). The nexus among long-term changes in lake primary productivity, deep-water anoxia, and internal phosphorus loading, explored through analysis of a 15,000-year varved sediment record. *Quaternary Science Reviews*, 233, 106222. <https://doi.org/10.1016/j.quascirev.2020.106222>.
- Tu, L., Moyle, M., Boyle, J. F., Zander, P. D., Huang, T., Meng, L., Huang, C., Zhou, X., & Grosjean, M. (2023). Anthropogenic modification of phosphorus sequestration in lake sediments during the Holocene: A global perspective. *Global and Planetary Change*, 229, 104222. <https://doi.org/10.1016/j.gloplacha.2023.104222>
- Turner, B. L., Condon, L. M., France, C. A. M., Lehmann, J., Solomon, D., Peltzer, D. A., & Richardson, S. J. (2016). Sulfur dynamics during long-term ecosystem development. *Biogeochemistry*, 128(3), 281-305. <https://doi.org/10.1007/s10533-016-0208-6>
- Twotone. (2025). *Twotone* [Software]. <https://twotone.io/>
- VAN NISPEN, T., & REBEL, K. T. (2025). «HARMONY IN COMPLEXITY» • A MUSICAL DATA SONIFICATION OF ONE CENTURY OF CLIMATE DATA. <https://doi.org/10.5281/ZENODO.15839860>
- Vázquez-Loureiro, D., Gonçalves, V., Sáez, A., Hernández, A., Raposeiro, P. M., Giralt, S., & Bao, R. (2019). Diatom-inferred ecological responses of an oceanic lake system to volcanism and anthropogenic perturbations since 1290 CE. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 534, 109285. <https://doi.org/10.1016/j.palaeo.2019.109285>.
- Vázquez-Loureiro, D., Sáez, A., Gonçalves, V., & Others. (2023). Recent global warming induces the coupling of dissimilar long-term sedimentary signatures in two adjacent volcanic lakes (Azores Archipelago, Portugal). *Quaternary Science Reviews*, 303. <https://doi.org/10.1016/j.quascirev.2023.107968>.

- Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). Springer-Verlag.
- Verburg, P. (2007). The need to correct for the Suess effect in the application of $\delta^{13}\text{C}$ in sediment of autotrophic Lake Tanganyika, as a productivity proxy in the Anthropocene. *Journal of Paleolimnology*, 37(4), 591-602. <https://doi.org/10.1007/s10933-006-9056-z>
- Vésteinsson, O., & McGovern, T. H. (2012). The peopling of Iceland. *Norwegian Archaeological Review*, 45(2), 206-218. <https://doi.org/10.1080/00293652.2012.721792>
- Vimeux, F., Ginot, P., Schwikowski, M., Vuille, M., Hoffmann, G., Thompson, L. G., & Schotterer, U. (2009). Climate variability during the last 1000 years inferred from Andean ice cores: A review of methodology and recent results. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 281(3-4), 229-241. <https://doi.org/10.1016/j.palaeo.2008.03.054>
- Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science*, 277(5325), 494-499. <https://doi.org/10.1126/science.277.5325.494>
- Voldstad, L. H., Alsos, I. G., Farnsworth, W. R., Heintzman, P. D., Håkansson, L., Kjellman, S. E., Rouillard, A., Schomacker, A., & Eidesen, P. B. (2020). A complete Holocene lake sediment ancient DNA record reveals long-standing high Arctic plant diversity hotspot in northern Svalbard. *Quaternary Science Reviews*, 234, 106207. <https://doi.org/10.1016/j.quascirev.2020.106207>
- Vollweiler, N., Scholz, D., Mühlinghaus, C., Mangini, A., & Spötl, C. (2006). A precisely dated climate record for the last 9 kyr from three high alpine stalagmites, Spannagel Cave, Austria. *Geophysical Research Letters*, 33(20), 2006GL027662. <https://doi.org/10.1029/2006GL027662>
- Waal, D. B., Verschoor, A. M., Verspagen, J. M. H., & Others. (2010). Climate-driven changes in the ecological stoichiometry of aquatic ecosystems. *Frontiers in Ecology and the Environment*, 8, 145-152. <https://doi.org/10.1890/080178>
- Walentowitz, A., Lenzner, B., Essl, F., Strandberg, N., Castilla-Beltrán, A., Fernández-Palacios, J. M., Björck, S., Connor, S., Haberle, S. G., Ljung, K., Prebble, M., Wilmshurst, J. M., Froyd, C. A., Boer, E. J., Nascimento, L., Edwards, M. E., Stevenson, J., Beierkuhnlein, C., Steinbauer, M. J., & Nogué, S. (2023). Long-term trajectories of non-native vegetation on islands globally. *Ecology Letters*, 26(5), 729-741. <https://doi.org/10.1111/ele.14196>

- Walker, B. N. (2023). The past, present, and promise of sonification. *Arbor*, 199(810), a728.
<https://doi.org/10.3989/arbor.2023.810008>
- Walsh, S., Riveros-Iregui, D., Arce-Nazario, J., & Page, P. (Eds.). (2020). *Land Cover and Land Use Change on Islands*. Springer. <https://doi.org/10.1007/978-3-030-43973-6>.
- Wang, M., Houlton, B. Z., Wang, S., Ren, C., Van Grinsven, H. J. M., Chen, D., Xu, J., & Gu, B. (2021). Human-caused increases in reactive nitrogen burial in sediment of global lakes. *The Innovation*, 2(4), 100158. <https://doi.org/10.1016/j.xinn.2021.100158>
- Wang, Y., Li, Y., Ye, X., Chu, Y., & Wang, X. (2010). Profile storage of organic/inorganic carbon in soil: From forest to desert. *Science of The Total Environment*, 408(8), 1925-1931.
<https://doi.org/10.1016/j.scitotenv.2010.01.015>
- Wang, Z., Liu, S., Pan, Y., Piao, S., Janssens, I. A., Yin, G., & Chen, A. (2017). Human-induced erosion has offset one-third of carbon emissions from land cover change. *Nature Climate Change*, 7, 345-349. <https://doi.org/10.1038/nclimate3263>
- Waters, C. N., Zalasiewicz, J., Summerhayes, C., Barnosky, A. D., Poirier, C., Gałuszka, A., Cearreta, A., Edgeworth, M., Ellis, E. C., Ellis, M., Jeandel, C., Leinfelder, R., McNeill, J. R., Richter, D. deB., Steffen, W., Syvitski, J., Vidas, D., Waple, M., Williams, M., ... Wolfe, A. P. (2016). The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science*, 351(6269), aad2622. <https://doi.org/10.1126/science.aad2622>
- Wei, J., Fu, D., Guo, S., Tian, T., Huang, Y., Li, Z., Wang, L., Jin, L., Ye, W., Ren, A., & Yin, S. (2024). Elementomics of 32 elements in cord serum depicts the risk of orofacial clefts: A case-control study in Shanxi, China. *Environmental Pollution*, 362, 125037.
<https://doi.org/10.1016/j.envpol.2024.125037>
- Welti, N., Striebel, M., Ulseth, A. J., Cross, W. F., DeVilbiss, S., Glibert, P. M., Guo, L., Hirst, A. G., Hood, J., Kominoski, J. S., MacNeill, K. L., Mehring, A. S., Welter, J. R., & Hillebrand, H. (2017). Bridging Food Webs, Ecosystem Metabolism, and Biogeochemistry Using Ecological Stoichiometry Theory. *Frontiers in Microbiology*, 8, 1298.
<https://doi.org/10.3389/fmicb.2017.01298>
- Whickham, H. (2016). *ggplot2: Elegant graphics for data analysis (R package version 3.4.0)* [Software].

- Whittaker, R. J., Fernández-Palacios, J. M., Matthews, T. J., Borregaard, M. K., & Triantis, K. A. (2017). Island biogeography: Taking the long view of nature's laboratories. *Science*, 357(6354), eaam8326. <https://doi.org/10.1126/science.aam8326>
- Wick, L., & Tinner, W. (1997). Vegetation Changes and Timberline Fluctuations in the Central Alps as Indicators of Holocene Climatic Oscillations. *Arctic and Alpine Research*, 29(4), 445. <https://doi.org/10.2307/1551992>
- Wieczorkowski, J. D., & Lehmann, C. E. R. (2022). Encroachment diminishes herbaceous plant diversity in grassy ecosystems worldwide. *Global Change Biology*, 28(18), 5532-5546. <https://doi.org/10.1111/gcb.16300>
- Wijesinghe, D. K., John, E. A., & Hutchings, M. J. (2005). Does pattern of soil resource heterogeneity determine plant community structure? An experimental investigation. *Journal of Ecology*, 93(1), 99-112. <https://doi.org/10.1111/j.0022-0477.2004.00934.x>
- Wild, M., Gauly, M., Zanon, T., Isselstein, J., & Komainda, M. (2023). Tracking free-ranging sheep to evaluate interrelations between selective grazing, movement patterns and the botanical composition of alpine summer pastures in northern Italy. *Pastoralism*, 13(1), 25. <https://doi.org/10.1186/s13570-023-00287-3>
- Williams, M. (2008). A new look at global forest histories of land clearing. *Annual Review of Environment and Resources*, 33, 345-367. <https://doi.org/10.1146/annurev.enviro.33.040307.093859>
- Williams, M., Zalasiewicz, J., Barnosky, A. D., Leinfelder, R., Head, M. J., Waters, C. N., McCarthy, F. M. G., Cearreta, A., Aldridge, D. C., McGann, M., Hamilton, P. B., Summerhayes, C. P., Syvitski, J., Zinke, J., Cundy, A. B., Fiałkiewicz-Kozieł, B., McNeill, J. R., Kuwae, M., Rose, N. L., ... Berrio, J. C. (2024). Palaeontological signatures of the Anthropocene are distinct from those of previous epochs. *Earth-Science Reviews*, 255, 104844. <https://doi.org/10.1016/j.earscirev.2024.104844>
- Williams-Hoffman, M., Johansen, M. P., Larcombe, P., Child, D. P., Hotchkis, M. A. C., Serrano, O., Lavery, P. S., Thiruvoth, S., & Masqué, P. (2025). Montebello Islands marine sediment retains nuclear weapons-derived radionuclide contamination 70 years after detonations. *Marine Pollution Bulletin*, 219, 118280. <https://doi.org/10.1016/j.marpolbul.2025.118280>

- Williamson, C. E., Saros, J. E., Vincent, W. F., & Smol, J. P. (2009a). Lakes and reservoirs as sentinels, integrators, and regulators of climate change. *Limnology and Oceanography*, 54, 2273-2282. https://doi.org/10.4319/lo.2009.54.6_part_2.2273.
- Williamson, C. E., Saros, J. E., Vincent, W. F., & Smol, J. P. (2009b). Lakes and reservoirs as sentinels, integrators, and regulators of climate change. *Limnology and Oceanography*, 54(6part2), 2273-2282. https://doi.org/10.4319/lo.2009.54.6_part_2.2273
- Willig, M. R. (2011). Biodiversity and Productivity. *Science*, 333(6050), 1709-1710. <https://doi.org/10.1126/science.1212453>
- Wood, C. V. (2014). *Validating a calcium tracer based tree-ring dating method for tropical wood* [Doctoral Thesis, University of St Andrews]. <https://hdl.handle.net/10023/6389>
- Wood, S. N. (2017). *Generalized Additive Models: An Introduction with R* (2.^a ed.). Chapman and Hall/CRC. <https://doi.org/10.1201/9781315370279>
- Xu, Q., Wang, T., Cai, C., Li, Z., Shi, Z., & Fang, R. (2013). Responses of runoff and soil erosion to vegetation removal and tillage on steep lands. *Pedosphere*, 23(4), 532-541. [https://doi.org/10.1016/s1002-0160\(13\)60046-6](https://doi.org/10.1016/s1002-0160(13)60046-6).
- Yeloff, D., Van Geel, B., Broekens, P., Bakker, J., & Mauquoy, D. (2007). Mid- to late-Holocene vegetation and land-use history in the Hadrian's Wall region of northern England: The record from Butterburn Flow. *The Holocene*, 17(4), 527-538. <https://doi.org/10.1177/0959683607076472>
- Yin, M., Gao, X., Tenuta, M., Li, L., Gui, D., Li, X., & Zeng, F. (2020). Enhancement of N₂O emissions by grazing is related to soil physicochemical characteristics rather than nitrifier and denitrifier abundances in alpine grassland. *Geoderma*, 375, 114511. <https://doi.org/10.1016/j.geoderma.2020.114511>
- Young, D. M., Baird, A. J., Charman, D. J., Evans, C. D., Gallego-Sala, A. V., Gill, P. J., Hughes, P. D. M., Morris, P. J., & Swindles, G. T. (2019). Misinterpreting carbon accumulation rates in records from near-surface peat. *Scientific Reports*, 9(1), 17939. <https://doi.org/10.1038/s41598-019-53879-8>

- Young, D. M., Baird, A. J., Gallego-Sala, A. V., & Loisel, J. (2021). A cautionary tale about using the apparent carbon accumulation rate (aCAR) obtained from peat cores. *Scientific Reports*, 11(1), 9547. <https://doi.org/10.1038/s41598-021-88766-8>
- Yu, X., Zhou, W., Liu, X., Xian, F., Liu, Z., Zheng, Y., & An, Z. (2010). Peat records of human impacts on the atmosphere in Northwest China during the late Neolithic and Bronze Ages. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 286(1-2), 17-22. <https://doi.org/10.1016/j.palaeo.2009.11.034>
- Zaehle, S. (2013). Terrestrial nitrogen–carbon cycle interactions at the global scale. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1621), 20130125. <https://doi.org/10.1098/rstb.2013.0125>
- Zalasiewicz, J., Williams, M., Fortey, R., Smith, A., Barry, T. L., Coe, A. L., Bown, P. R., Rawson, P. F., Gale, A., Gibbard, P., Gregory, F. J., Hounslow, M. W., Kerr, A. C., Pearson, P., Knox, R., Powell, J., Waters, C., Marshall, J., Oates, M., & Stone, P. (2011). Stratigraphy of the Anthropocene. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 369(1938), 1036-1055. <https://doi.org/10.1098/rsta.2010.0315>
- Zanella, A., Harrison, C. M., Lenzi, S., Cooke, J., Damsma, P., & Fleming, S. W. (2022). Sonification and sound design for astronomy research, education and public engagement. *Nature Astronomy*, 6(11), 1241-1248. <https://doi.org/10.1038/s41550-022-01721-z>
- Zangrando, A. F. J., & Borrero, L. A. (2024). A pre-European archaeology in Malvinas/Falkland Islands? A review. *The Journal of Island and Coastal Archaeology*, 19(2), 433-447. <https://doi.org/10.1080/15564894.2023.2233582>
- Zargar, M. A., Riyaz, M., Hussain, S. M., Nazir, A., Hamid, S., Gojree, I. A., & Parray, K. A. (2025). Pollen and spores as proxies for palaeoenvironment reconstruction: A review of sediment-based research. *Journal of the Palaeontological Society of India*, 70(1), 42-60. <https://doi.org/10.1177/05529360251318072>
- Zeileis, A., & Grothendieck, G. (2005). zoo: S3 infrastructure for regular and irregular time series. *Journal of Statistical Software*, 14. <https://doi.org/10.18637/jss.v014.i06>
- Zetter, S., Garcés-Pastor, S., Lammers, Y., Brown, A. G., Walsh, K., Goslar, T., Lavergne, S., Coissac, E., Consortium, P., Tribsch, A., Heintzman, P. D., & Greve Alsos, I. (2025). SedaDNA shows

that transhumance of domestic herbivores has enhanced plant diversity over the Holocene in the Eastern European Alps. *The Holocene*, 35(4), 383-396.

<https://doi.org/10.1177/09596836241307304>

Zhang, B. L., Zhang, Z. P., Shi, S. M., Shi, H. J., DeLeon, P. A., & Shum, W. (2023). Dynamic elementomics of single-cell ICP–MS-derived signals in normal and calcium pump PMCA4-deficient mouse epididymal sperm during capacitation. *Metallomics*, 15(10), mfad059. <https://doi.org/10.1093/mtomcs/mfad059>

Zhou, G., Eisenhauer, N., Du, Z., Lucas-Borja, M. E., Zhai, K., Berdugo, M., Duan, H., Wu, H., Liu, S., Revillini, D., Sáez-Sandino, T., Chai, H., Zhou, X., & Delgado-Baquerizo, M. (2025). Fire-driven disruptions of global soil biochemical relationships. *Nature Communications*, 16(1), 1190. <https://doi.org/10.1038/s41467-025-56598-z>

Zhou, J., Leavitt, P. R., Zhang, Y., & Qin, B. (2022). Anthropogenic eutrophication of shallow lakes: Is it occasional? *Water Research*, 221, 118728. <https://doi.org/10.1016/j.watres.2022.118728>

References for aesthetics and illustrations



Fra Mauro. (c. 1450/1459). Mappamondo di Fra Mauro. Biblioteca Nazionale Marciana, Venice.



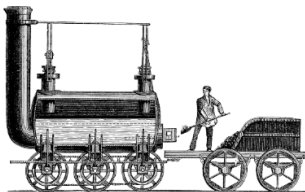
Bayeux Tapestry. c. 1070s. Bayeux Museum, Bayeux, France.



Pontifical de Guillaume Durand (Guillaume Durand), approx. 1390, Bibliothèque Sainte-Geneviève, Paris, ms. 143, fol. 77v)



Luttrell Psalter, Add MS 42130, commissioned by Sir Geoffrey Luttrell, England (East Anglia), c. 1325-1340. British Library, London.



Blücher locomotive from George Stephenson (1814)

