

Institute of Biology

The relative contribution of the five pedogenesis factors to soil formation and soil organic matter incorporation across environmental gradients

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by

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factors to soil formation and soil organic matter
incorporation across environmental gradients”**

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“The soil is the great connector of our lives, the source and destination of all.”

- Wendell Berry

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Prologue

The Swiss Mountain Soil Ecology Project, a unique personal initiative, aims to consolidate and analyze the diverse research conducted throughout my PhD studies. This project, though not an official entity, is distinct in its approach, integrating various methodologies and findings into a cohesive framework to enhance our understanding of soil dynamics in Switzerland's mountainous regions.

The project employs a multifaceted approach, including:

- Historical analysis: utilizing a 37-year-old soil library to trace long-term soil organic carbon (soc) changes and pedogenesis changes.
- Elevation gradients: investigating how soil properties and processes vary with altitude, shedding light on temperature and precipitation effects on soil formation.
- Slope models: examining the influence of slope orientation on soil development through variations in solar radiation and moisture.
- Reciprocal transfers: analyzing the impact of relocating plant materials between different environments to understand decomposition processes.

While this initiative offers valuable insights into SOC dynamics, soil mineralogy, and ecosystem functioning, it also faces limitations such as geographical specificity and methodological challenges. It is imperative that future research builds upon these findings and addresses these limitations by expanding geographical scope and refining analytical techniques, thereby advancing our understanding of soil dynamics.

Overall, this personal endeavor highlights the importance of understanding soil systems in the context of climate change and environmental variability, and it sets the stage for continued exploration and advancement in soil science.



Swiss Mountain Soil
Ecology Project

Abstract

Climate change is expected to challenge the future persistence of soil organic carbon (SOC) in terrestrial ecosystems. Considering the complexity of soil organic carbon change, plant-soil interactions, climatic conditions, and biotic factors are essential to understanding ecosystem functioning and soil formation. Over the past few decades, anthropogenically induced climate change, habitat destruction, and ecological disturbances have led to significant shifts in socio-environmental dynamics, resulting in altered soil properties and ecosystem dynamics. These changes are expected to have major impacts on the services soil provides to humans, threatening the persistence of many species and, thus, the overall health of ecosystems. Investigating SOC changes in a changing world is crucial for understanding contemporary environmental systems.

In this thesis, I aim first to understand how changing environments drive SOC changes in soils over decades, looking at soils from an environmental gradient perspective, from lakeshores to alpine meadows. Second, I investigated how changing environmental conditions – using elevation gradients – drive the decomposition dynamics of organic matter in the context of climate change. Decomposition dynamics are not only influenced by climate warming; they are also expected to change along elevation as the vegetation cover changes and migrates upwards to track optimal temperatures under warming. Thus, I am using elevation with north and south-facing slopes in the Swiss Alps to simulate future climatic scenarios. The study of soils across time and environmental gradient to predict SOC change across is presented in Thematic 1 and 2. The investigation on decomposition dynamics using elevation gradients for climatic variations together with north-south facing slopes and tea bags is presented in Thematic 3 and 4.

Also, to further investigate the effect of plant organ chemistry phytochemistry in decomposition dynamics, I used handmade litter bags filled with local plant material to show how the phytochemistry of leaves and roots influences litter decomposition in a litter transplant experiment (Thematic 3). Finally, to look over the last but not least soil forming factor, I also looked at microarthropod diversity along elevation gradients to better explain local ecological indicators of soil biodiversity (Thematic 4).

Keywords: decomposition, elevation gradients, pedogenesis, soil organic carbon, soil.

Résumé

Le changement climatique devrait remettre en question la persistance future du carbone organique du sol (SOC) dans les écosystèmes terrestres. Compte tenu de la complexité de l'évolution du carbone organique du sol, les interactions plante-sol, les conditions climatiques et les facteurs biotiques sont essentiels pour comprendre le fonctionnement des écosystèmes et la formation des sols. Au cours des dernières décennies, le changement climatique induit par l'homme, la destruction des habitats et les perturbations écologiques ont entraîné des changements significatifs dans la dynamique socio-environnementale, ce qui s'est traduit par une modification des propriétés des sols et de la dynamique des écosystèmes. Ces changements devraient avoir un impact majeur sur les services que les sols rendent à l'homme, menaçant la persistance de nombreuses espèces et, par conséquent, la santé globale des écosystèmes. L'étude des changements du SOC dans un monde en mutation est cruciale pour la compréhension des systèmes environnementaux contemporains. Dans cette thèse, j'ai d'abord cherché à comprendre comment les changements d'environnement entraînent des changements de SOC dans les sols au fil des décennies, en examinant les sols du point de vue d'un gradient environnemental, des rives des lacs aux prairies alpines. Deuxièmement, j'ai étudié comment les conditions environnementales changeantes - en utilisant les gradients d'altitude - conduisent la dynamique de décomposition de la matière organique dans le contexte du changement climatique. La dynamique de décomposition n'est pas seulement influencée par le réchauffement climatique ; on s'attend également à ce qu'elle change en fonction de l'altitude, à mesure que le couvert végétal se modifie et migre vers le haut pour suivre les températures optimales sous l'effet du réchauffement. J'utilise donc l'altitude avec des pentes orientées vers le nord et le sud dans les Alpes suisses pour simuler des scénarios climatiques futurs. L'étude des sols à travers le temps et le gradient environnemental pour prédire le changement de SOC est présentée dans les thèmes 1 et 2. L'étude de la dynamique de décomposition en utilisant les gradients d'altitude pour les variations climatiques ainsi que les pentes orientées nord-sud et les sachets de thé est présentée dans les thèmes 3 et 4.

En outre, pour approfondir l'étude de l'effet de la phytochimie des organes végétaux sur la dynamique de décomposition, j'ai utilisé des sacs de litière faits à la main et remplis de matériel végétal local pour montrer comment la phytochimie des feuilles et des racines influence la décomposition de la litière dans le cadre d'une expérience de transplantation de litière (thème 3).

Enfin, pour examiner le dernier facteur de formation du sol, mais non le moindre, j'ai également étudié la diversité des microarthropodes le long des gradients d'altitude afin de mieux expliquer les indicateurs écologiques locaux de la biodiversité du sol (thème 4).

Mots-clés : décomposition, gradients d'altitude, pédogenèse, carbone organique du sol.

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Introduction

Ecology seeks to elucidate the interactions between biotic entities and their abiotic environment, emphasizing the spatio-temporal dynamics that shape plant and soil community composition (Bardgett & Van Der Putten, 2014). Understanding these dynamics—whether influenced by environmental factors or biotic interactions—is increasingly critical in the context of climate change, especially regarding species distribution across elevation gradients (Lenoir & Svenning, 2015). Recent studies have demonstrated that climate change significantly impacts species distributions, affecting ecological interactions and ecosystem functions (Pecl et al., 2017). These shifts have profound implications for Soil Organic Matter (SOM) dynamics and mineralization processes, both of which are crucial for CO₂ sequestration in terrestrial ecosystems (Bradford et al., 2016). For example, changes in temperature and moisture regimes due to climate change can accelerate SOM decomposition, altering soil carbon sequestration and release (Crowther et al., 2016).

Plants play a pivotal role in soil organic matter dynamics and carbon cycling through various processes such as photosynthesis, decomposition of leaf and root residues, and the release of root exudates (Hütsch et al., 2002). By capturing atmospheric CO₂ and transferring carbon to the soil through plant residue decomposition, plants significantly contribute to SOM, thereby enhancing soil structure and fertility (Singh & Rengel, 2007). Soil organisms, including arthropods and earthworms, further decompose this organic material, mixing it with soil and forming stable aggregates that improve nutrient availability (Lavelle et al., 2004; Le Bayon et al., 2021). Microbes, such as bacteria and fungi, use specific enzymes to break down complex organic substances, leading to complete mineralization and nutrient release (Pritsch & Garbaye, 2011; Rashid et al., 2016; Romaní et al., 2006).

This microbial activity is essential for enhancing soil quality, fertility, and long-term carbon storage, which helps mitigate atmospheric CO₂ levels (Tian et al., 2019). Overall, plants and soil microorganisms are crucial for maintaining soil resilience and combating climate change through their influence on carbon sequestration and SOM dynamics (Rodrigues et al., 2023).

Understanding these mechanisms is vital for predicting and addressing climate-induced disruptions to ecosystem functioning and the carbon cycle. Plants contribute to SOM by adding organic residues like leaves, roots, and exudates, which decompose and enrich the topsoil, playing a central role in soil pedogenesis (Kögel-Knabner et al., 2023).

With their distinct horizons or layers, soil profiles develop over time under the influence of five key factors: climate, time, parent material, topography, and biological activity (Jenny, 1994). Climate affects soil formation through temperature and precipitation, impacting weathering and organic matter decomposition (Certini & Scalenghe, 2023).

Time allows for the gradual development of soil profiles, while parent material determines the initial mineral composition and affects soil texture (Mitchell & Soga, 2005). Topography influences water drainage and erosion, leading to variations in organic matter accumulation and horizon development (Rosenbloom et al., 2001).

Soil pedogenesis is driven by interrelated processes that shape soil profiles and affect their physical and chemical properties. Weathering breaks down parent material into finer particles through physical, chemical, and biological means, forming the mineral base of the soil (Anderson, 1988; Wilson, 2004). Organic matter accumulates from the decomposition of plant residues and animal remains, enriching the soil with humus and enhancing its fertility (Biswas & Kole, 2017; Kononova, 2013).

Leaching removes soluble substances from the soil, potentially leading to nutrient loss (Anderson, 1988; Shepherd & Bennett, 1998). Illuviation and eluviation describe the movement of minerals and nutrients within the soil profile, with eluviation referring to removal from upper layers and illuviation to accumulation in lower layers (Moody, 2006; Phillips & Lorz, 2008). Soil structure develops as these processes interact, creating distinct horizons or layers within the soil profile (Rabot et al., 2018). Biological activity from soil organisms, such as microbes, earthworms, and plant roots, further influences soil structure, nutrient cycling, and organic matter decomposition.

These factors collectively shape the soil profile and impact its fertility and structure.

Soil organic matter (SOM) includes particulate organic matter (POM), derived from the decomposition of plant and animal residues, and mineral-associated organic matter (MOM), formed by the binding of organic materials to soil minerals (Cai et al., 2023; Mikutta et al., 2019). Both POM and MOM are essential for soil health and its ability to support plant growth.

Understanding the dynamic interactions between soil organic carbon (SOC) changes, plant-soil interactions, climatic conditions, and biotic factors is crucial for comprehending ecosystem functioning and pedogenesis (Schmidt et al., 2011). Recent research emphasizes the significant role of microbial community composition and function in mediating SOC decomposition under various climatic conditions (Lange et al., 2021). Additionally, plant diversity and root exudates have been shown to influence soil microbial activity and SOC dynamics, highlighting their importance in soil health and ecosystem stability (Ho et al., 2017).

This thesis emphasizes the urgent need to deepen our understanding of Soil Organic Carbon (SOC) in the face of climate change's impending challenges. It adopts an interdisciplinary approach to explore ecosystem functioning and pedogenesis, focusing on the intricate dynamics of SOC, plant-soil interactions, climatic conditions, and biotic factors (**Figure I**). The study specifically investigates how climatic variations influence decomposition processes and SOC changes in natural soils.

By examining these interactions, this research aims to enhance our comprehension of ecosystem functioning and the factors driving pedogenesis under changing climatic conditions. The study provides nuanced insights into soil evolution and environmental resilience by analyzing SOC changes over recent decades and evaluating the contributions of vegetation inputs, soil communities, and climatic conditions.

With a rigorous focus on fieldwork and methodological precision, this thesis offers a robust foundation for developing informed conservation and management strategies. It emphasizes the role of organic matter (OM) as a central thematic, highlighting its impact on soil structure, fertility, and overall ecosystem health. This comprehensive approach aims to improve our strategies for managing natural soils amidst contemporary environmental shifts.

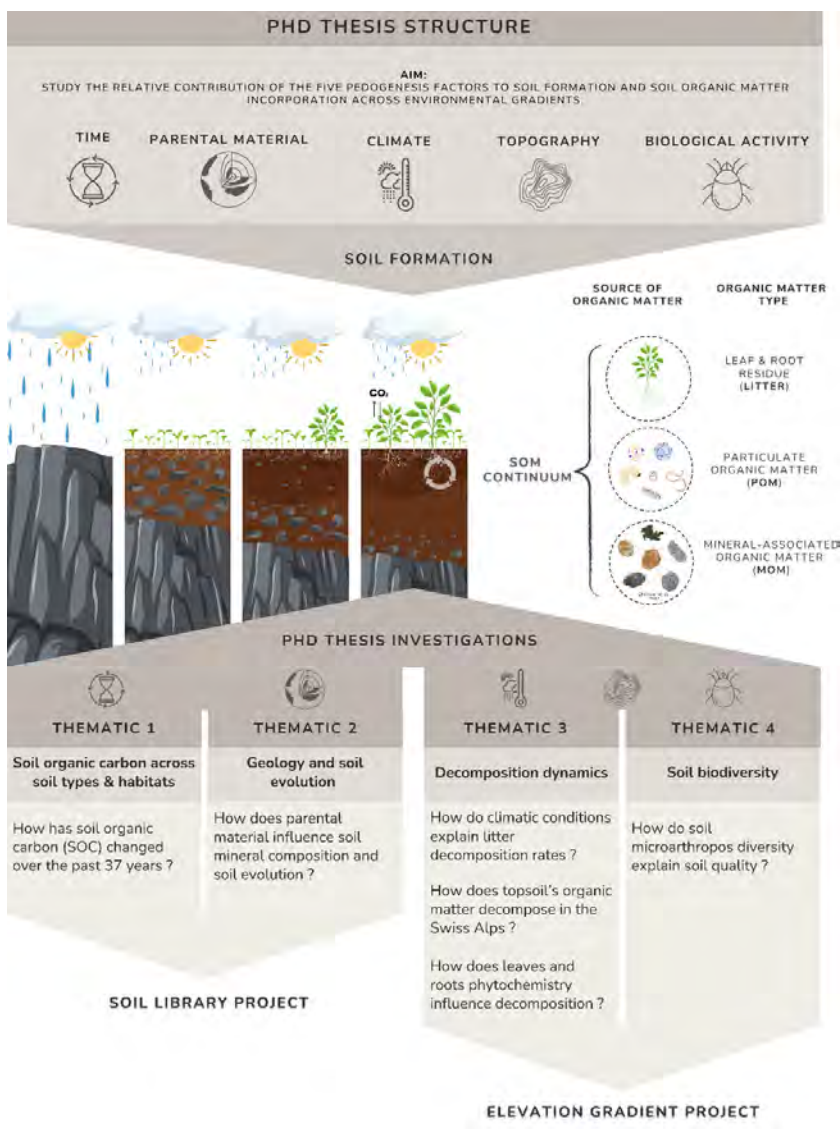


Figure I. Structure of the Ph.D. thesis. This figure graphically represents the main objectives of the thesis, illustrating the five-key soil pedogenesis factors that influence soil formation and the Soil Organic Matter (SOM) continuum. The thesis addresses these factors through four thematic areas: Thematic 1 and 2 focus on Soil Organic Carbon (SOC) changes over time and the influence of parental material on Mineral-Associated Organic Matter (MOM), employing both synchronic and diachronic approaches. Thematic 3 and 4 examine litter decomposition and the role of soil microarthropods in soil quality, utilizing an elevation gradient approach. This multi-faceted methodology provides a comprehensive understanding of SOC dynamics, organic matter contributions, and soil quality across different environmental contexts.

Understanding how climate change impacts Soil Organic Carbon (SOC) and its interactions with plant and soil communities is crucial for advancing ecological science. This thesis addresses this need by investigating how natural soils store SOC across different temporal and spatial scales and evaluating the effects of climate warming on plant litter and tea bag decomposition. The research employs both synchronic and diachronic approaches, examining SOC changes over decades and assessing decomposition rates along elevation gradients. To achieve this, the thesis integrates methods from ecology and pedology, including reciprocal transplant experiments that simulate future climate scenarios. Specifically, Thematic 1 and 2 focus on soil evolution and SOC dynamics over time (diachronic approach), while Thematic 3 and 4 explore how climate-induced elevation gradients affect decomposition rates and soil quality (synchronic approach). The thesis is structured around two main projects: the soil library project, which adopts a diachronic approach to study SOC over several decades, and the elevation gradient project, which uses a synchronic approach to investigate the impact of climate warming on decomposition dynamics. Each thematic area addresses one of the five key pedogenic factors related to organic matter incorporation into the soil. The thesis is organized as follows: it begins with a review of the current state of knowledge and identifies existing research gaps. Each thematic area is then explored separately, focusing on specific aspects of soil pedogenesis and organic matter dynamics. Thematic 1 examines the time factor and SOC evolution, Thematic 2 investigates the influence of parent materials on Soil Organic Matter (SOM), Thematic 3 analyzes decomposition dynamics, and Thematic 4 assesses soil quality using the QBS-Ar index and soil microarthropod communities. Results are presented as articles within each thematic section, highlighting the objectives and findings of the research.

Thematic 1 - Soil organic carbon changes over decades

Recent socio-environmental changes, driven by human activities, climate change, and ecological disturbances, have significantly altered soil properties and ecosystem dynamics (Amundson et al., 2015). Research has increasingly focused on how Soil Organic Carbon (SOC) has changed over recent decades, a key aspect of understanding contemporary environmental systems (Jackson et al., 2017).

Studies have demonstrated that land use changes, such as deforestation and urbanization, can substantially reduce SOC stocks (Gao et al., 2024; Lal, 2016).

Climate change, characterized by rising temperatures and shifting precipitation patterns, exacerbates these effects by accelerating the decomposition of soil organic matter (SOM) and increasing CO₂ emissions, which in turn intensify global warming (Crowther et al., 2016).

Extreme weather events, including droughts and floods, further disrupt soil structure and microbial activity, influencing SOC dynamics (Finley et al., 2018). Additionally, soil management practices play a crucial role in SOC content, with sustainable practices like no-till farming and organic amendments enhancing SOC sequestration and soil health, while conventional practices often lead to SOC depletion and soil degradation (Paustian et al., 2016; Sanderman et al., 2017). Understanding SOC changes is essential for developing strategies to mitigate climate change, enhance soil fertility, and ensure the sustainability of both agricultural and natural ecosystems. This thesis investigates SOC changes over recent decades, focusing on how climate change and ecological disturbances have influenced SOC dynamics.

By utilizing a soil library with samples from the past 30 years, this research explores the roles of soil types and environmental variations in driving SOC changes, with an emphasis on the underlying physicochemical properties responsible for these shifts.

In Thematic 1, the study examines the spatio-temporal relationships between soils and vegetation across Switzerland, aiming to understand the effects of time and climate on soil evolution. This involves comparing the physicochemical properties of the same soil profiles sampled over 20-30 years. The hypothesis posits that soil development varies according to local climatic conditions, with colder and more humid environments potentially hindering pedogenic processes, regardless of vegetation type.

To address these aims, the research employs both diachronic and synchronic approaches across the Swiss landscape. The diachronic approach involves comparing historical soil profiles from a soil library with contemporary samples from 2020, leveraging a collection of over 300 georeferenced soil profiles spanning up to 40 years (**Box 1**).

This approach highlights how factors such as land use changes, climate variability, and soil management practices affect SOC dynamics. On the other hand, the synchronic approach analyzes soil profiles from 2020 within and across different habitats to understand spatial variations in SOC and how these relate to climatic conditions.

Overall, this research employs a combination of descriptive, analytical, and experimental methodologies to explore soil formation and SOC dynamics across Switzerland's diverse terrain. The Swiss landscape's geological substrates and environmental conditions, including its elevation gradients, provide an ideal setting for disentangling the effects of local climate from geological and ecological factors.

This comprehensive approach aims to enhance our understanding of soil evolution and contribute to more effective soil management and conservation strategies in the face of ongoing environmental changes.

This study provided valuable insights into how soil dynamics might evolve in response to environmental changes over time. By examining soil properties across various landscapes in Switzerland, the research highlighted how soils could potentially adapt to ongoing climatic and land use shifts. Specifically, the variations observed in soil organic carbon content and carbon-to-nitrogen ratios between older and more recent samples shed light on how soil carbon levels may fluctuate with changing environmental conditions. These findings offer critical predictions that can inform future land management strategies and the development of sustainable practices aimed at preserving soil health and maintaining ecosystem functionality in the face of global environmental challenges.

Box 1. What can a historical soil collection reveal about soil development?

Discover the University of Neuchâtel's soil library, a comprehensive archive of over 4,000 soil samples collected between 1983 and 2014. Curated by Professor Emeritus Jean-Michel Gobat and his team, this collection includes soil profiles from as early as 1982, alongside detailed records in lab books, field notes, and theses. This historical dataset provides a unique opportunity to study soil formation and changes over time, offering valuable insights into how soil properties have evolved under different climatic conditions.

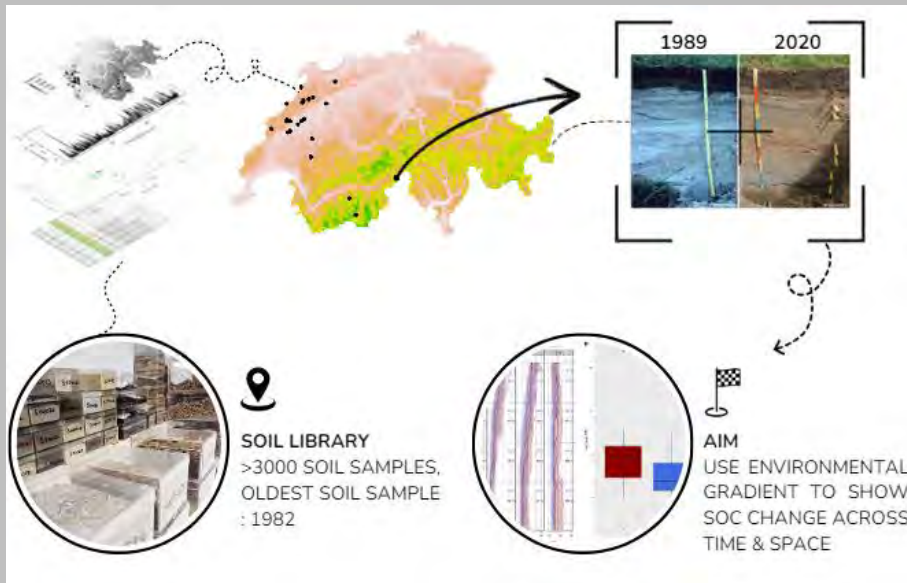


Figure II. The soil library project. This diagram outlines the critical phases of the soil library project. It includes steps such as data filtering, mapping selected study sites, and a detailed case study of the Binntal Fluvisol in Valais, Switzerland, showcasing historical and recent soil profile images. The diagram also highlights the collection of statistical data to analyze changes in soil properties over time.

Thematic 2 - Parental material driving soil mineral composition

The mineral composition, texture, and chemical properties of parent material fundamentally shape soil fertility, nutrient availability, and microbial communities, which in turn impact plant growth and ecosystem productivity (Jenny, 1994). Geological substrates form the bedrock of soil development, directly influencing soil pH, nutrient retention, and water-holding capacity (Hahm et al., 2014). For instance, soils derived from limestone tend to be alkaline, whereas those from granite are typically acidic (Kinzel, 1983).

The texture of parent material, including particle size distribution, affects soil structure and drainage properties (Osher & Buol, 1998). Clay-rich soils retain water but may suffer from poor aeration, while sandy soils drain well but hold less moisture (Betti et al., 2016; Wäldchen et al., 2012). These variations impact root penetration, soil moisture, and nutrient diffusion, all of which are crucial for plant growth (Das & Ghosh, 2024; Osman, 2018).

Additionally, the chemical properties of parent materials, particularly their nutrient composition, play a critical role in determining soil fertility and microbial activity (van der Heijden et al., 2008; Bardgett & van der Putten, 2014).

For example, basalt-derived soils are often rich in nutrients, supporting robust plant growth, whereas quartz-derived soils may require additional nutrients for effective agricultural use (Gillman et al., 2002). The interplay between plants and soil microorganisms further influences nutrient cycling and organic matter decomposition (Bardgett & Van Der Putten, 2014; Van Der Heijden et al., 2008).

In my research, I explored how geological foundations shape soil evolution within the Swiss landscape. Leveraging the extensive dataset from the soil library, I investigated the role of geological substrates in soil formation and composition.

This analysis focused on the bottom horizons of soils across Switzerland's varied landscapes, with particular attention to mineral substrates and parent materials. My objective was to show the relationships between geological history and soil organic carbon (SOC) dynamics. My research aimed to uncover the long-term implications of geological heritage on soil health, fertility, and ecosystem resilience. By highlighting the complexities of soil evolution within Switzerland, my work contributes to a deeper understanding of geological processes, soil formation dynamics, and ecosystem functioning.

This exploration offers valuable insights into how geological foundations influence soil evolution and have implications for land management, conservation, and sustainable development.

In Thematic 2, I focused on the mineral composition of soil samples from the soil library to investigate the contribution of parental material to soil formation and evolution. I compared samples from siliceous and calcareous bedrocks to understand different soil evolution scenarios (Abtahi, 1980; Musso et al., 2019). Additionally, I analyzed soil samples from the 2020 field campaign, examining texture and vegetation diversity indices. My hypothesis was that different parental materials affect pedogenesis and soil evolution through their influence on vegetation cover and topographical aspects. This chapter aims to provide insights into how geology, topography, and superficial formations across Switzerland contribute to soil evolution, shedding light on the spatiotemporal relationships between soils and vegetation under various climatic conditions.

Thematic 3 - mountains as natural laboratories for organic matter decomposition studies

The Swiss Alps, with their diverse topographic features and climatic gradients, offer a unique setting for studying topsoil organic matter (OM) decomposition. These high-altitude ecosystems, characterized by temperature fluctuations and varied soil properties, significantly influence microbial activity and organic matter turnover rates (Becker et al., 2007). **In Thematic 3** I focus on the steep elevation gradients in the Alps create microclimatic variations that affect soil temperature and moisture, leading to spatial heterogeneity in decomposition processes (Bardelli et al., 2018; Gessner et al., 2010; Praeg et al., 2020).

Alpine environments are particularly sensitive to climate change due to their reliance on temperature, limited species adaptation, and snow and ice dynamics (Smith et al., 2009). Thawing permafrost and shifting precipitation patterns further heighten this sensitivity, making alpine ecosystems early indicators of broader climate impacts (Alexander et al., 2016; O'Donnell et al., 2010). Changes in temperature and precipitation at high altitudes can accelerate soil organic matter (SOM) decomposition and alter carbon storage dynamics (González-Domínguez et al., 2019; Yvon-Durocher et al., 2010).

Additionally, shifts in snow cover duration and snowmelt timing affect soil thermal regimes and microbial activity, influencing organic matter turnover (Hagedorn et al., 2010).

Research done in the Swiss Alps has highlighted the critical role of vegetation cover in mediating SOM dynamics (Canedoli et al., 2020; Galluzzi et al., 2024; Greinwald et al., 2021). Alpine plants contribute to the soil organic carbon pool through their root systems and litter inputs, impacting microbial communities involved in decomposition (Bardgett, 2005; Condrón et al., 2010).

Variations in plant species composition along elevation gradients can affect litter quality and decomposition rates (Cornelissen et al., 2007). Understanding these processes is essential for assessing the resilience of mountain ecosystems to global environmental changes and for informing conservation strategies worldwide (Gottfried et al., 2012).

Decomposition is a fundamental ecological process that recycles nutrients and organic matter, crucial for maintaining ecosystem functionality and carbon cycling. Plant secondary metabolites (PSMs) reflect how climatic conditions influence litter decomposition rates and SOM dynamics in alpine environments (Sun & Fernie, 2023; Zhang et al., 2019). The chemical composition of plant tissues—such as lignin content, nitrogen concentration, and secondary metabolites—plays a significant role in shaping decomposition dynamics by affecting substrate quality, microbial communities, and enzymatic activities (Aber & Melillo, 1982; Chomel et al., 2016; Cornwell et al., 2008; Luo et al., 2023; Ransedokken et al., 2024; Zhu et al., 2024).

Climatic conditions, including temperature and moisture availability, drive enzymatic activities, microbial biomass turnover, and organic matter breakdown. Increased temperatures generally enhance microbial respiration and decomposition rates, although drought and excessive rainfall can inhibit microbial activity or create anaerobic conditions, respectively (Borken & Matzner, 2009; Conant et al., 2011; Davidson & Janssens, 2006; Karhu et al., 2014; Qu et al., 2023; Schulze et al., 2009). Changes in seasonal patterns, such as earlier snowmelt and prolonged dry periods, can further alter decomposition timing and rates, impacting carbon fluxes and nutrient cycling (Rustad et al., 2001).

Understanding these climatic influences is crucial for predicting soil carbon dynamics and developing strategies to manage soil health under changing conditions. In examining the role of topography, this research focused on how elevation gradients and slope orientations interact with climatic factors to influence decomposition rates. Using tea bag experiments (**Box 2**), I discovered that solar radiation is a major driver of decomposition, with higher radiation levels significantly accelerating litter breakdown, surpassing other climatic factors such as temperature and moisture.

Box 2. Tea time for soil: unveiling decomposition dynamics

We used a unique approach to explore how different factors influence organic matter breakdown: standardized tea bags—green tea and rooibos. We assessed how soil composition, climate conditions, and microbial activity affect the decomposition process by analyzing these tea bags in various soil environments. This multi-faceted experiment combines soil analysis, microbial tests for carbon degradation, and soil respiration measurements to reveal the intricate dynamics of organic matter breakdown in different settings.

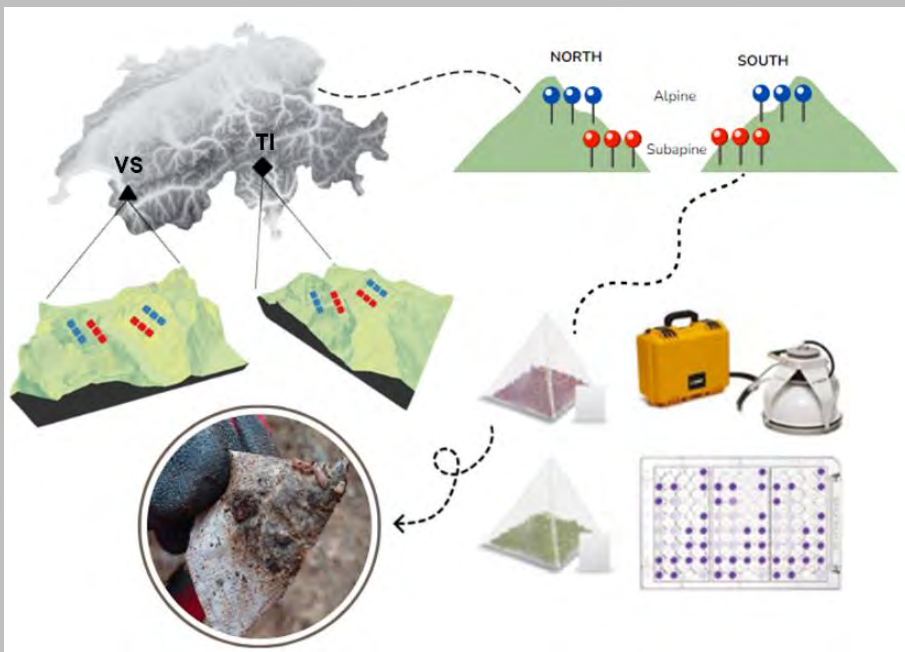


Figure III. Tea bag experiment. This diagram illustrates the key stages of the tea bag experiment designed to investigate organic matter decomposition. It includes a map highlighting the two regions where field campaigns were conducted. The experimental design shows north and south-facing transects across subalpine and alpine sites. Additionally, the figure presents a graphic representation of the methods employed—standardized litter (green tea and rooibos tea), soil analyses, microbial tests for carbon degradation, and soil respiration measurements—to explore the impacts of soil characteristics, climate, and microbial activity on organic matter breakdown.

To deepen our understanding of how plant inputs and climatic conditions influence soil organic matter (SOM) cycling, I conducted another experiment involving plant samples from high and mid-elevation transects.

I collected shoots and roots from prominent plant species and utilized a litter transfer experiment to investigate the effects of different types of plant litter on SOM dynamics. In this experiment, I reciprocally transplanted hand-made litter bags containing either allochthonous (external) or autochthonous (local) plant litter into the soil. To analyze the contributions of these litter types, I performed phytochemical analyses using High-Performance Liquid Chromatography (HPLC). This approach aimed to elucidate how vegetation inputs, influenced by climatic conditions, affect SOM dynamics by focusing on the role of phytochemicals. The study also explored how climate variations impact soil microbial communities and decomposition processes.

By examining how different litter types affect decomposition at the local scale, the research provided insights into the complex dynamics of litter breakdown and its implications for soil health and carbon cycling (see **Box 3**).

Additionally, I investigated the role of plant secondary metabolites (PSMs), such as alkaloids, phenolic compounds, and terpenes, in decomposition dynamics. These compounds, which enter ecosystems through various pathways, impact decomposition based on their chemical properties. The reciprocal litter transfer experiments and high-resolution mass spectrometry analysis revealed that phytochemical diversity and composition significantly influence decomposition rates. Specifically, litter decomposed more slowly in non-native environments due to mismatched interactions between phytochemicals and soil biota.

This comprehensive analysis provides valuable insights into the impacts of climate change on organic matter decomposition and ecosystem functioning, emphasizing the importance of ongoing research to manage and mitigate these effects effectively. Understanding how different types of litter decompose under varying environmental conditions is key to comprehending ecosystem functionality and nutrient cycling.

My research explored how litter characteristics, environmental factors, and microbial activity drive decomposition rates in mountain ecosystems. By analyzing the effects of specific litter traits on decomposition across elevation gradients, the study aimed to reveal the underlying factors influencing these rates.

This work advances our knowledge of decomposition processes and highlights the resilience and dynamics of mountain ecosystems in response to environmental changes. While traditional theories suggest that decomposition rates decline with latitude and elevation, recent studies emphasize the significant role of plant chemistry (Smith et al., 2020).

Decomposition efficiency often improves in native environments due to specialized decomposer communities (Jones & Smith, 2019). To investigate these dynamics, I characterized climatic conditions at various sites, performed reciprocal litter transfer experiments, and utilized untargeted metabolomics. Leaves and roots from ten dominant species across 24 sites were analyzed using ultra-high-performance liquid chromatography with quadrupole time-of-flight mass spectrometry (UHPLC-QTOFMS) to determine their chemical composition and diversity. This research enhances our understanding of how plant communities adapt to climate change and its impact on nutrient cycling and carbon storage in mountain ecosystems.

Box 3. Unpacking litter dynamics: the litter reciprocal transfer experiment

Through our reciprocal litter transfer experiment, we explore how litter decomposition rates and plant phytochemistry shift along elevation gradients. By collecting and analyzing leaves and roots using UHPLC-QTOFMS, we delve into the intricate phytochemical composition and diversity of plant organs.

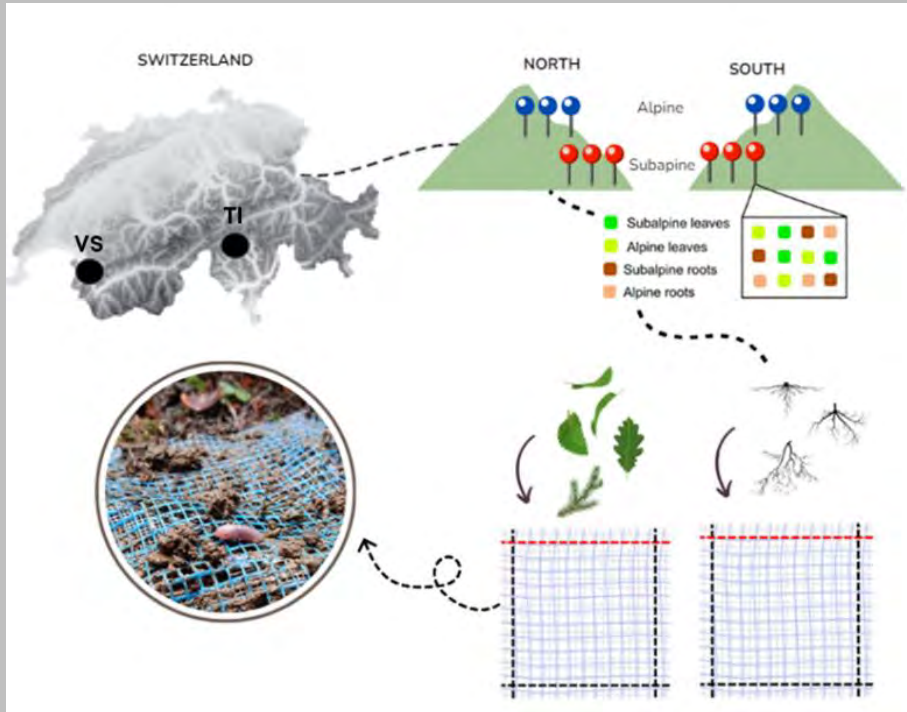


Figure IV. Reciprocal litter transfer experiment. This diagram provides a detailed overview of the reciprocal litter transfer experiment. It features a map that highlights the two regions where the field campaigns were carried out, showcasing the geographical scope of the study. The figure also includes a schematic of the experimental design, illustrating the layout of north and south-facing transects at both subalpine and alpine elevations. Additionally, it presents a detailed view of the litterbag composition and distribution, demonstrating how different types of litter were transplanted across various sites. This comprehensive visualization captures the experimental approach used to investigate the impacts of litter type and elevation on decomposition rates and phytochemical diversity.

Thematic 4 - Functional diversity of soil microarthropods

Soil microarthropods, such as mites and Collembola, play a crucial role in litter decomposition by interacting with microbial communities and organic matter (Fujii & Takeda, 2017; Heneghan et al., 1999; Liu et al., 2023). Their diverse functional roles impact nutrient mineralization rates, microbial biomass dynamics, and soil carbon stabilization mechanisms (Coleman et al., 2024; Sagi & Hawlena, 2021; Seastedt, 1984). By fragmenting and consuming leaf litter and other organic materials, these microarthropods increase the surface area available for microbial colonization and enzymatic action, thereby facilitating the release of essential nutrients like nitrogen and phosphorus (Bezerra & de Matos Andrade, 2021).

Additionally, their digestive systems contain enzymes and symbiotic microorganisms that further decompose organic matter, making nutrients more accessible to plants and microbes (Berg et al., 2004; Karmakar et al., 2016). Microarthropods also regulate microbial populations through predation on fungi, bacteria, and protozoa, which helps maintain microbial diversity and resilience (Moore et al., 1988; Shade et al., 2012; Taylor et al., 2010). Their physical activities, such as burrowing and excretion, stimulate microbial activity by redistributing organic matter and microorganisms within the soil matrix (Coleman & Wall, 2007; Le Bayon et al., 2021; Villani et al., 1999). Furthermore, these organisms contribute to soil carbon stabilization by aiding in the formation of soil aggregates and humus, protecting organic matter from rapid decomposition and enhancing long-term carbon storage (Lehmann et al., 2017; Maaß et al., 2015; Santorufo et al., 2024).

Understanding the ecological roles of different soil microarthropod groups enriches our knowledge of belowground food webs and their impact on ecosystem functioning.

For instance, mites serve as decomposers, predators, and fungivores, breaking down organic matter and regulating microbial populations (Walter & Proctor, 2013), while Collembola feed on fungi, bacteria, and decaying plant material, playing a vital role in nutrient cycling and soil structure formation (Rusek, 1998).

In Thematic 4. I examined how soil microarthropod biodiversity influences soil organic matter (SOM) dynamics across varying climatic conditions. Using an LI-COR system for soil respiration measurements and Bait Lamina tests for biological activity, I assessed the QBS-Index to evaluate arthropod community health. I hypothesized that climatic conditions and soil biodiversity significantly affect SOM recycling, predicting that harsh climates and lower functional biodiversity would lead to changes in the carbon-to-nitrogen ratio.

To test this hypothesis, I investigated arthropod communities in experimental plots ranging from low to high elevation, employing the MacFadyen extractor for soil core analysis and applying the QBS-AR index for soil quality assessment (**Box 4**). This study aimed to describe local soil communities, elucidate the impacts of climatic conditions and soil biodiversity on SOM dynamics, and understand their roles in pedogenesis. By identifying individual arthropods to the order or class level and assigning Ecological Morphological Index (EMI) values, ranging from 1 (no adaptation to soil) to 20 (perfect adaptation to soil), I sought to reveal the correlation between arthropod diversity, environmental conditions, and decomposition rates.

My study provides valuable insights into the intricate relationships between climatic factors and soil microarthropod communities, offering a deeper understanding of their collective impact on ecosystem dynamics.

By revealing how variations in elevation and environmental conditions influence arthropod diversity and their role in organic matter decomposition, the research advances our knowledge of soil health and nutrient cycling. Our findings enhance our comprehension of how climate change and altitude-related factors affect soil ecosystems, emphasizing the critical role of arthropods in modulating soil processes. This integrated perspective not only enriches our understanding of soil biodiversity but also informs strategies for ecosystem conservation and management in the face of environmental change.

Box 4. Decoding soil quality through microarthropod diversity

Soil functioning and productivity hinge on the intricate roles of detritivores, such as soil microbes and invertebrates, which break down organic matter and recycle essential nutrients. In this study, we delve into the world of soil microarthropods across the Swiss Alps to understand how community composition influences organic matter decomposition and soil quality.

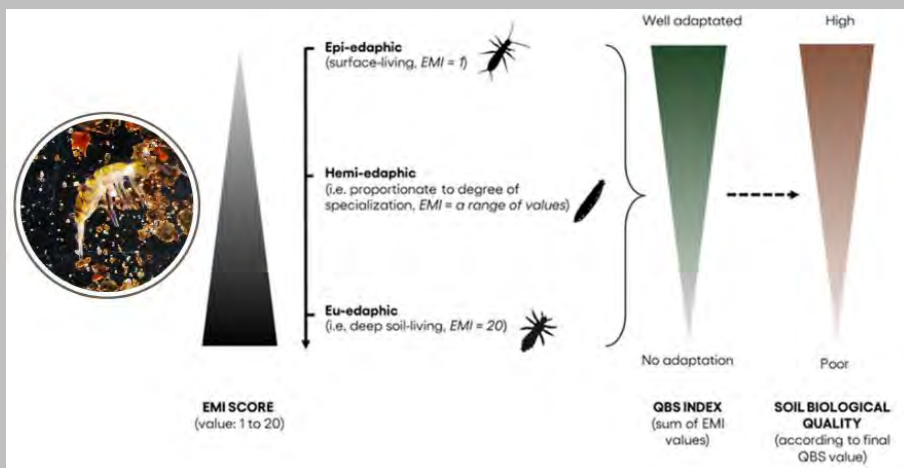


Figure V. The QBS-Ar Index. This diagram illustrates the QBS-Ar index, which assesses soil quality based on soil arthropods' ecological and morphological traits. It details how various arthropod categories — epi-edaphic, hemi-edaphic, and eu-edaphic — are scored on a scale from 1 to 20 according to their degree of specialization to soil environments. The combined scores of these ecological categories produce the QBS index value, reflecting the adaptability and health of the soil ecosystem based on its microarthropod community. This index helps to interpret the impact of environmental variables on soil biological quality.

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Thematic 1: Soil organic carbon across soil types & habitats

Temporal changes in soil properties: insights from a 37-year-old Swiss soil library

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matter.



Abstract

The soil formation equation states that over time, soils, under the influence of climate, topography, parent material, and vegetation, undergo qualitative and structural changes, ultimately developing into unique soil types and profiles. Although this process is conserved globally, it remains unclear to what extent in various environments soil profiles – either different or from the same taxonomic group - undergo similar changes over comparable timespans. To address this gap, we employed a diachronic approach to investigate the factor time of the soil formation process by looking at temporal changes in soil physicochemical properties using a Swiss soil library covering the most characteristic features of the Swiss landscape. Utilizing a comprehensive soil library initiated in 1982, we re-analyzed 28 archived and modern soil profiles -a total of 256 soil horizons - from natural and semi-natural habitats. The results obtained for soil properties, including pH, organic matter content, cation exchange capacity, and carbon-to-nitrogen ratio done in 2020 for both archived and modern soil samples were compared to track changes over up to 37 years. We found that distinct soil types such as Cambisols, Fluvisols, and Gleysols exhibit unique characteristics shaped by local geomorphology and environmental factors, with significant variations observed in the carbon-to-nitrogen ratio, indicating subtle shifts in nutrient dynamics in relation to carbon and nitrogen inputs and soil decomposition dynamics. We also found significant variation in how much the physicochemical properties of soil profiles changed over time, with predictable patterns significantly related to climate. We showed that soils in habitats with warmer temperatures, more solar radiation, and increased humidity were the most susceptible to change. By elucidating how time and climate influence soil properties, this research contributes to more accurate forecasts of climate change impacts on soil organic carbon decomposition forecast proposing new perspectives on how one can use soil to take stock of the changes that have taken place over time underlining the role of soil communities in future changes in the integration of organic matter in the soil.

1. Introduction

Soils are crucial natural resources that support the health of entire ecosystems, as well as human well-being, through a variety of emergent properties, such as carbon storage, water retention or maintaining habitats for soil biodiversity (Dazzi & Lo Papa, 2022; Dror, Yaron, & Berkowitz, 2022; Eswaran, Lal, & Reich, 2019; Lal, 2015; Telo da Gama, 2023). The formation and evolution of soils, known as pedogenesis, are influenced by a complex interaction of biotic and abiotic factors including climate, topography, parent mineral material, vegetation, and soil microorganisms, as well as time (Jenny, 1994; Lehmann & Rillig, 2015; Lehmann & Kleber, 2015). Understanding how these factors affect pedogenesis across different ecosystems is essential for preserving soils and the services they provide, especially in the face of rapid environmental changes (Drenning, 2021). Nonetheless, one of the main challenges in understanding soil physicochemical changes is that the interactions among various pedogenesis factors vary across ecosystems. This leads to different trajectories in soil formation and significantly affects the variation in soil carbon content and distribution across ecosystems (Davidson & Janssens, 2006). For example, tropical rainforest soils exhibit high organic matter due to elevated plant productivity and decomposition, whereas arid region soils show low organic matter and high salinity due to minimal rainfall and vegetation (Asner et al., 2005). Along these lines, topography impacts soil formation through erosion and deposition, while parent mineral material influences the soil's physical and chemical properties, affecting carbon storage (Anderson, 1988; Basile-Doelsch et al., 2020; Gregorich et al., 1998; Kögel-Knabner & Amelung, 2021). Hence, understanding variation in soil changes across habitats can help better predict changes in the services provided during land use and climate change across ecosystems (Briones, 2014; Wall et al., 2012; Wang et al., 2021).

A diachronic approach, involving the study of soil changes over time, is essential for understanding the long-term dynamics of soil properties and their responses to environmental changes (Fujisaki et al., 2017; Trevisani & Bogunovic, 2022). Chronosequences, which according to (Walker et al.) (2010) represent “a set of sites formed from the same parent material or substrate that differs in the time since they were formed”, have been advocated for studying soil development and carbon dynamics (Galluzzi et al., 2024; Walker et al., 2010).

Studies using chronosequences have examined soil development and evolution following natural disturbances such as volcanic eruptions, landslides, and glacier retreats (Rasigraf & Wagner, 2022). However, one limitation of using chronosequences is that they may not accurately reflect the rate and direction of soil development in other regions or under different environmental conditions.

In contrast, using soil libraries—consisting of well-documented, stored soil samples collected over time – enables the analysis of changes in soil properties across ecosystems. Therefore, in principle, through precise glocalization, one could analyze the properties of the same soil profile at different time points and identify trends and patterns in soil carbon content and other properties, contributing to more accurate predictions of future soil changes (Jandl et al., 2014; Li et al., 2020). In this regard, the National Cooperative Soil Survey Soil Characterization Database and the GlobalSoilMap project, among others, have been instrumental in tracking changes in soil organic carbon content due to land use changes and other factors (Arrouays et al., 2020).

For instance, studies have shown that organic matter in the upper soil horizons changes rapidly due to various processes such as accumulation, decomposition, and incorporation (Cotrufo & Lavelle, 2022; Lehmann & Kleber, 2015; Rumpel & Kögel-Knabner, 2011; Schmidt et al., 2011). Hence, soil libraries could help refine models for better predicting future soil changes across ecosystems (Nunes et al., 2021).

In this study, we asked whether soil profiles and their inherent physicochemical properties change similarly across ecosystems over several decades. To address this question, we utilized a soil physical library from the University of Neuchâtel, Switzerland, to investigate changes in soil types and their properties over time across different climatic conditions and environmental gradients. By accurately describing horizon-by-horizon soil profiles' changes from diverse habitats, including grasslands, forests, and riparian areas, we aimed to determine if soil libraries can reveal broad changes in soil physicochemical properties and how these changes vary according to soil types across environments.

We hypothesized that soil variables related to soil organic carbon show significant variation over time, particularly in the uppermost layers, and that different climatic conditions will generate variation in the rate of these changes. Specifically, we predicted that ecosystems with higher levels of disturbance (i.e., young soils, such as Fluvisols) or with higher biological activity in warmer and more humid habitats (i.e., Leptosols and Umbrisols) would show higher levels of change. In contrast, older soil types, such as Podzol, would show litter physicochemical and structural change. An important caveat of our study is that, over the approximately four decades covered by our soil library, the climate in the Central European Alps has been changing rapidly (Barros et al., 2014; Gobiet et al., 2014). This likely exerts significant abiotic pressure, potentially accelerating soil evolution (Karmakar et al., 2016).

2. Material and Methods

2.1. The soil library and selection of soil profiles

We used both synchronic and diachronic approaches to investigate variations in soil properties across the landscape and through time. The synchronic approach compares soil profiles across habitats (spatial), while the diachronic approach compares the same soil profiles at different time points (temporal). This was achieved using a physical soil library initiated by one of our co-authors (J.-M. Gobat) in 1982 at the University of Neuchâtel, Switzerland. This soil library now includes more than 4000 referenced soil samples taken for each horizon described in the field, dried in an oven at 40°C, sieved at 2mm, and stored in a dark and temperate environment in plastic boxes. Most of these archived soil samples originated within Switzerland.

We followed a multistep selection protocol to address our aims of comparing modern and archived soils, as shown in **Figure S1. 1**. First, we only selected natural and semi-natural habitats across Switzerland, representing a wide range of continental to temperate conditions. Second, we only selected soil profiles whose data was as complete as possible and contained valid reference information, including precise GPS coordinates, vegetation cover, soil type, and habitat. This information was necessary to retrieve the original soil location precisely.

Third, we selected soil profiles that originated from a variety of habitats, here including the alpine habitat (above 2000 meters above sea level), grasslands, forests, riparian, and low-elevation lakeshore habitats. Finally, we only selected those profiles in which all soil samples were sufficient to re-perform the necessary analyses in 2020 and referenced for the entire soil profile.

Based on these selection criteria, we obtained 37 complete soil profiles spread across Switzerland's three major bioclimatic zones: the Jura, the Plateau, and the Alps. Next, we removed all soil profiles containing a single horizon and soil profiles from which we could not trace back their original documentation, either in the form of a thesis, a report, or a peer-reviewed publication. Ultimately, we obtained 28 complete soil profiles that were surveyed and analyzed in 2020, including 6 Cambisols, 7 Fluvisols, 7 Gleysols, 1 Leptosol, 1 Luvisols, 5 Podzols, and 1 Umbrisol (see **Figure 1.1**, **Figure 1.2**, **Figure S1.1**, **Figure S1.2**, and **Figure S1.3**)

To ensure that the storage of the archived soil samples did not significantly alter their physicochemical properties over time, we used – as a reference - the loss on ignition (LOI) method (Allen et al., 1974) to compare initial archived results with those of 2020.

The LOI method estimates the total organic matter in the soil (SOM), for which the basic technique did not change during the past 40 years. We randomly selected several profiles from the archived soil samples list. Then, by performing the loss of ignition analysis on all soil samples again in 2020 (i.e., weighting the sample before and after burning the sample at 450°C) and by obtaining comparable results on the stored samples, we assumed that little to no alteration happened during sample storage (see **Table S1.1**).

2.2. Soil sampling and analyses

During the summer of 2020, we visited all 28 initial soil profile locations, re-dug a soil profile, and described and classified the soil profile horizons following the FAO Guidelines for soil description (Jahn et al., 2006). We collected soil samples for every layer (organic and mineral horizons), removing coarse elements > 2 cm and roots.

Soil description included the following descriptors: horizon depth, colour (Munsell soil colour chart), coarse elements ($> 2 \text{ mm}$), structure (particular, massive, fragmented, build), texture (sand $2\text{mm} - 50 \text{ }\mu\text{m}$, silt $50 - 2 \text{ }\mu\text{m}$, clay $< 2 \text{ }\mu\text{m}$) and parental material. In addition, we determined the relative abundance of carbonates in situ by the HCl 6M test and soil pH Hellige (for details on the modern soils, see **Table S1. 2Table S1. 3**).

The archived and modern soil samples were subsequently analyzed in parallel. We retrieved seven different parameters on all soil samples: (1) pH, measured in distilled water and KCl with a Metrohm 827 pH meter (Metrohm AG, Herisa, Switzerland). (2) Soil organic matter, using the LOI method (Allen et al., 1974) and corrected by the 'Howard' correction factor (Howard & Howard, 1990). (3) Soil total cationic exchange capacity (CEC), using the 'cobalt hexamine trichloride' method (Ciesielski & Sterckeman, 1997). (4) Total carbonates (CaCO_3) using a Calcimeter Bernard method and HCl 6M. (5) Total carbon (C_{tot}) and nitrogen (N_{tot}), with an elemental analyzer (FLASH 2000, Thermo Scientific, Waltham, Massachusetts, USA). (6) carbon-to-nitrogen ratio (C: N) by calculation. And (7) Soil relative humidity (Rh) after drying the soils at 105°C for three days.

2.3. Extraction of climatic variables

To obtain the site-specific climatic niche, for each site, we extracted environmental data at a 20 m resolution from Swiss maps, including growing degree days (hereafter referred as the temperature axis), annual mean solar radiation, and potential evapotranspiration (hereafter referred as moisture) from associated environmental layers, since these variables have been shown to explain best the Alpine climatic conditions (Körner, 2007; Pellissier et al., 2013; Pellissier et al., 2016).

Values for degree days and potential evapotranspiration were calculated from meteorological stations using a Digital Elevation Model (DEM) at 20m resolution and interpolated based on Zimmermann & Kienast (1999).

2.4. Statistical analysis

We performed all statistical analyses with R software, version 3.5.1 (R Development Core Team 2020).

We used algorithms for quantitative pedology, the *aqp* package (Beaudette et al., 2013) to visualize and analyze soil horizons and profiles between archived and modern soil profiles. To visualize initial soil similarities based on the measured soil parameters, we computed a summed, depth-segment-aligned dissimilarity matrix (using the *profile_compare* function in the *aqp* package) to a maximum depth of 40 cm. We selected soil pH, soil organic matter (SOM), organic carbon (C_{org}), total nitrogen (N_{tot}), and the carbon-to-nitrogen ratio (C:N) as the key physicochemical properties anticipating these would exhibit faster changes. Based on this matrix, we computed a divisive hierarchical clustering (*diana* in the package *cluster*) and visualized it using the *hclust* function. Initial soil profiles (those from the soil libraries) and their physicochemical similarities tree were then mapped on a Swiss map using the *phylo.to.map* function in the package *phytools* (Revell, 2012).

Relative to our research questions, we selected the most relevant packages as follows: have different metrics related to OM of soils changed when comparing the modern and archived soils? To address this question, the *aqp* package compared changes across all profiles for all soil physicochemical parameters (except total carbonates, for which field tests showed too little or no reaction).

First, we computed a depth-wise summary (medians $\pm$ 25 and 75 percentiles) of horizon-level attributes using the *slab* function in *aqp* to visualize average changes in soil properties between archived and modern profiles. Second, we computed the horizon depth-weighted mean value for each parameter and each soil horizon. Differences between archived and modern soils for each variable were then tested using linear models with soil age class as a fixed factor and soil profile as the blocking factor.

Do soil physicochemical properties change over time? If so, do they vary across environmental gradients? To test for the effect of climate on soil changes, we first performed a principal component analysis (PCA) on all climatic variables. We then extracted pairwise distances between each archived and its corresponding modern soil from the dissimilarity matrix as computed above. Finally, we performed a linear regression analysis between the first and second PCA axes, separately with the distance axis.

3. Results

3.1. Climate effect on soil profiles' change over time

The environmental PCA (**Figure S1. 2** and **Figure S1. 3**) indicates that the selected soil profiles from the soil library ($n = 28$) and homologous modern soil profiles are relatively well spread and grouped along the environmental gradient from cold (frost days) and humid (humidity = average evapotranspiration, precipitations = average precipitations) to warm (degree-days) and dry (solar radiations). This also indicates that archived and modern soil profiles are under the same climate conditions as homologous profiles are close to each other. In addition, we show that the coordinates placement method for archived soil samples collected before 1989 was done accurately.

Moreover, observations made during the fieldwork and the physicochemical analyses on archived and modern soil samples also attest to the accuracy of the information referenced in the soil library and its corresponding archived documents.

3.2. Did soils change over decades?

The divisive hierarchical clustering of 28 soil profiles, based on five physicochemical parameters (soil pH, soil organic matter (SOM), organic carbon (C_{org}), total nitrogen (N_{tot}), and the carbon-to-nitrogen ratio (C:N), reveals distinct clusters among soil profiles across Switzerland (**Table 1. 1**, **Figure 1. 1**).

Table 1. 1. Sites of soil profiles. Shown are the names of the study locations, with their corresponding coordinates (WGS84), the environment in which the soil profile was found, the soil class based on the World Reference Base for Soil Resources (WRB) nomenclature, and the year in which the soil was archived in the soil library. The ID corresponds to what is shown in Figure1. Environments considered were alpine grassland, beech forest, lakeshore forest, mesic grassland, pine forest, riparian forest, and subalpine grassland.

Location	ID	Environment	Latitude	Longitude	Archived profile soil calss ¹	Year
Bevaix	Bev	Beech forest	551848	197176	Cambisol (Calcaric)	1992
BinntalBlatt1	Bi1	Alpine grassland	665320	136478	Arenic Dolomitic Fluvisol	1989
BinntalBlatt2	Bi2	Alpine grassland	665230	136346	Stagnic Histic Dolomitic Fluvisol	1989
BinntalBlatt3	Bi3	Alpine grassland	664586	136996	Epihistic Reductic Gleysol	1989
BinntalBlatt4	Bi4	Alpine grassland	665681	136160	Cambic Umbrisol	1989
BoisRaiguel	Boi	Beech forest	575974	222550	Podzol	1985
Chasseral	Cha	Subalpine grassland	570360	220088	Luvisol (Calcaric)	1985
Chasseron	Cho	Subalpine grassland	531751	189291	Luvisol (Calcaric)	1985
Chevroux	Che	Lakeshore forest	560088	194080	Reductic Gleysol	1983
Cheyres1	Ch1	Lakeshore forest	551945	186936	Reductic Gleysol (Humic)	1983
Cheyres2	Ch2	Lakeshore forest	549781	185146	Reductic Gleysol	1983
Cudrefin1	Cu1	Lakeshore forest	570454	202848	Reductic Gleysol	1983
Cudrefin2	Cu2	Lakeshore forest	566618	199560	Stagnic Gleysol	1983
Gorgier	Gor	Beech forest	548619	196886	Luvisol	1984
Goumois	Gou	Mesic grassland	563463	233844	Cambisol	1986
Nava	Nav	Alpine grassland	615108	115154	Cambisol	1988
Pontins	Pon	Pine forest	563650	197225	Podzol (Calcaric)	1983
Portablan	Por	Beech forest	565942	219653	Epihistic Reductic Gleysol	1984
Posieux1	Po1	Riparian forest	575320	178790	Fluvisol (Calcaric)	1987
Posieux2	Po2	Riparian forest	575370	178630	Fluvisol (Brunic, Calcaric)	1987
Raimeux1	Ra1	Beech forest	600154	239411	Podzol	1988
Raimeux2	Ra2	Beech forest	600154	239408	Stagnic Gleysol on Podzol	1988
RocheDevant	Roc	Alpine grassland	547615	197748	Hyperskeletal Leptosol	1984
Rossens1	Ro1	Riparian forest	573562	158998	Fluvisol (Oxyaquic, Calcaric)	1989
Rossens2	Ro2	Riparian forest	573269	158230	Fluvisol	1989
Saignolis	Sai	Pine forest	548632	215407	Podzol	1995
Worben	Wor	Riparian forest	589798	215812	Fluvisol (Brunic, Calcaric)	1989
Zermatt	Zer	Alpine grassland	622457	97439	Cambisol	1989

¹For additional nomenclature and name change across modern and archived sampling see Tables S1 and S2.

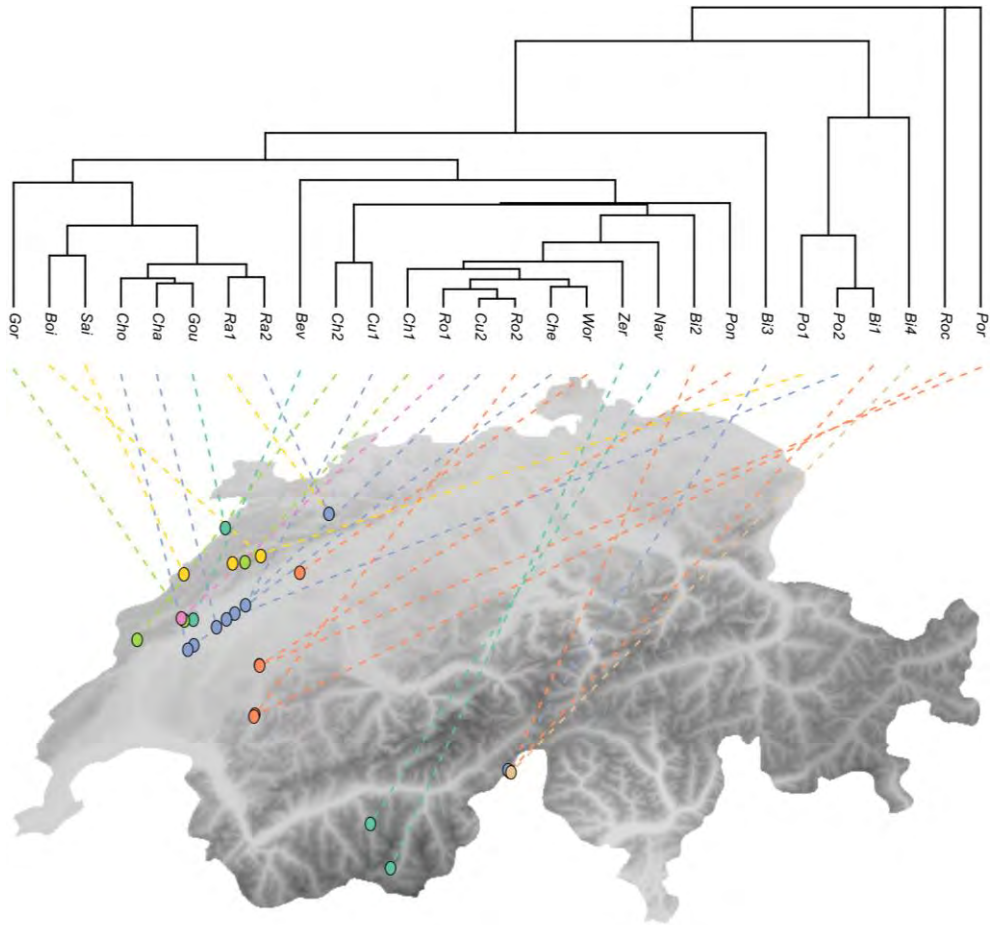


Figure 1.1 Location of 28 soil profiles. Shown is the divisive hierarchical clustering of 28 soil profiles based on five soil physicochemical parameters: including soil pH, soil organic matter (SOM), organic carbon (Corg), total nitrogen (Ntot), and the carbon-to-nitrogen ratio (C: N). Soil profile locations are visualized on a map of Switzerland. Soils are colour-coded based on soil classes as determined by the World Reference Base for Soil Resources (WRB): Cambisols (turquoise), Fluvisols (orange), Gleysols (purple), Leptosols (pink), Luvisols (green), Podzols (yellow) and Umbrisols (brown).

These results highlight the diversity of soil types within regions, showcasing unique characteristics and variations across different landscapes. In total, we identified seven Cambisols, including one previously classified as a Luvisol in the soil library but renamed as a Cambisol in 2020, as well as seven Fluvisols, seven Gleysols, and five Podzols.

Additionally, we found one Umbrisol, one Leptosol, and one Luvisol (**Figure 1. 2**). The varied nature of these soils emphasizes the diversity of soil types across the Swiss landscape.

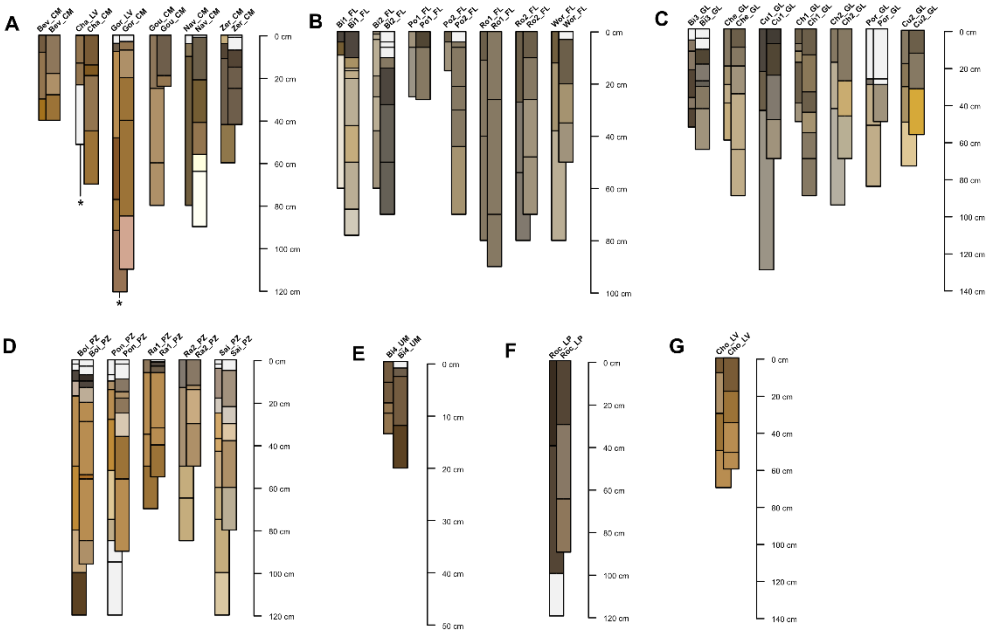


Figure 1. 2 Soil profile collection of archived and modern soil groups. The figure shows a numerical generation of all archived soil profiles (background) and the modern soil profiles (foreground). Panel (A) shows all Cambisols for archived and modern soil profiles. Three archived soils were not described as Cambisols but are still shown side by side these three soils' profile is highlighted with a star (*). Archived and modern soil profiles' numerical generation are shown for: Cambisols (A), Fluvisols (B), Gleysols (C), Podzols (D), Umbrisols (E), Leptosols (F), and Luvisols (G). The first three letters of the name represent the location as described in Table 1. The last two letters represent the soil class: Cambisols (CM), Fluvisols (FL), Gleysols (GL), Podzols (PZ), Umbrisols (UM), Leptosols (LP), and Luvisols (LV). Colours indicate the horizon Munsell colour codes for organo-mineral and mineral horizons are represented, the white colour indicates all histic organic horizons (H, Hf, Hm), the organic horizons formed in oxic conditions (OF, OH), or when the colour was not recorded at the bottom of the profile because of the rocky substrate. The organic horizons (OL) on the surface are not shown here.

Cambisols (**Figure 1. 2A**; n=7) feature subsurface horizons with varied degrees of pedogenetic alteration, from weak to relatively strong. These soils were observed in pastures, grasslands, and forests across diverse landscapes. All Cambisols exhibited cambic horizons with varying degrees of brownification processes.

Notably, in the Swiss Alps (Nav and Zer), two Cambisols were found on scree and steep slopes (**Soil descriptions**). Additionally, two soil profiles (Cha and Gou) displayed altered subsurface horizons in the Jura Mountains under grasslands. Comparison of archived and modern soil profiles revealed that except for two Cambisols (Cha_CM and Gor_CM), which were previously classified as Luvisols in the soil library, the reference soil group remained consistent.

Fluvisols (**Figure 1. 2B**; n=7;) were predominantly located in ecosystems with frequent alluvial deposits characterized by heterogeneous sandy textures. These soils primarily developed in carbonated sedimentary rock environments. Riparian Fluvisols near the Sarine River (Po1, Po2, Ro1, Ro2) and Aar River (Wor) originated from calcareous parent material. In alpine settings such as the Swiss Alps (Bi1 and Bi2), Fluvisols formed from alluvial deposits derived from the North Pennine Trias dolomite. Comparing old and modern profiles, Fluvisols retained their classification over nearly four decades, showing minimal differentiation between those from recent riparian deposits and older flood-prone alluvial valleys (Ro1). However, older Fluvisols displayed higher organic matter content, exhibited deeper profiles with thicker layers, and sustained finer surface sands than the recent soil profiles.

Gleysols (**Figure 1. 2C**; n=7), characterized by gleyic properties and reducing conditions, were predominantly found in low-elevation lakeshore environments along the southern shore of Lake Neuchâtel and alpine swamps like the Binntal Valley (Bi3). These soils exhibit hydromorphic features, varying in water saturation levels with principal and supplementary qualifiers. Due to intermittent groundwater saturation, one profile initially identified as a Stagnosol (Cu2) was alternatively described as a Gleysol to emphasize its varying saturation characteristics (**Appendix B. Table S37-S39, and Figure S21**).

Podzols (**Figure 1. 2D**; n=5) with spodic horizons were observed in pine forests in the Jura mountains. These soils demonstrated diverse characteristics reflected in principal and supplementary qualifiers. Across archived and modern profiles, the reference soil group remained consistent (Boi, Pon, Ra1, Ra2, Sai).

One unique Umbrisol profile (**Figure 1. 2E**; n=1) featured a surface horizon with significant organic matter content and low base saturation, situated southwest of Ofenhorn peak in the Binntal Valley (Bi4).

One unique Hyperskeletal Leptosol (**Figure 1. 2F**; n=1) was identified in 2020 (Roc), composed of hard technic material and less than 20% fine earth, located in a limestone scree-filled cirque at Roche-Devant. This soil profile corresponded closely with its description in the soil library, which was previously also classified as a Leptosol.

Lastly, in 2020, only one soil profile remained in the Luvisol class (**Figure 1. 2G**; n=1, Cho). Luvisols are indeed characterized by an argic horizon starting before 100 cm depth (WRB, 2022). Following this definition, we reclassified two archived Luvisols (Gor_LV, Cha_LV) as modern Cambisols (**Figure 1. 2A**; Gor_CM, Cha_CM).

To summarize, the comparative analyses of soil profiles across Swiss landscapes reveal persistent classifications for most soil classes over nearly four decades, with a notable evolution for specific soil characteristics. Fluvisols, for instance, maintained a consistent classification across archived and modern profiles, showing minor variations in granulometry and clay content across different environments. Conversely, soils exhibiting gleyic properties demonstrated subtle changes, exemplified by the Cu2 profile reclassified as a Gleysol due to intermittent groundwater saturation and variable clay content.

3.3 Changes in soil physicochemical parameters

The soil segmentation analyses highlighted changes in physicochemical parameters between archived and modern across soil depth (**Figure 1. 3**). Overall, soil pH tended to become more alkaline from top to bottom, moving from an average of 7 to 8 below 60 cm of depth (**Figure 1. 3**, pH). Along the same lines, the total organic matter decreased from an average of 9.6 % to 1.1 % at the bottom (**Figure 3**, SOM), total nitrogen decreased from 0.39 to 0.02 % (**Figure 1. 3**, Ntot), and total carbon from 7.8 to 0 (**Figure 1. 3**, Ctot).

On the other hand, the carbon-to-nitrogen ratio remained constant throughout the soil profiles, from 12.6 to 15.8 on average (**Figure 1.3**, C: N).

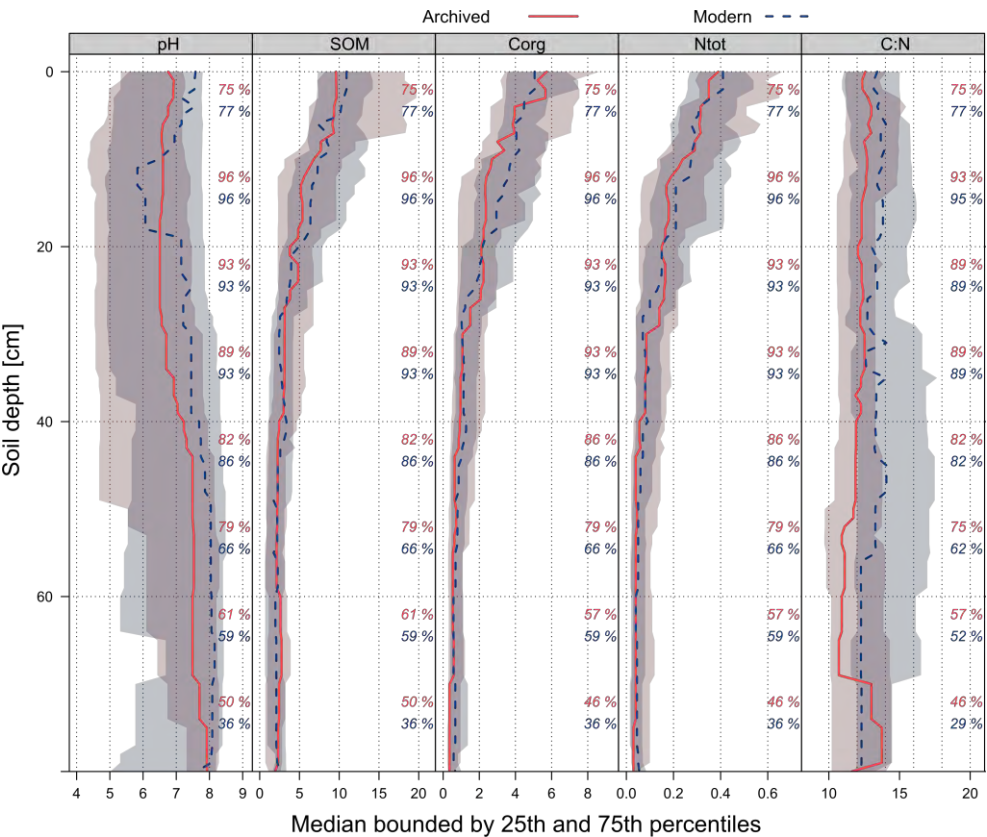


Figure 1.3 Depth-wise aggregation of archived and modern soil profiles, for pH, soil organic matter (SOM), organic carbon (Corg), total nitrogen (Ntot), and carbon-to-nitrogen ratio (C: N). Lines represent median values and shaded areas represent the 25th and 75th percentiles around the median values calculated for each variable across all 28 soil profiles. Blue colours represent the archived soil profiles, and red colours represent the modern soil profiles.

Weighted means' comparisons between archived and modern soils show that all soil parameters measured to a total depth of 40 cm did not change across time (**Figure 1.4**, and **Figure S1.4**), except for the C:N ratio, which significantly increased from an average of 12.5 to an average of 13.7 across all soil profiles (**Figure 1.4**, and

Table S1. 4, Time effect: $p = 0.036$).

Figure 1. 4 illustrates the absolute differences in key soil parameters between archived and modern soil profiles across various soil classes: Cambisols, Fluvisols, Gleysols, Leptosols, Luvisols, Podzols, and Umbrisols. All soil types were heterogeneously distributed across the axis for pH, showing no particular grouping. However, Cambisols (Bev, Nav, Gor), Fluvisols (Bi2, Po1), Podzols (Pon, Sai, Boi), Luvisol (Cho), and Gleysol (Ch2) all exhibited a decrease in pH over 37 years. In contrast, the remaining 18 soil profiles showed increased soil pH. In terms of soil organic matter (SOM), a similar trend of heterogeneous distribution is observed, with decreases in SOM for Cambisols (Nav, Cha, Gor, Bev), Fluvisols (Ro1, Ro2), Podzols (Ra1, Sai, Boi), Gleysols (Bi3, Che, Ch1, Por), Luvisol (Cha), and Leptosol (Roc).

The other 13 profiles displayed an increase in SOM content. Lastly, the carbon-to-nitrogen ratio (C:N) was lower for Cambisols (Gor, Nav), Fluvisols (Bi1, Bi2, Ro1, Ro2), Gleysols (Bi3, Ch1), and Luvisol (Cho), while the remaining 10 profiles exhibited a higher C:N ratio.

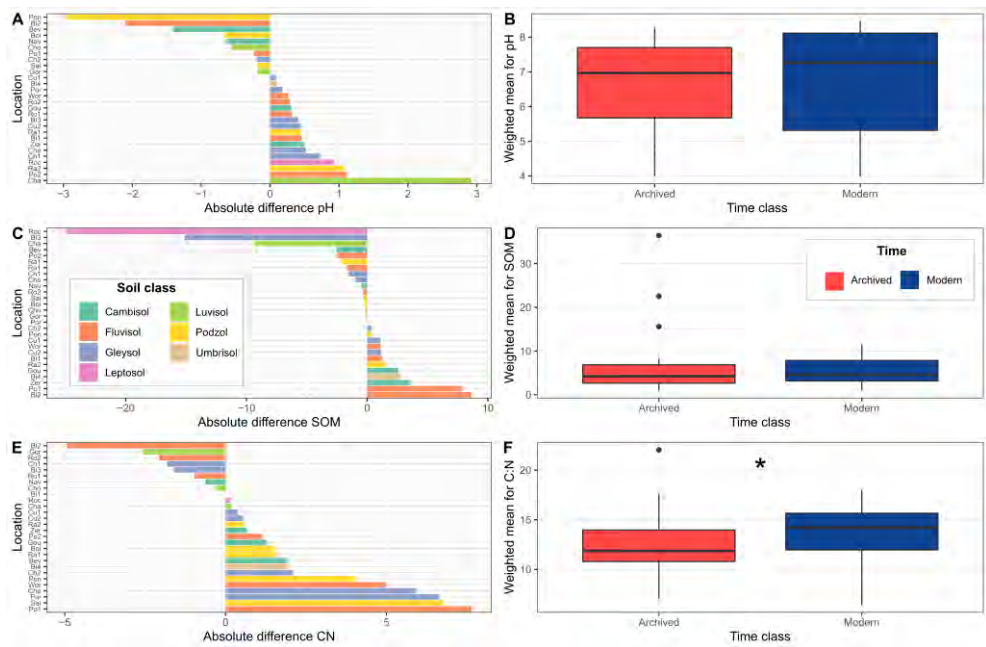


Figure 1. 4 Soil physicochemical parameters change over time. Shown are the absolute differences between modern and archived soil parameters based on the horizon depth weighted means for the first 30 cm, including pH, soil organic matter (SOM), and carbon-to-nitrogen ratio (C: N) with the left bar plots representing the absolute differences (modern minus archived value) for each soil profile. Positive values indicate an increase, while negative values indicate a decrease in the soil parameter. Colours indicate soil classes: Cambisols (turquoise), Fluvisols (orange), Gleysols (purple), Leptosols (pink), Luvisols (green), Podzols (yellow), and Umbrisols (brown). Panels on the right represent average differences between archived and modern soils. Colours indicate the time class: archived (red) and modern (blue). Asterisks indicate significant differences between time classes ($p < 0.05$).

3.4 Soil physicochemical properties change across climatic gradients

When correlating the first two axes of the PCA with the average physicochemical distance between modern and archived soil profiles (**Figure 1. 5A**), our analysis revealed significant negative correlations with both the first (**Figure 1. 5B**, PCA1, $n = 28$, $r = -0.61$, $p = 0.03$) and the second **Figure 1. 5C**, PCA2, $r = -0.56$, $p = 0.001$) axis of climate-based principal component analysis (PCA).

These findings suggest that soils exhibiting the most remarkable changes are in regions characterized by lower elevations, warmer and drier conditions (correlated with PCA1), and areas with lower solar radiation levels (correlated with PCA2). This result indicates that environmental factors such as temperature, moisture, and solar exposure play crucial roles in modifying soil physicochemical properties over time.

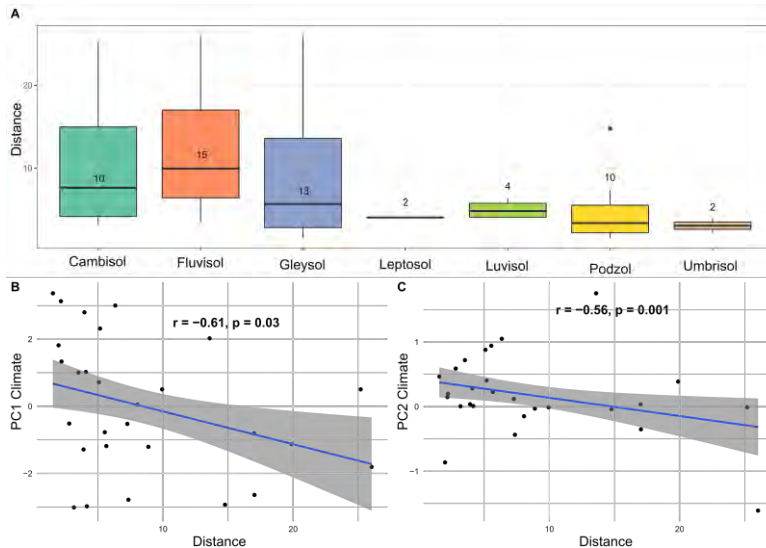


Figure 1. 5 Physicochemical distance between archived and modern soil profiles. Shown are (A) Boxplots averaging the physicochemical distance between time classes (archived and modern) and soil classes based on soil pH, cation-exchange-capacity (CEC), soil organic matter content (SOM), organic carbon (Corg), total nitrogen (Ntot) and the carbon-to-nitrogen ratio (C: N). Colours indicate the different soil classes: Cambisols (turquoise), Fluvisols (orange), Gleysols (purple), Leptosol (pink), Luvisols (green), and Podzols (yellow), and Umbrisols (brown). Boxplots represent, from bottom to top, minimum, first quartile, median, third quartile, and maximum, and dots represent the outliers. Scatterplots (B, C) show the linear regression between the physicochemical distance and the principal component (PCA) 1 and 2 of the climate for each site, respectively. The blue line and shaded grey area represent the linear fit and the confidence intervals, respectively.

4. Discussion

4.1 Soil evolution over time: profile-level observations

We investigated various ecosystems to determine whether soils have remained stable or undergone significant transformations over 37 years. Although our selection of soil profiles is not exhaustive relative to the highly heterogeneous landscape of the Central European Alps (Gobat & Guenat, 2019) and is constrained by the availability of our soil library, it still captures a wide array of pedogenetic processes. Our research demonstrates significant soil diversity within the relatively small biogeographical area investigated (**Figure 1. 1**). By characterizing the presence or absence of specific diagnostic horizons, we were able to precisely assign names to the different modern soil types and compare topological changes over time. From each reference soil group (WRB, 2022), we discriminated two main soil ages in our dataset: the youngest soils (Fluvisol, Leptosol, Umbrisol) periodically disturbed and/or rejuvenated by environmental constraints, and the oldest soils (Cambisol, Gleysol, Luvisol, Podzol). With few exceptions, most of the names assigned to the soils, whether young or old, remained unchanged, indicating minimal changes at the soil profile level. This is not entirely surprising, as pedogenetic processes that significantly alter soil types typically extend over periods longer than four decades (Jenny, 1994). However, slight variations were observed in situ, which are discussed below.

The Fluvisols predominate in the alluvial zones (Bi1, Po1), and display significant textural variations linked to the alluvial dynamics, which have remained active over the last 37 years in our study area. Erosion and sediment deposition periodically rejuvenate the profiles near active channels, stripping topsoil and/or creating deposition gradients with varying grain sizes over time (Ro1, Bi2). Pedogenesis can evolve rapidly in an alluvial environment, mainly when the soils are rich in bases, especially calcium. This ion effectively ensures the organo-mineral complex establishment and, consequently, the formation of aggregates (Le Bayon et al., 2017; Rowley et al., 2018; Schomburg et al., 2018). Therefore, profiles from limestone and dolomitic deposits (Po1, Bi1) would be particularly conducive to rapidly establishing a stable structure in cambic horizons. However, such an evolution is naturally disturbed and prevented by the fluvial dynamics that constantly rejuvenate the soils.

This explains why, in some cases, Fluvisols can become brownified until becoming Cambisols when the alluvial index decreases, moving or rising away from the river (terraces) or when the main riverbed changes (Blume et al., 2002; Le Bayon et al., 2013; Petts & Gurnell, 2005; Schilling et al., 2018), but this was not the case in our study.

Concerning the Umbrisols and Leptosols, speculations about their dynamics are in our case very limited, as our database contains only one example in each case). However, focusing on each of the two cases we propose hypotheses for future development. First, Umbrisols, enriched in organic matter with low base saturation, are usually prevalent in acidic environments such as high-altitude coniferous forests (Zech et al., 2022). Their development is linked to climate conditions influencing organic matter decomposition rates and leaching processes over time (Musielok et al., 2022). In our database, the Cambic Umbrisol identified in 1989 was also identified as a Cambic Umbrisol in 2020. The "Cambic" qualifier indicates that the soil has maintained its structuring characteristics over time. This structure is twofold: small aggregates embedded in larger ones.

When the larger aggregates are crushed, the smaller ones appear (commonly known as "fluffy structure" due to aluminum ions). The persistence of this fluffy structure over 31 years reflects a remarkable degree of soil stabilization. This stabilization is particularly noteworthy in mountainous regions, where soils are primarily used for pasture or forestry. In these areas, maintaining soil stability is crucial for sustainable land use, as it prevents erosion, preserves soil fertility, and supports the productivity of pasturelands and forests, which are vital for local economies and ecosystems. Yet, the consistent classification as Cambic Umbrisol, when comparing archived and modern soils, suggests that despite potential environmental pressures and land use changes (in terms of pastoral or forestry activities), the soil has preserved its essential characteristics (organic matter content and structural stability). This enduring stability highlights certain soil types' capability to maintain their functions and services despite environmental changes (Gregor et al., 2018). This finding emphasizes the value of long-term soil monitoring and the need to account for both stable and dynamic aspects of soil properties in environmental assessments.

In contrast to the soil types described above, due to their shallow development in rocky and erosive settings, Leptosols represent weakly developed soils, typical of the initial phases of soil formation (Zech et al., 2022). These soils were located in a glacier retreats cirque filled with limestone scree, where the potential for pedogenetic evolution is very low. The weathering of the region's hard limestone and the fresh scree's setting create highly unfavourable conditions for the rapid development of thick soil horizons, which explains why this soil has remained virtually unchanged for 36 years. Still, this hypothesis needs to be confirmed with a much broader set of similar case studies.

Therefore, according to our initial predictions, the oldest soils in our dataset showed little changes over the three to four decades of our study. However, we observed that Cambisols, in particular, undertake pedogenetic changes in line with their environmental contexts. The topography strongly influenced Cambisols on steep slopes (Nav, Zer) in the Swiss Alps. Also, compared with other profiles, such as Nav from 1992, the results suggest that the variation in soil profile-specific location influenced the observed changes, mainly linked to the colluviation processes and site coordinates. The thicknesses of colluvium vary considerably across sites because they depend strongly on different factors such as the type of colluviation process, the length of time and periodicity, the type of source material, topography, land cover, human impact, and so on (Miller & Juilleret, 2020). In the field, the parental material was observed to crumble very quickly, which could explain the colluvial input between 1988 and 2020 because of the rock's erosivity.

In contrast, Cambisols found in the Jura mountains (Cha, Gor, Gou) showed relative stability (i.e., same horizons, same thickness, no change in pedogenesis process) under grassland conditions, indicating prolonged maturation and resilience to environmental disturbance. However, the soil profile of the Bev, located near Lake Neuchâtel, shows signs of disturbance due to human activities, leading to a reduction in soil organic matter and the presence of anthropogenic waste, which contrasts with its previous state.

Finally, we noted that the Bev soil, currently classified as Cambisol, could have been designated with an additional qualifier such as "technical" if human influence on the topsoil layers was to be confirmed.

Also, it seems premature to classify it as a technosol at this stage, given the emphasis on anthropogenic disturbance and the observed decrease in surface organic matter resulting from human reworking.

Luvisols, distinguished by clay translocation processes that form clay-enriched horizons (illuviation), were prominent in the Jura region. Luvisols are generally fertile soils mainly found in the humid mid-latitudes (Zech et al., 2022) and often found in the Swiss Jura Mountains submitted to loess deposits (Martignier et al., 2015; Martignier & Verrecchia, 2013; Zárate, 2017). Moderate slopes, clay-rich parent materials, and high precipitation facilitate their development (Weil & Brady, 2017). Clay illuviation is driven by the leaching of soluble substances from upper horizons under humid conditions (Finke, 2012; Lavkulich & Arocena, 2011). These soils exhibited variable horizon development, influenced by local climate and erosion dynamics, providing insights into their long-term evolutionary trends (Gómez-Guerrero & Doane, 2018).

In our study, two Luvisols were reclassified as Cambisols. However, as migration of clays up the profile is, of course, impossible, and in an evolving pedological sequence, a Luvisol never becomes a Cambisol again, it is therefore very likely that the identification of these two soils in 1984 and 1985 was erroneous, and that the Cambic horizon was not correctly identified in situ.

Gleysols, found in waterlogged environments along lake shores and alpine swamps, exhibit distinct horizon sequences shaped by leaching and translocation processes (Blume et al., 2016; Hewitt et al., 2021). Their evolution is closely tied to hydrological stability on the Swiss Plateau, influenced by the corrections of Jura waters that occurred in the 19th and 20th centuries and intermittent groundwater saturation in the Jura, which significantly impact nutrient cycling and soil fertility dynamics (Bresson, 1978; Duchaufour, 1977; Weil & Brady, 2017; WRB, 2022; Zech et al., 2022).

The Cu₂ Gleysol exemplifies the challenges in soil classification based on water conditions dynamics and seasonal variations. Seasonally impeded water percolation plays a crucial role in forming Gleysols, affecting redox dynamics, especially in the presence of clays and fine silts. While our study shows low clay content across all profiles, variations in Gleysols specific horizons are linked to water saturation and redox processes.

Silt content exhibits high variability, particularly in reductive and rust-stained horizons, indicating its role in influencing redox conditions and suggesting significant impacts of hydrological factors on soil development over time. Following FAO guidelines for soil description, soil layers can be attributed with 'r' or 'g' to denote reddish or greyish colours indicative of water content dynamics (Jahn et al., 2006). The French soil system further distinguishes horizons like the G horizon, characterized by prolonged water saturation, and the g horizon with mottling and rust-coloured spots from fluctuating water circulation (Baize & Girard, 2009). Understanding these dynamics is crucial for accurate soil mapping and ecological understanding in global waterlogged environments (IUSS, 2022).

Podzols, often regarded as the ultimate evolution of soil under specific ecological conditions, are expected to maintain stable acidic conditions, resulting in well-defined horizons with organic-rich surface layers and spodic subsoils (Brock et al., 2020; Buurman & Jongmans, 2005). As plant litter decomposes in the O horizon, it produces organic acids such as fulvic and humic acids, which form strong complexes with metal ions.

These complexes are transported downward by percolating water, where in zones of higher pH or less organic material, they dissociate, precipitating iron and aluminium in the B horizon. This process creates a spodic horizon enriched with organic matter, iron, and aluminium oxides (Weil & Brady, 2017; Zech et al., 2022). Unchanged Podzols over time include the Sai, Rai1, Rai2, and Pon profiles. The Sai profile, examined in 1995 and 2020 under a Sphagno-Piceetum pine forest, exhibited highly pronounced acidic conditions in the upper horizons, proving an ongoing podzolization process. Interestingly, a basic pH in the lower horizons suggests a calcareous substrate, a regional peculiarity noted earlier (archives from Vadi & Gobat, 1998).

Podzolization involves the downward movement of organic acids, iron, aluminium, and other soluble compounds from the upper soil layers, forming a profile characterized by a bleached E horizon and an enriched B horizon. The Rai1 profile, observed in 1988 and 2020 within a subalpine forest with substantial deadwood, was shown to maintain a pH = 4 all the way down to 32 cm of depth, with slight increases in surface organic matter and decreases in clay content since 1988, despite sandy soil and earthworm activity (**Appendix B. Table S60**).

The Rai2 profile, also found within a subalpine forest, exhibited redox phenomena throughout, indicating water influence, with a persistent organomineral Ag horizon and fluctuations in organic matter. The Pon profile, established in 1984 in a Sphagno-Piceetum pine forest, shows typical podzol characteristics with increased organic horizon thickness and redox features extending beyond 30 cm by 2020, maintaining acidic surface pH and declining clay content.

Lastly, the Boi Podzol, from 1985 under a beech forest, while in 2020 under spruce, likely indicating land use change, showed evolving horizons and stable acidic conditions promoting podzolization, with increased clay and organic matter contents over decades. Together, therefore, the analyses of these soil profiles highlight the resilience and evolution of Podzols under varying environmental conditions, demonstrating both stability and subtle changes over time, thus confirming their status as one of the ultimate soil formations under specific ecological contexts.

4.1.2 Climate influence on soil properties

The negative correlations between soil physicochemical properties and the two axes of a climate-based principal component analysis (PCA) illustrated in **Figure 1. 5** provide significant insights into the influence of climatic factors on soil dynamics. Elevated PCA values correspond to increased warmth and aridity (PCA 1) and possibly reduced solar radiation (PCA 2), which correlate with diminished physicochemical distances. It has been postulated and observed that soils in warmer habitats change more rapidly than those in colder habitats, such as along elevation and latitudinal gradients (Chersich, 2018). Whether drier environments also facilitate soil physicochemical changes is less intuitive.

Theory predicts that moderate humidity levels favour the biological activity of plants and soil biota, ultimately leading to more rapid modifications in soil attributes (Butenschoen et al., 2011; Valencia et al., 2018). However, our findings are closely linked to our experimental design. In our study region of the Swiss Alps, warmer lowland conditions are typically associated with drier climates compared to the colder, more humid high-elevation habitats (Körner, 2021; Scherrer & Körner, 2011). Therefore, we speculate that the most significant changes observed in low-elevation soils, specifically in areas with warmer, drier, and sunnier conditions, are due to these climatic differences.

Thus, our study confirms that climate influences the rate of soil evolution, although these observations cannot yet be disentangled from other factors such as elevation, geological bedrock, or vegetation composition.

4.2 Variability in soil properties over time: horizon-level analysis

In addition to profile-level assessments, we conducted detailed analyses of soil properties, focusing on the surface horizons most sensitive to environmental changes (Sulman et al., 2020).

By combining field observations with analytical measurements of physicochemical properties from 28 profiles resampled 25 to 37 years apart, we evaluated changes in soil properties likely to vary over time. Specifically, we focus our discussion on the studied proxies for soil carbon change; soil organic matter (SOM), organic carbon (C_{org}), and carbon-to-nitrogen ratio (C:N), as the other measured properties showed overall little change. Weighted mean comparisons between archived and modern soils revealed consistent temporal patterns in SOM and C_{org} values between archived and modern profiles aligned with existing literature, confirming the reliability of our soil library and reinforcing the study's findings (Arthur & Okae-Anti, 2022; Gaudinski et al., 2000). Unique variations were noted in specific profiles, such as the Leptosol profile (Roc), which exhibited pronounced fluctuations in SOM content attributed to its steep slope location within a cirque. The observed variability in soil organic carbon (SOC) content across profiles highlights the influence of climatic variability and land use practices on soil carbon dynamics.

Fluvisols and Cambisols exhibited significant fluctuations in SOC content, and Gleysols showed consistent SOC accumulation patterns, while Leptosols had stable SOC levels despite their shallow profiles and erosive environments. The most pronounced changes concerned the C:N ratio (**Figure 1. 3**). In young soils and/or rejuvenated soils, such as Fluvisols, the C:N ratio tended to fluctuate over time. We propose that this fluctuation is influenced by the ongoing deposition of organic material and the variable decomposition rates observed in these habitats. Conversely, the more stable C:N ratio observed in old soils, like Podzols, is likely driven by the organic matter's long-term accumulation and decomposition.

Thus, our comparative analysis highlights the differential impact of vegetation and climate changes on soil organic matter and its subsequent effects on soil properties in young versus old soils.

5. Conclusion

While vegetation changes can be observed within a human generation, significant soil-level transformations typically occur over longer timescales. Indeed, the literature indicates that soil changes generally are minimal throughout a human generation, except in exceptional cases such as the Anthrosoles or the Fluvisols. Yet, thanks to detailed horizon-level analyses, we could highlight significant variation in soil physicochemical changes, even within 37 years, across climatic niches and elevation gradients.

In the last 37 years, soil science has experienced a surge in new analytical techniques such as FTIR (Fourier-transform infrared spectroscopy), laser technology, advanced machinery, and sophisticated tools like thin sections and laser granulometry bolstered by artificial intelligence. These advancements have revolutionized data interpretation, significantly enhancing our understanding of soil dynamics. However, it's crucial to note that these tools complement rather than replace field observations.

Accordingly, the trained eye of a pedologist remains indispensable as taxonomy evolves alongside technological advancements. Nonetheless, while our study provides valuable insights into soil development across diverse environments, several methodological limitations warrant consideration in interpreting the findings.

The wide range of soil types and environmental conditions mainly introduces complexity, potentially confounding results, and complicates broad generalizations. Despite these challenges, our study's inclusion of reference soil groups ensures a robust framework for comparative analysis, enhancing the study's applicability and validity and ultimately emphasizing the complex interactions among climatic, topographic, and other ecological factors in shaping soil dynamics.

6. Acknowledgments

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Thematic 2: Geology and soil evolution

Mineralogical indicators of soil evolution in Swiss soils

This chapter of the PhD thesis is currently in preparation. Please be advised that the analysis of the clay samples through X-ray Diffraction is still ongoing. Consequently, the results presented herein are mostly descriptive and any analysis should only be considered preliminary. As such, any conclusions drawn should be considered preliminary and may be subject to change as further analysis is completed.

In process with clay analysis ongoing:

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Abstract

Switzerland's geological history is characterized by sediment deposition, alpine uplift, Jura folding, massif erosion, and extensive glaciations, and led to a diverse array of soil landscapes shaped by central geological units such as the Jura, Swiss Plateau, Northern Alps, and Southern Alps. These geological processes have significantly influenced the mineralogical composition of soils, being one of the factors in soil formation which has been further modulated by climate, topography, and biological activity. Despite a comprehensive understanding of how geological and climatic factors impact soil formation, a notable gap exists in the longitudinal study of soil mineralogical changes over extended periods for different soil types. Specifically, there is limited insight into how these factors interact over time and space to influence soil mineralogy and how soil types evolve in response to climatic and geological shifts and how this can bring small scale mineralogical information about soil mineralogical composition at two different time points. To address this gap, we utilized X-ray diffraction (XRD) and a swiss soil library cover a wide range of environments to study soil mineralogy by comparing historical and modern soil samples 37 years apart, to detect traces of a differentiated mineralogical soil evolution pattern. Specifically, we stated that soil that had more time to evolve would be considered as "older" than soils that had less time to evolve which were considered as "young". Specifically, we hypothesized that climatic and geological changes would be reflected in soil mineralogy, with older soils displaying advanced weathering processes. Specifically, we hypothesize that older soils show higher levels of phyllosilicates and clay, indicating advanced pedogenesis as expressed in Cambisols, Gleysols, one Luvisol, and Podzols. In contrast, younger soils would be characterized by a predominance of primary minerals such as feldspaths and plagioclases, with evidence of early-stage clay formation predominantly in Leptosol, Fluvisol, and Umbrisol. Our findings show that soil types mineralogy undergo changes at different rates, and that older soils are indeed characterized by advanced weathering processes, as evidenced by higher levels of phyllosilicates and clay, compared to younger soils, which are dominated by primary minerals. However, further work is needed to investigate the exact nature of clays across the different soil samples which might allow a more precise and better understanding of how mineralogy of soil changes over space and time.

1. Introduction

Multiple historical events have shaped Switzerland's geology, including sediment deposition, the uplift of the Alps and the folding Jura, massif erosion, and glaciations (Champagnac et al., 2009; Pfiffner, 2014). These processes have divided Switzerland into four distinct geological units: (1) the tabular and folded Jura in the north and northwest, composed of limestone, marl, clay, and gypsum/anhydrite; (2) the Swiss Plateau's Molassic basin, filled with sandstone, pudding, silt, and marl; (3) the Northern Alps with the Helvetic domain predominantly made of marl and limestone; and (4) the Central and southern Alps with a crystalline base mainly composed of granites and gneiss (Nagra, 2024). These geological events, in conjunction with the site-specific topography, climate, and biological activity, have contributed to shape the diverse soil landscapes of Switzerland (Antonelli et al., 2018; Huggett, 1998; Jenny, 1994; Phillips, 2021). Indeed, surface formations, including soil, alterite and sedimentary formations, play a crucial role in geomorphological dynamics and soil formation processes (Bauer & Velde, 2016; Zinck, 2023). Specifically, soil formation, in this regard, involves the transformation of primary minerals from bedrock into secondary minerals, such as clays, oxides, and hydroxides. This process, known as weathering, is crucial for pedogenesis and the resulting variety of soil properties (Churchman & Lowe, 2012; Righi & Meunier, 1995; Wilson, 2004).

Therefore, the evolution of soils varies significantly due to the distinct properties of their parent materials (Michalet, Gandoy, Joud, Pagès, & Choler, 2002). For instance, calcareous bedrock, such as limestone, weathers rapidly under acidic conditions, leading to the formation of soils rich in calcium carbonate and clay minerals like kaolinite (Osman, 2013). These soils often exhibit good fertility and structure but may be prone to compaction and erosion. Conversely, siliceous bedrock, composed mainly of quartz and silicates, weathers more slowly, resulting in soils with higher sand content and lower nutrient availability (White, 1995). These soils tend to be more acidic, less fertile, but generally offer better drainage and are less prone to compaction (Gray & Murphy, 1999).

As soils mature, ongoing weathering processes typically increase the relative abundance of phyllosilicates and goethite, while quartz and feldspars, being more resistant to weathering, decrease in concentration (Allen & Fanning, 1983; Velde, Meunier, Velde, & Meunier, 2008).

This mineralogical shift serves as an important indicator of soil development and aging, consistent with findings in other studies on soil evolution and weathering (Egli, Merkli, Sartori, Mirabella, & Plötze, 2008; Zehetner et al., 2024).

Moreover, recent research has highlighted the significant impact of climate change on soil properties and processes, including how variations in precipitation and temperature affect weathering rates and organic matter decomposition (Galluzzi, Plaza, Priori, Giannetta, & Zacccone, 2024; González-Domínguez et al., 2019; Qafoku, 2015). Nevertheless, there remains a notable gap in longitudinal studies examining soil evolution over extended periods.

In this context, we define old soils as those exhibiting complex and advanced pedogenetic processes such as brunification (forming a clay-humus complex with an iron bridge), clay leaching (Moody, 2006), or podzolization. In contrast, young soils are characterized by simpler processes like organic matter accumulation, decarbonation, waterlogging, and material input, which may later lead to brunification and material export (Lavelle & Spain, 2001). At our latitudes, most soils are relatively recent in formation, when compared to tropical soils. In this regard, Central European soils mostly all started during the Holocene, from around 11,700 years ago to the present, and under post-glacial climatic conditions and vegetation. Yet, soils can have evolved over much longer periods; the Pleistocene soils were formed between approximately 2.6 million and 11,700 years ago, shaped by alternating glacial and interglacial periods (Studer, Koller, Loew, & Lateltin). Older than these soils, are the Pliocene soils, dating from about 5.3 million to 2.6 million years ago, and the Miocene soils, which originated from around 23 million to 5.3 million years ago, show significant weathering associated with the geological conditions of the Miocene epoch (Studer et al.). Residual soils, dating back more than 23 million years, are the oldest, formed through prolonged bedrock weathering and commonly found in stable landforms.

Recent advancements in X-ray diffraction (XRD) technology have greatly improved our understanding of soil and clay mineralogy, providing a valuable tool for analysing mineral compositions and gaining insights into soil evolution and pedogenesis (Hong et al., 2023; Hubert, Caner, Meunier, & Lanson, 2009).

For example, studies using XRD have revealed how clay minerals influence soil processes and how the mineralogical composition impacts soil properties such as fertility, structure, and hydrology (Aboudi Mana, Hanafiah, & Chowdhury, 2017; Harris & Norman White, 2008; Zhou et al., 2018). Moreover, XRD is used to determine how the mineralogy of parent material undergoes physico-chemical changes in respect to in soil chemistry and physical properties (Böhlert, Mirabella, Plötze, & Egli, 2011; Kumari & Mohan, 2021).

For instance, XRD analysis has shown that soils derived from crystalline rocks in the Alpine region typically contain higher levels of illite and chlorite, while soils from sedimentary rocks in the Swiss Plateau are richer in smectite and kaolinite (Martignier, Nussbaumer, Adatte, Gobat, & Verrecchia, 2015). These differences in mineral composition are essential for understanding soil formation and evolution across diverse landscapes. The question remains of how different soil types, spread across a wide range of climatic and topographic diversity are similarities in their mineral composition, and whether recent climate changes can impact the mineral composition over relatively short periods of times, hence independently of the long-term geological processes.

We addressed these questions by studying 28 soil profiles spread across the diverse geological and topographical landscapes of Switzerland, and from which we have samples dating back up to 37 years. We used XRD analysis to compare soil types comprehensively, focusing on their mineralogical composition to understand how soils have evolved over time. We hypothesized that climate significantly influences soil evolution, reflected in varying soil types and mineral compositions. Specifically, we anticipated that advanced weathering would be indicated in old Swiss soils by higher relative percentages of phyllosilicates and goethite alongside lower percentages of quartz and feldspaths. In contrast, younger Swiss soils are expected to show a predominance of primary minerals and early-stage clay formation.

Specifically, we asked: (1) How different soils, in different environment (either old or young) display different mineralogies? We analysed climatic data to correlate mineral composition with soil types and pedoclimatic contexts. (2) How does soil mineralogy change over short periods as a function of soil type? We investigated the variations in primary and secondary minerals across different soil types to understand their evolutionary phases better. For this thesis, because we did not obtain the full dataset of the XRD analyses, we mainly focus on the second question.

2. Materials and methods

We integrated field-based sampling with laboratory analyses to assess the impact of various rock types and pedogenic processes on soil mineralogy. Soil samples were collected from representative sites across Switzerland, covering a range of rock types. Each sample underwent detailed mineralogical analysis using XRD to identify key minerals such as quartz, goethite, and phyllosilicates (kaolinite, montmorillonite). These analyses allowed us to trace the influence of geological and pedogenic factors on soil formation, such as hydrolytic weathering, leaching, and oxidation.

By integrating these data, we aimed to understand how different soil types—including Cambisol, Fluvisol, Gleysol, Podzol, Umbrisol, Luvisol, and Leptosol—transition through their developmental phases as they age, based on various rock parent materials and under diverse climatic and topographic conditions. **Figure 2.1** summarizes all the concepts addressed in this study.

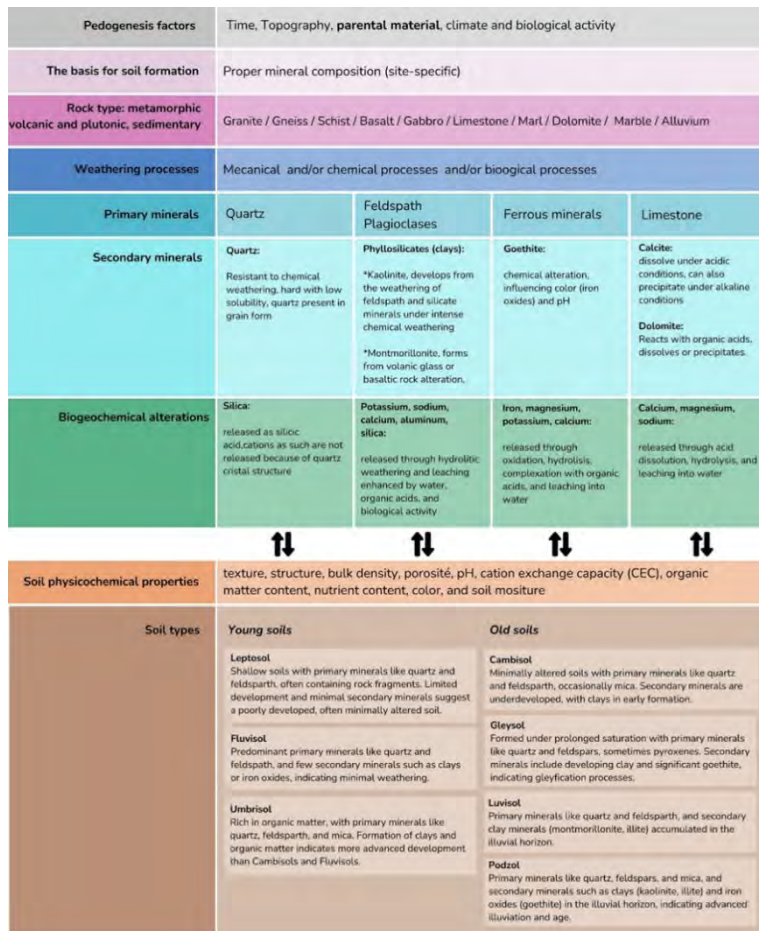


Figure 2. 1 Conceptual model of Swiss soil formation and mineralogical composition. This figure illustrates the interplay between various soil formation rock types, mineralogy, and pedogenic processes. It shows how different rock types—metamorphic (e.g., Granite, Gneiss, Schist), volcanic and plutonic (e.g., Basalt, Gabbro), and sedimentary (e.g., Limestone, Marl, Dolomite, Marble, Alluvium)—contribute to soil mineral composition. Key minerals are highlighted: quartz, which is resistant to chemical weathering and low in solubility; goethite, affecting soil color and pH through chemical alteration; and phyllosilicates such as kaolinite and montmorillonite, formed from the weathering of feldspath, silicate minerals, or volcanic glass. The figure also depicts how weathering processes—hydrolytic weathering, leaching, oxidation, and complexation—release minerals like silica, iron, magnesium, potassium, and calcium. Soil types are represented, including Cambisol (young soils with primary minerals), Fluvisol (with minimal weathering), Gleysol (formed under prolonged saturation), Podzol (advanced illuviation), Umbrisol (organic matter-rich), Luvisol (with secondary clay accumulation), and Leptosol (shallow and minimally developed). The diagram integrates pedogenic factors such as time, topography, parental material, climate, and biological activity, and illustrates their impact on soil physicochemical properties, including texture, bulk density, pH, cation exchange capacity (CEC), organic matter content, nutrient content, and soil moisture.

2.1 Study sites and data collection

We used archived soil samples from a 37-year-old soil library, which includes soil profiles representing diverse regions and soil types across Switzerland. These historical profiles were meticulously chosen to reflect a broad geographical and pedological range. In 2020, we revisited the original sampling sites to collect new, homologous soil profiles. This excavation replicated the original sampling methods as closely as possible to ensure comparability between historical and recent samples. Our objective was to investigate the long-term evolution of soil mineralogy and clay content over the past four decades by comparing the bottom horizons of both old and new soil profiles. Each soil profile was described and classified according to the “Référentiel pédologique” guidelines (Baize & Girard, 2009) and the Guidelines for Soil Description (Jahn, Blume, Asio, Spaargaren, & Schad, 2006) and subsequently translated into the World Reference Base for Soil Resources (WRB, 2022) classification system. Key descriptors included horizon depth, color (using the Munsell soil color chart), coarse fragments (>2 mm), soil structure, and texture (sand 2 mm - 50 μm , silt 50-2 μm , clay <2 μm). Additional in situ measurements were taken to assess relative carbonate content using 6M HCl, soil pH with a Hellige meter, and biotic indicators such as root presence and animal droppings. In our study, a total of 56 soil samples were analyzed to provide a comprehensive overview of soil changes and continuity over time.

2.2 Soil analysis

Soil samples were dried at 40°C, and then sieved at 2 mm. Clays were identified through laser granulometry (Gee & Bauder, 1986; Pansu & Gautheyrou, 2003). XRD analyses of the whole rock samples were conducted at the Geological Institute of the University of Lausanne, following the procedure described by Adatte et al. (1996) and Kübler (1983). Approximately 20 grams of each rock sample were initially crushed with a jaw crusher to produce small chips (1 to 5 mm). Subsequently, about 5 grams of each sample were dried at 60°C and ground into a homogeneous powder with smaller particle sizes than 40 μm . For XRD analysis, 800 milligrams of the powdered sample were pressed into a powder holder using a glass plate.

XRD analysis was performed using an XTRA ARL Diffractometer, with methods based on Ferrero (1965, 1966), Klug and Alexander (1974), Kübler (1983), and Rolli (1990). The semi-quantitative analysis of the bulk rock mineralogy was conducted using XRD patterns of random powder samples and external standards. Details of the equipment and settings are provided in the supplementary materials. Raw data files generated by SCINTAG (.RD format) were transformed into calculated files (NI format) using the DMS program (v. 2.63) with graphic-normal display. The calculations included Fourier noise filtering, background subtraction, and Ka2 stripping. Measurements were performed on these calculated files.

3. Data analysis

All analyses were performed in R v.4.1.1 (R Core Team, 2013; Team, 2020). Also, it is important to note that a subset of the samples remains under XRD analysis for clay mineral identification. Consequently, our current analysis is limited to the data available from the recently excavated soils (2020) and from a subset of 16 soils from the soil library. As a result, while our study aims to understand soil evolution from a mineralogical perspective, it is not yet robust due to the incomplete dataset. However, we can still describe and analyse the differences among the existing soil profiles. Once the XRD results for the remaining samples are completed, we will integrate this data to conduct more comprehensive analyses and provide a thorough understanding of the soil profile characteristics.

3.1 Site-specific climatic, topographical and lithological variables

We extracted climatic and topographic variables using raster layers from Zimmermann et al. (1999). These layers included radiation, elevation, degree days, potential evapotranspiration, precipitation, and frost days. We extracted climate variables at specific soil sample locations using the `extract` function in the `raster` package (Hijmans et al., 2015), allowing us to append climate information to each soil profile. Principal Component Analysis was then performed using the `dudi.pca` function from the `ade4` package (Dray & Dufour, 2007) and visualized with `fviz_pca_biplot` from the `factoextra` package (Kassambara & Mundt, 2017). Lithology data for each soil sample were gathered from Macrostrat online database (Peters, Husson, & Czaplewski, 2018).

A principal component analysis (PCA) was performed to ordinate soil profiles based on their climatic niche, and color-coded based on the lithological substrate using the factoextra package in conjunction with ggplot2 (Wickham, Chang, & Wickham, 2016).

3.2 Soil profiles similarities based on soil mineralogical information

To address the question of how different soil profiles across the Swiss landscape converge or diverge in terms of their mineral properties, we first visualized similarities among soil profiles in terms of mineralogical variables (clay content, phyllosilicates, quartz, potassic feldspath, sodic plagioclases, calcite, dolomite, goethite, and non-quantified (organic matter, amorphous or poorly crystallized products: e.g., iron hydroxides) using a PCA and with cluster dendrograms. The dissimilarity matrix was constructed, and the corresponding dendrogram were constructed using the profile_compare function in the aqp package (Beaudette, Roudier, Beaudette, & RcolorBrewer, 2024). The different soil profiles were then visualized using the plotSPC function from the aqp package to illustrate the distribution of soil types across different profiles. We then performed a redundancy analysis (rda function in vegan, Oksanen (2010)), and asked if the multivariate set of the mineral content varies significantly according to the “old” versus “young” soil classification (as shown in **Table S2. 1**).

3.3 Short-terms changes in mineral composition

To explore how much the multivariate mineral composition has changed within each soil profile (i.e., comparing the data from the soil library with data from the recent – 2020 - sampling), we ordinated the data using non-metric multidimensional scaling (NMDS; with metaMDS function in vegan), and visualised the change by connecting the same soil profile across the two sampling dates; longer segments indicating larger amount of change in the mineral composition. We then tested the interactive effect of sampling time (soil library versus the 2020 sampling) and soil type on the mineral composition with a permutational multivariate analysis of variance (PERMANOVA; adonis2 function in vegan). For both the NMDS and the PERMANOVA, the Euclidean distance was used.

4. Preliminary results

This analysis presents preliminary results and is intended to provide an initial understanding of soil processes and phases across different soil types. The findings should be interpreted cautiously, as they are based on initial data and may be subject to revisions as further research is conducted. The conclusions drawn here are exploratory and serve as a foundation for more detailed investigations.

4.1 Soil diversity, lithology and climate

The principal component (PCA) analysis of the climatic variables of the soil profiles, shows that soil can be grouped according to their lithology, with different ecological environments (**Figure S2. 1** and **Table S2. 1**), with PC1 and PC2 explaining 85,8% of the total variance. Alluvium, moraine, calcareous sedimentary rocks, and gravel and sand mineralogies are clustered together and representative of warm and dry environmental conditions. In contrast, metamorphic rocks and one biogenic carbonate samples are clustered together and representative of very cold and wetter environmental conditions. Ecological environment reflected the observed climatic niche, with soils distributed and clustered along the PCA axis 1 with Alpine soil grouped, except for the Cambisol (Nav) from the Val d'Anniviers in the canton Valais (VS) and the Leptosol (Roc) from the region Neuchâtel (NE). Alluvial soils were found in very hot and dry climatic conditions degree days highly influencing their distribution and lithology. The two Cambisols found near Lake Neuchâtel (Bev and Gor), in forest environments 900 m to 3km, respectively, distant from the lakeshore were also characterized by hot and dry climatic conditions. Grasslands soils exhibit a heterogeneous distribution, with soil profiles from various geographical regions and ecological environments. For instance, the Luvisol from Chasseron in Vaud (VD) is grouped with soils from Binntal (VS), while the Cambisol du Chasseral (NE), influenced by the cold climate of Chasseral, and the Cambisols du Theusseret in the Jura (JU), affected by heat, also show notable similarities.

4.2 Mineralogical similarity across different soil types

In terms of the mineralogical composition, we observed that soils that group together do not necessarily belong to the same soil type (Figure 2. 2 and Figure S2. 2), highlights considerable diversity in soil mineralogies, independently of the soil nomenclature.

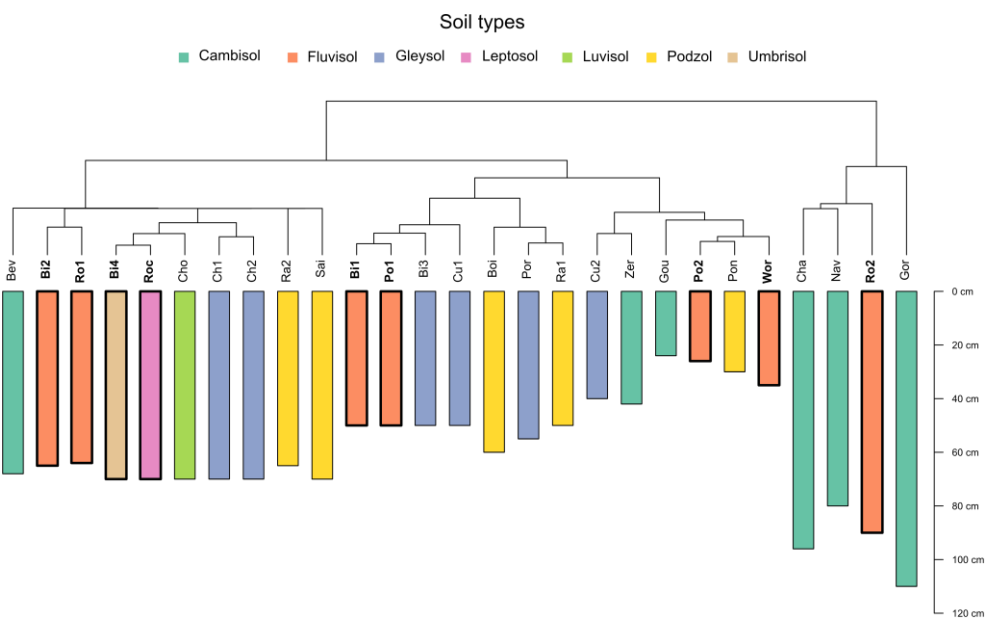


Figure 2. 2 Soil samples analysis and mineralogical dissimilarity. This dissimilarity matrix highlights differences in mineral content across soil samples, focusing on key minerals such as phyllosilicates, quartz, potassic feldspaths, sodic plagioclases, calcite, and dolomite. The matrix is accompanied by depth intervals for bottom horizon thicknesses for all soil profiles. Colors represent different soil types: Cambisols (green), Fluvisols (orange), Gleysols (blue), Leptosols (pink), Luvisols (lime green), Podzols (yellow), and Umbrisols (tan).

Yet, some trends of mineral composition emerge characteristic of soil types (Figure 2. 3 and Figure S2. 2). For instance, Podzols from various regions cluster together, reflecting their shared characteristics, such as high clay and phyllosilicates (Figure 2. 3). In contrast, soils like the Gleysol (Cu2) from Cudrefin and the Raimeux Podzol (Ra1) from Canton Bern, despite being from different regions, show significant similarity, as evidenced by their lower dissimilarity score of 14.6.

On the other hand, the Cambisol (Nav) from Roches de Nava and the Fluvisol (Ro1) from Canton Fribourg display intermediate dissimilarity, while the Podzol (Sai) from Canton Neuchâtel and the Fluvisol (Wor) from Canton Bern show a wide range of dissimilarity scores, reflecting greater variability in their mineralogical traits. Together, these results indicate a substantial variability in soil mineralogical characteristics across the sampled locations.

Figure 2.3 Soil age. The PCA biplot illustrates the distribution of minerals identified in each soil sample. Each point represents a soil sample, with colors indicating the different conceptual soil ages with old soils: Cambisols, Gleysol, Luvisol, Podzol (red), and young soils (Leptosol, Fluvisols, and Umbrisol (blue). The plot visually differentiates these soil ages based on their mineralogical composition. The sample codes reflect the site names and soil type abbreviations, providing context for the data points.

Accordingly, Podzols, Cambisols (except the Zermatt sample), and Luvisols tend to share similar mineralogical traits and compositions, clustering towards clay, phyllosilicates, and quartz.

Conversely, Gleysols, Fluvisols, Umbrisols, and Leptosols are clustered towards calcite and dolomite, indicating that these soils are characterized by lower clay and phyllosilicates and higher levels of calcite and dolomite.

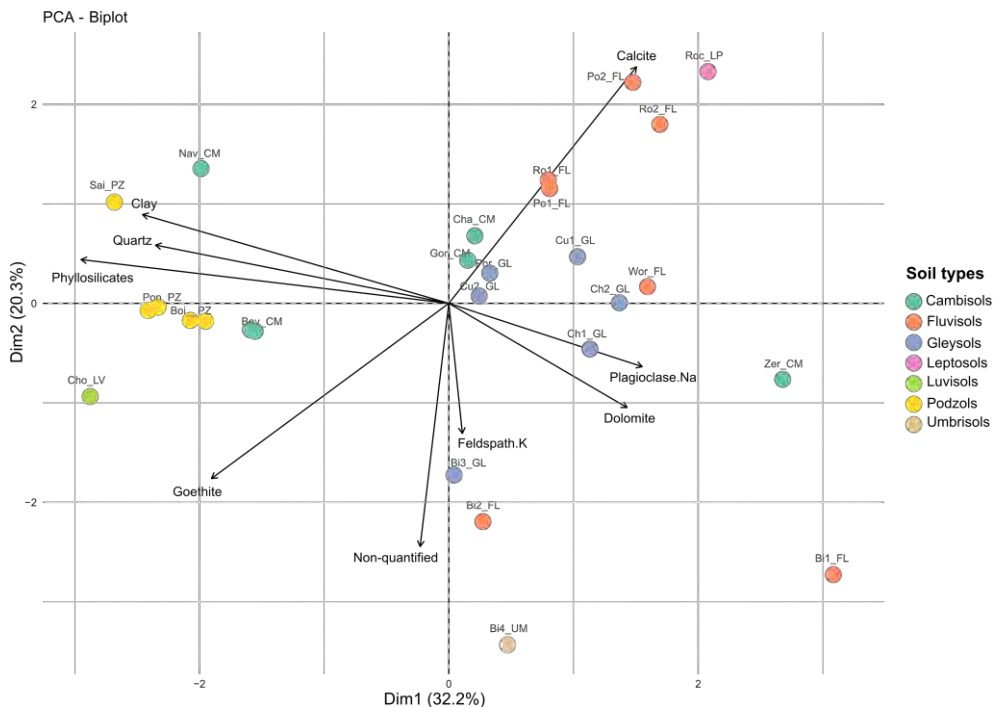


Figure 2. 4 Soil mineral distribution. The PCA biplot illustrates the distribution of minerals identified in each soil sample. Each point represents a soil sample, with colors indicating different soil environment groups: Cambisols (light green), Fluvisols (orange), Gleysols (purple), Leptosols (pink), Luvisols (light green), Podzols (yellow), and Umbrisols (brown). The plot visually differentiates these soil types based on their mineralogical composition. The sample codes reflect the site names and soil type abbreviations, providing context for the data points.

4.2 Mineralogical changes over 37 years

Although so far, we could only analyse 16 pairs samples (2020 - soil library, **Figure 2. 5**), we can see that some soils show greater changes in their mineralogical composition than others, notably certain Fluvisols (Bi1, Bi2 Po1, Po2 and Wor), Leptosol (Roc), Gleysol (Cu2) and Umbrisol (Bi4).

Whereas other soils types, such as Podzols (Boi, Ra1, Sai), Cambisols (Gou), Fluvisols (Ro1, Ro2, Ch2) and Gleysols (Cu1) show only minimal changes. Yet, for now, this variability in the extent of change was not supported by the PERMANOVA analysis (sampling time effect: $F_{1,31} = 0.17$, $p = 0.96$, soil type effect: $F_{5,31} = 2.65$, $p = 0.01$, and the interaction: $F_{5,31} = 0.56$, $p = 0.91$).

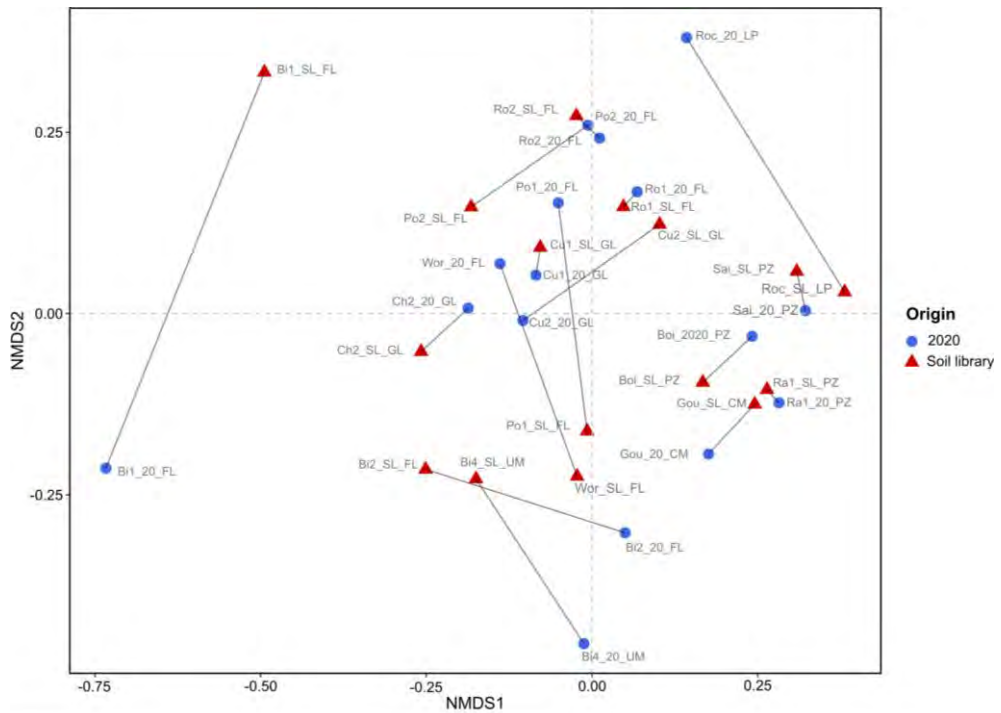


Figure 2. 5 Soil mineralogical changes across time. Shown is a non-metric multidimensional scaling (NMDS) ordination plot illustrating the origin of soil samples. Points are colored to differentiate soil oring from 2020 soil samples (blue) and the soil library samples (red). The distance between 2 points is indicate by a black line.

5. Discussion

We employed both diachronic and synchronic approaches to interpret historical and recent soil samples, focusing on their mineralogical composition and the impact of climatic conditions. Our goal was to develop hypotheses regarding the evolution of these soils over time and to identify reliable indicators of soil development. By categorizing soil types into "old" and "young", we aimed to validate our predictions and deepen our understanding of soil evolution.

5.1. Climate and weathering effects on soil types

Our preliminary results underscore the crucial role of both climate and geological factors in shaping soil characteristics. We observed that soils from similar ecological environments —such as alpine, forest, grassland, alluvial, and lakeshore — tend to cluster according to their lithology. However, some environments, like alluvial, grassland, and forest, exhibit more variability.

In alpine environments, for example, we found that soils (e.g., Nav and Zer Cambisols, Bi1 and Bi2 Fluvisols, Bi3 Gleysol, and Bi4 Umbrisols) originating from different lithologic substrates, such as metamorphic rocks, are grouped based on geographic location (Baumann, Robl, Prasicek, Salcher, & Keil, 2018). Specifically, soils from the dolomitic region of Binntal (Bi1, Bi2, Bi3, Bi4) with high precipitation and humidity, the basaltic region of Zermatt (Zer) with lower rainfall and humidity, and the Val d'Anniviers (Nav) with extremely cold conditions exhibit distinct clustering patterns.

Similarly, we observed a broader diversity of soil types in forest environments, likely due to ecological succession (Walker, Wardle, Bardgett, & Clarkson, 2010). Forests that have achieved a stable equilibrium or climax state typically feature more mature soils, such as Podzols (Sai, Ra1, Ra2, Boi, Pon). In contrast, younger and more disturbed forests, such as Cambisols, often exhibit less mature soils (Gor and Bev). This highlights that while Cambisols are still undergoing brunification — a complex soil formation process — they represent less mature soil development compared to the more stabilized Podzols (Ismail-Meyer, Stolt, & Lindbo, 2018). This stability in forest ecosystems is reflected in consistent climatic conditions, including balanced radiation, precipitation, humidity, elevation, frost days, and degree days (Bonan, 1989). The lithology, including biogenic carbonates for Podzols and moraine, gravel, and sand for Cambisols, further explains the mineralogical maturity of these soils (Fabio, Daniela, & Zerboni, 2023; Indraratne, 2020). Instead, for grassland, we sampled in heterogeneous climatic conditions, ranging from very cold (Nav) to warm and dry (Gou) condition. Biogenic carbonates in these soils may result from calcium accumulation in plant tissues, which is returned to the soil upon decomposition, along with microbial activity that promotes carbonate mineral formation through precipitation (Dupraz et al., 2009; Hinsinger, 2013).

Our study of alluvial soils (Ro1, Ro2, Po2, and Wor Fluvisols) underscores the significant influence of temperature and water on their characteristics. Despite originating from different regions, these soils clustered together, likely indicating a similar influence of environmental factors on the formation of these soils. This clustering can be attributed to vulnerability to erosion indexes and dynamics, which reflect the ongoing processes of sediment deposition and erosion typical of alluvial environments (Ahmed, Howlader, Hoque, & Pradhan, 2021; Modak, Mandal, Mandi, & Ghosh, 2023).

The constant regeneration and reworking of these alluvial systems contribute to the similarities observed in soil profiles, underscoring how these dynamic processes shape soil characteristics and lead to similar clustering patterns across diverse locations.

5.2 Mineralogical indicators of soil evolution

Our study aims to deepen the understanding of soil evolution and mineral content in Switzerland by using XRD analysis of clay minerals. XRD helps us assess soils' mineralogical composition and texture, revealing how geological substrates affect soil formation and weathering. Combining XRD data with geological and geomorphological evidence will clarify how mineral composition interacts with soil formation processes and environmental factors, especially glacial dynamics. This approach highlights how mineral content, such as high phyllosilicates indicating advanced weathering in humid climates or high quartz content suggesting less weathered soils in semi-arid regions (very hot and dry climate, although in our latitudes the climate is more temperate), serves as a key indicator of soil evolution. In our analysis, we found that the presence of potassic feldspath and sodic plagioclases, which weather into secondary minerals, suggests that soils with these minerals are younger or less weathered than soils with significant clay formation. Additionally, goethite, a ferrous mineral, often indicates advanced soil weathering and maturity, especially in well-drained soils like Gleysols or Ferralsols, where iron oxides are prevalent (Wu, Amelung, Xing, Bol, & Berns, 2019). This finding is consistent with our preliminary results, where soils classified as older or younger based on mineralogical composition were clustered together, irrespective of soil type (**Figure 2.2** and **Figure 2.3**).

More mature soils, such as Podzols (Sai, Boi, Ra1, Ra2, Pon), Luvisol (Cho), and Cambisols (Nav and Bev), exhibit higher levels of clay, phyllosilicates, quartz, and unquantified materials like organic matter and poorly crystallized products (e.g., iron hydroxides).

Conversely, soils considered less mature are grouped based on high calcite, dolomite, and sodic plagioclase content and potassic feldspath. This grouping includes some older soils, suggesting that the "young" and "old" soil categories may overlap, with some old soils exhibiting characteristics of younger soils or soils in transition. Notably, a small cluster of soils—including Leptosol, Cambisols (Cha, Gor), and one Fluvisol (Ro1)—differentiates itself from the other groups. This cluster represents an intermediary phase, indicating soils transitioning between youthful and more mature phases.

This intermediate group encompasses Cambisols, Leptosols, Fluvisols, and Gleysols, reflecting soils that are becoming more mature or stable, regardless of their initial classification.

Finally, our preliminary analysis highlights how mineralogical composition reflects soil evolution and the influence of geological and environmental factors. Climate significantly impacts soil mineral composition through direct and indirect effects on weathering processes (Qafoku, 2015; Taylor, Banwart, Valdes, Leake, & Beerling, 2012). In humid climates, intense weathering accelerates the breakdown of primary minerals like feldspaths and plagioclases into secondary minerals such as clay (Singh et al., 2018) and goethite (Wilson, 2004).

In contrast, with minimal rainfall, the semi-arid climates observed allow primary minerals like quartz to persist, resulting in slower chemical weathering (Bland et al., 1998; Wackett, Yoo, Amundson, Heimsath, & Jelinski, 2018). Limestone-rich areas, where calcite and dolomite weather to create alkaline conditions, experience variations in leaching and organic matter decomposition influenced by precipitation and seasonal changes (Caserini, Storni, & Grosso, 2022; Sadooni & Al Awadi, 2009). Wetland areas with high moisture and waterlogging often yield Gleysols, characterized by grey or blue-grey hues from reduced iron oxides (Bedard-Haughn, 2011).

Cold and acidic conditions favor the development of Podzols, where leaching removes iron and aluminum from the upper horizons, creating a distinctive leached horizon below (Sanborn, Lamontagne, & Hendershot, 2011). Climate-driven weathering processes are crucial in determining various soil types' mineralogical and pedological characteristics.

Taken together these first results thus highlight that soil evolution and pedogenesis process can also be understood within the framework of mineral composition changes across the landscape.

5.3 Soil changes over short time periods

The mineral composition of soil samples reveals significant insights into soil age and type, as depicted in **Figure 2. 3**, **Figure 2. 4**, and **Figure 2. 5**. For instance, Podzols from the 2020 samples (Sai, Ra1, and Ra2) exhibited increased clay content compared to older samples from the soil library, suggesting recent changes in soil formation. In contrast, Cambisols (Gou) demonstrated a reduction in clay content over time, likely due to ongoing weathering and leaching processes.

Fluvisols showed divergent trends: those from Ro1 and Ro2 had elevated calcite levels, probably due to calcite-rich sediment deposition or arid conditions, while Fluvisols from Binntal experienced decreased dolomite content, likely due to higher organic matter and dissolution from organic acids.

Some Fluvisols (Ch2) also had reduced sodium-rich plagioclases due to weathering and alteration processes that formed clay minerals and released sodium ions. Groundwater chemistry, including acidity and ion exchange capacity, may further influence these processes, especially in soils near lakeshores. Notable changes were observed in Fluvisols from Bi1, Bi2, Po1, Po2, and Wor, with factors such as sandy texture, vertical and horizontal water dynamics, and sediment mixing contributing to these variations. For instance, the sandy texture and dolomitic origin of Bi1, coupled with increased percolation, influenced weathering, while Bi2's thick organomineral horizon and vertical water movement were key factors. The differences in Po1 and Po2, are influenced by horizontal water dynamics and potential erosion, contrasted with those in Bi1 and Bi2.

Additionally, Roc's changes were linked to calcareous rock fragmentation and sediment mixing, Cu2's oxidation-reduction phenomena from vertical water table movements, and Bi4's to weathering late Pleistocene and Holocene deposits. Conversely, minimal changes were noted in Podzols (Boi, Ra1, Sai), Cambisol (Gou), Fluvisols (Ro1, Ro2, Ch2), and Gleysols (Cu1), suggesting stability due to long-term environmental conditions and soil maturity. These findings underscore the complex interplay of soil formation factors and environmental conditions, highlighting the nuanced variations within soil types and the challenges in deciphering soil pedogenesis.

5.4 Understanding soil complexity: mineralogy and organic matter

As Phillips (2017) proposed, soil convergence and divergence are fundamental concepts in understanding soil development. Convergence occurs when soils from different locations become similar due to comparable environmental conditions and pedogenetic processes, such as similar climate or biological influences. This means that despite differing initial conditions, soils can evolve to have similar characteristics. Conversely, divergence happens when soils with similar starting conditions develop distinct characteristics due to varying environmental factors, such as differences in climate or topography.

Phillips highlights that both convergence and divergence are essential for understanding soil complexity and emphasizes the need for diachronic (over time) and synchronic (across locations) analyses to fully grasp how soils evolve and vary.

Our preliminary results reflect key principles of soil formation by revealing distinct clustering patterns among soil types based on their mineralogical composition. This clustering emphasizes the complexity inherent in soil development, where even soils classified under the same type can exhibit considerable variability due to differing developmental stages or processes. For instance, mature soils such as Podzols and Luvisols, characterized by high levels of clay and phyllosilicates, signify advanced weathering and extensive soil development. These soils typically undergo prolonged weathering, which results in the accumulation of clay minerals and transforming primary minerals. In contrast, less mature soils display varying levels of calcite, dolomite, and potassic feldspaths, indicative of various developmental phases.

This variability underscores the ongoing nature of soil evolution and the dynamic interaction between soil types and environmental factors (**Figure 2. 2, Figure 2. 3**). In addition to mineralogical composition, the role of organic matter, specifically mineral-associated organic matter (MOM) and particulate organic matter (POM), further elucidates the complexity of soil formation. MOM is tightly bound to soil minerals, influencing soil structure, stability, and nutrient availability (Mikutta et al., 2019).

In soils such as Podzols and Luvisols, the degree of weathering significantly influences the nature and stability of organic matter. In Podzols, where advanced weathering and leaching processes have occurred, the POM tends to be concentrated in the upper, more acidic horizons, forming less stable humus due to the high acidity and leaching (Zech, Schád, & Hintermaier-Erhard, 2022). This results in relatively lower fertility and less stable organic matter than Luvisols. In contrast, Luvisols benefit from high clay content, promoting stable MOM complexes' formation. The interaction between clay minerals and organic matter in Luvisols enhances the stability of humus, thereby contributing to the soil's overall fertility and structural integrity (Zech et al., 2022). This stability reflects the advanced developmental stage of Luvisols, where clay and organic matter interactions result in well-preserved and fertile soil profiles. The differences in organic matter stabilization between these soil types underscore their distinct developmental stages and the varying impacts on soil fertility and structure.

On the other hand, POM, which consists of decomposed plant material and other organic residues, tends to be more prevalent in younger or less weathered soils. For instance, in soils with significant amounts of calcite or dolomite, the presence of POM reflects ongoing organic input and decomposition, contributing to soil fertility and structure (Calero, García-Ruiz, Torrús-Castillo, Vicente-Vicente, & Martín-García, 2022).

The interaction between POM and soil minerals in these less mature soils highlights the transitional phases of soil development, where organic matter is actively integrated into the soil matrix. The presence and distribution of MOM and POM in soil profiles also reveal insights into soil formation processes and environmental conditions.

For example, soils with high MOM content, such as mature Podzols, typically experience more intense weathering, whereas soils with significant POM, like some Cambisols, indicate ongoing organic matter accumulation and soil development. Overall, integrating the analysis of mineralogical composition with the study of MOM and POM provides a more comprehensive understanding of soil development. It illustrates how different stages of soil maturity and environmental influences interact to shape soil properties and characteristics. This approach highlights the intricate relationships between soil mineralogy, organic matter dynamics, and soil formation processes, offering valuable insights into the evolution of soil types over time.

Our findings underscore the complex interplay between soil minerals and organic matter in shaping soil profiles. By considering both mineralogical traits and organic matter dynamics, we gain a deeper understanding of soil evolution and the factors driving soil variability across different environments. **Figure 2. 6** highlights the dynamic nature of soil types, illustrating how they undergo various developmental phases influenced by climatic and environmental processes.

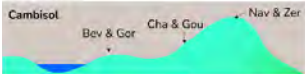
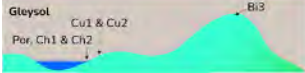
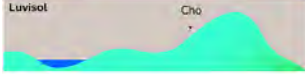
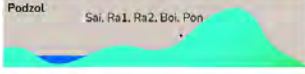
Soil type across the Swiss landscape	Processes involved & SOM		Phase
Old soils			
	Simple & complex processes	• Acidification • Decarbonation • Brownification POM : ++ MOM : +	Intermediate phase of formation with primary mineral weathering influenced by climate and hydrology
	Simple processes	• Clogging • OM accum. POM : +++ MOM : +	Changing phases influenced by periodic clogging with vertical water movement and climate
	Complex processes	• Acidification • Illuviation • Eluviation POM : + MOM : +	Intermediate to long-term phase , soil developed under temperate climates with clay illuviation; may exhibit variations based on seasonal changes.
	Complex processes	• Acidification • Eluviation • Chelation • Podzolisation POM : +++	Long-term phase with strong acidification and weathering under cold and humid climatic conditions.
Young soils			
	Simple processes	• Fragmentation • OM accum. & integration POM : +++ MOM : +	Early to long-term phase with weathering and erosion processes dominating; soil development influenced by climatic and geological conditions
	Simple & complex processes	• Flooding • Material inputs/outputs • Brownification POM : + MOM : +	Changing to intermediate phase frequently affected by periodic flooding; mineral depositions or erosion and soil formation influenced by hydrological dynamics.
	Complex processes	• Acidification • Brownification • Chelation POM : +++ MOM : +++	Long-term phase , soil developed in humid and temperate climates; influenced by high organic matter accumulation and soil acidification

Figure 2. 6 Conceptual table of soil processes and phases across the Swiss landscape. This figure presents a conceptual table summarizing the primary soil formation processes and developmental phases for four distinct soil types: Luvisols, Leptosols, Fluvisols, and Umbrisols. The table categorizes each soil type according to the main processes influencing its development, such as climatic modification, flooding, and acidification. For each soil type, it details key processes and phases, illustrating how different factors contribute to soil formation and evolution. The graphic on the left, depicted in turquoise, shows the Swiss landscape and the location of different soil types within it. Sites are categorized based on their proximity to the lake, with royal blue indicating the lake's location at its lowest point (400m altitude). Sites on the right bank of the lake border it, while samples from the left bank represent alluvial sites. Soil profiles are illustrated with varying symbols to indicate the relative abundance of Particulate Organic Matter (POM) and Mineral-Associated Organic Matter (MOM), where "+" symbols denote their theoretical and hypothetical contents.

We categorize these developmental phases into four distinct stages, each reflecting different aspects of soil formation. The early phase represents the beginning of soil development, characterized by the onset of several formation processes. During this phase, soils start to establish their primary characteristics as basic mineralogical and organic processes begin. This stage sets the groundwork for the more complex development phases that follow. In the intermediate phase, soils experience both simple and complex formation processes.

These processes can persist for varying durations, leading to a more defined set of soil characteristics. The intermediate phase is marked by a blend of evolving mineralogical traits, reflecting ongoing environmental changes. This phase's soil shows a mixture of developing properties as they evolve towards more mature forms. The long-term phase is characterized by advanced and complex soil formation processes. Soils such as Podzols and Umbrisols, which undergo extensive weathering and transformation, are examples of long-term development. These soils develop highly complex profiles due to prolonged and intense formation processes. Conversely, Leptosols exhibit significant fragmentation with minimal organic matter development, representing simpler yet sustained developmental processes over time.

Finally, in the changing phase, the predominant movement of water significantly influences soil development. Fluvisols, with their horizontal water movement, exhibit characteristics shaped by sedimentation and depositional processes. In contrast, Gleysols, influenced by vertical water movement, display unique properties related to saturation and reduction conditions. This phase highlights the role of hydrological dynamics in determining the formation and state of soils.

5.3 Limitations and future perspectives

Preliminary analyses have underscored how soil mineral composition reflects both soil development and environmental impacts. However, future research should integrate X-ray diffraction analysis with detailed clay mineral studies to deepen our understanding of how mineralogical changes are affected by environmental factors, and the geological settings. Further limitations include the potential inadequacy of soil libraries in capturing long-term historical changes and the possibility that recent samples from 2020 may not fully represent past climatic conditions or historical weathering processes. Additionally, soil libraries and modern samples might not cover all soil types and conditions across Switzerland, particularly in less sampled or highly variable regions.

To address these limitations, future research should employ advanced analytical techniques such as XRD, scanning electron microscopy (SEM), and inductively coupled plasma mass spectrometry (Moor, Lymberopoulou, & Dietrich) combined with historical data and high-resolution spatial analysis (Sahu, Reddy, Kumar, & Nagaraju, 2015).

Radiocarbon dating would be another complementary initiative in this direction (Scharpenseel & Schiffmann, 1977; Van der Plicht, Streurman, & Van Mourik, 2019). Analyzing the radiocarbon content could provide insights into soil organic carbon dynamics, the age of soil carbon, and its turnover and stability.

Such data is crucial for improving carbon cycling models and assessing the role of soils in climate change mitigation. The findings from this project will enhance our understanding of soil organic carbon's age and behavior, contributing to better soil management practices and climate policy in Switzerland. Expanding the dataset to include diverse soil types and conditions, alongside exploring non-linear dimensionality reduction and temporal dynamics, will offer a more comprehensive view of soil evolution. This approach will elucidate the complex interplay between mineral composition, soil formation processes, and environmental influences, ultimately providing a clearer picture of soil development and its broader implications.

7. Conclusion

Our study poses the foundations to clarify the complex interplay between soil mineral composition and the processes shaping soil formation and evolution. By analyzing key minerals such as phyllosilicates, quartz, feldspaths, plagioclases, calcite, and goethite, we can gain insights into soil weathering and the influences of climatic and geological conditions. Elevated phyllosilicates suggest advanced weathering typical of humid tropical environments, while high quartz content points to less weathered soils from arid regions. The presence of feldspaths and plagioclases, which transition into secondary minerals alongside calcite, indicates soil development in less weathered or carbonate-rich settings. Our approach, which includes both horizon-level and whole soil profile analyses, is essential for drawing robust conclusions about soil development and identifying trends in soil formation. Although soil libraries and recent samples from 2020 offer valuable information, they have limitations, such as potential gaps in historical soil changes and incomplete coverage of soil variability across Switzerland. To address this, future research should integrate current data with historical records, long-term monitoring, and high-resolution spatial analyses. Also, measuring radiocarbon levels across various soil profiles could deepen our understanding of soil organic carbon dynamics, turnover, and stability.

Combining ^{14}C data with mineralogical and environmental analyses will provide a comprehensive view of soil evolution and its response to climatic and geological factors. In summary, integrating detailed mineralogical analysis with historical and spatial data, alongside innovative ^{14}C studies, enhances our understanding of soil formation processes and their interaction with environmental changes. These insights are crucial for advancing research into soil evolution and assessing the role of soils in climate change mitigation and management.

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Thematic 3: How do climatic conditions explain litter decomposition rates?

Solar radiation explains litter degradation along alpine elevation gradients better than other climatic or edaphic parameters

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Abstract

Organic matter (OM) decomposition has been shown to vary across ecosystems, suggesting that variation in local ecological conditions influences this process. A better understanding of the ecological factors driving OM decomposition rates will allow to better predict the effect of ecosystem changes on the carbon cycle. While temperature and humidity have been put forward as the main drivers of OM decomposition, the concomitant role of other ecosystem properties, such as soil physicochemical properties, and local microbial communities, remains to be investigated within large-scale ecological gradients. To address this gap, we measured the decomposition of a standardized OM source – green tea and rooibos tea – across 24 sites spread within a full factorial design including elevation and exposition, and across two distinct bioclimatic regions in the Swiss Alps. By analyzing OM decomposition via 19 climatic, edaphic or soil microbial activity-related variables, which strongly varied across sites, we identified solar radiation as the primary source of variation of both green and rooibos teabags decomposition rate. This study thus highlights that while most variables, such as temperature or humidity, as well as soil microbial activity, do impact decomposition process, in combination with the measured pedo-climatic niche, solar radiation, very likely by means of indirect effects, best captures variation in OM degradation. For instance, high solar radiation might favor photodegradation, in turn speeding up the decomposition activity of the local microbial communities. Future work should thus disentangle the synergistic effects of the unique local microbial community and solar radiation on OM decomposition across different habitats.

1. Introduction

The global carbon cycle is at the base of the functioning of most ecosystems (Schimel, 1995; Stuart Chapin et al., 2009; Shukla et al., 2019) and is primarily driven by climatic (temperature and precipitation) factors (Bardgett et al., 2008; Lal, 2013; Wagg et al., 2021; Jungkunst et al., 2022). Because climate change is accelerating, understanding climate's effects on the carbon cycle is of primordial importance (Davidson and Janssens, 2006). Among many, one of the critical events driving the carbon cycle, is the rate at which organic matter (OM) decomposes once it reaches the topsoils' layers.

Indeed, OM added to the soils can take two main pathways: incorporation into soil organic layers or mineralization (Angst et al., 2021). In the first pathway, OM may persist in soils, sometimes for thousands of years (Schmidt et al., 2011), where it will be integrated into the organo-mineral layers, stocking up the soil's organic carbon bank (Man et al., 2022). In the second pathway, the decay of dead plant and animal material (i.e., litter) transforms complex organic molecules into simpler organic and inorganic molecules. Then, via the consumption by detritivores, litter is transformed into energy, and CO₂ is released back into the atmosphere. Therefore, OM decomposition fuels energy flow within the soil biota, i.e., the macro- and mesofauna, but especially the microbial (bacterial and fungal) communities (Krishna and Mohan, 2017).

Organic matter decomposition is influenced by various biotic and abiotic factors (Bhatnagar et al., 2018; Woolf and Lehmann, 2019). For instance, plant litter quality has been shown to influence decomposition rates, in which more recalcitrant molecules should slow down the decomposition process, whereas litter containing high nitrogen to lignin ratio should accelerate it (Murphy et al., 1998; Cornwell et al., 2008; Berg, 2014; Chomel et al., 2016; Lu et al., 2017; Djukic et al., 2018). Moreover, other facets of the ecosystems have been shown to also affect OM decomposition across habitats (Schmidt et al., 2011), including soil physicochemical properties (Liu et al., 2006; Ge et al., 2013; Delgado-Baquerizo et al., 2015), temperature and precipitations (Meentemeyer, 1978; Aerts, 1997; Fierer et al., 2005; Aerts, 2006) and soil communities' (i.e., decomposers) activity (Bray et al., 2012; Tresch et al., 2019; Sokol et al., 2022).

In addition, while each variable can affect OM decomposition independently, Bradford et al. (2016) proposed to also consider the concomitant action of multiple ecological factors simultaneously.

Therefore, predicting the relative influence of the different components of the ecosystem on OM decomposition in the soils remains a hard nut to crack (Carrenho et al., 2020). In this context, large-scale ecological gradients can be used to tease apart the effect of different ecological factors on OM decomposition (Krishna and Mohan, 2017).

For instance, decomposition rates have been shown to decrease with latitude (Zhang et al., 2008) and elevation (Sundqvist et al., 2011), likely due to a decrease in temperature and time of the growing season. However, along ecological gradients, multiple variables co-vary with climate, making it difficult to disentangle the contribution of each variable (Zhu et al., 2019). For instance, plant community beta diversity - and the inherent phytochemical composition - co-vary with other variables such as temperature and humidity (Defossez et al., 2021).

To resolve this conundrum, one way is to harmonize leaf litter decomposition studies by using a common source of litter for measuring OM decomposition across different ecosystems. In this regard, Keuskamp et al. (2013) developed the tea bag method, using standardized tea types (green tea and rooibos tea as substrate) to explore the effect of local factors on litter decomposition, independently of the site-specific vegetation differences in phytochemistry (Defossez et al., 2021). For example, Didion et al. (2016) contrasted teabags' degradation rates and decomposition of local litterbags along an elevation gradient. They observed the slowest decomposition rates at the high-elevation site, independently of the litter quality. Therefore, elevation alone bears poor explanatory power for studying variation in OM decomposition.

However, by studying OM decomposition across multiple orthogonal axes, in conjunction with a standardized litter decomposition assay, might help tease apart the relative importance of the different ecological factors, such as climatic and soil factors, driving variation in OM decomposition.

Therefore, to further shed light on the relative contribution of different ecological factors (biotic and abiotic parameters, see **Table S3.2**) driving OM decomposition across habitats, we took advantage of the natural climatic and edaphic variation along the steep elevation gradients of the Alps (Hagedorn et al., 2019). Specifically, we asked which edaphic, climatic, or microbial activity-related variables, best explain OM decomposition rates across sites.

To address this question, we measured litter decomposition using the teabag approach (Keuskamp et al., 2013). We assessed the effect of different climatic and edaphic variables across two regions (northern Prealps versus southern Alps), two elevation zones (alpine versus subalpine), and two expositions (north versus south). Specifically, we hypothesized that by generating variation in ecological variables potentially driving OM decomposition using a common litter source, it would be possible to identify key variables best-explaining variation in OM decomposition. Ultimately, by dissecting the relative role of biotic and abiotic factors driving soil OM degradation, this work should provide additional information on how to estimate the rate of carbon turnover across ecosystems, and the effect of climate change key natural ecosystem processes.

2. Materials and methods

2.1. Study sites and climatic variables

To identify the climatic and edaphic drivers of leaf OM decomposition, we performed a litter bag experiment using two standardized tea types [Rooibos and Green tea (Keuskamp et al., 2013)] across 24 sites in the Alps. The experiment was replicated across two distinct bioclimatic regions (the Northern Prealps in the canton of Valais in Switzerland, and the Southern Alps, in the canton of Ticino in Switzerland, **Figure 3. 1**). In each region, we selected two elevation transects facing each other, a north and a south-facing slope. Within each elevation transect, we randomly selected three plots, at the subalpine level [approximately 1,500 m above sea level (asl)] and the alpine level (about 2,100 m asl). Each plot was distant from the other by at least 100 m ($N = 2 \text{ regions} \times 2 \text{ expositions} \times 2 \text{ elevations} \times 3 \text{ replicates} = 24 \text{ plots}$). Plot size varied according to the vegetation type; at the subalpine level, dominated by conifer forests, the vegetation plots were 400 m² (20 m × 20 m), whereas, at the alpine level, dominated by alpine grasslands, the vegetation plots were 25 m² (5 m × 5 m).

To assess the site-specific climate, for each site, we extracted environmental data, including elevation, number of degree-days, solar radiation, number of frost days, and potential evapotranspiration (hereafter referred to as moisture) from associated environmental layers (Pellissier et al., 2016).

We calculated values for temperature (degree-days) and moisture from meteorological stations using a Digital Elevation Model (DEM) at 25 m resolution and interpolated the following (Zimmermann and Kienast, 1999).

We estimated solar radiation values using the tool implemented in ArcGIS 10 (Zimmermann and Kienast, 1999).

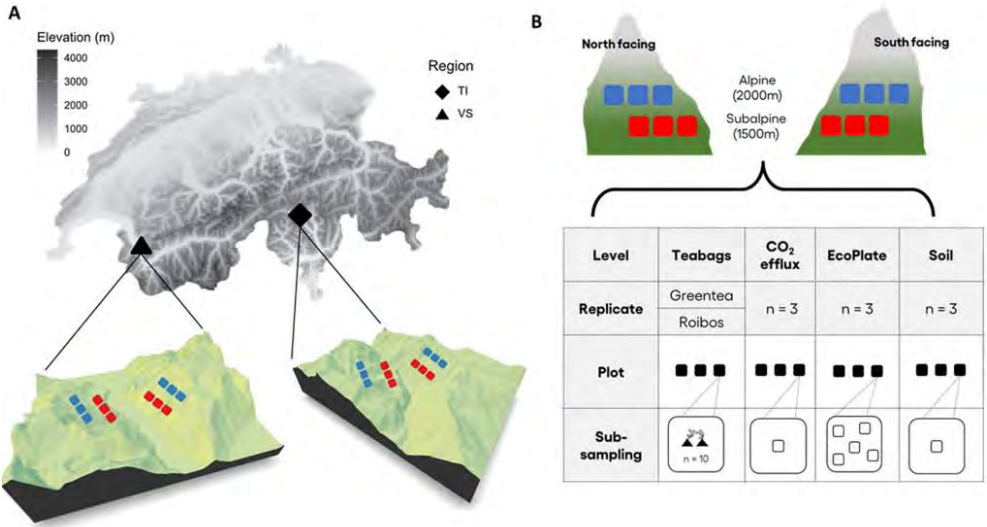


Figure 3.1 Study sites and experimental design. (A) Map of Switzerland showing the location of the two regions where the study took place; Valais (VS, black triangle) transect in the Northern Alps, and Ticino (TI, black diamond) in the Southern Alps. In both regions, we established a north- and a south-facing altitudinal transect. (B) The elevation transects were divided into two elevation zones; a subalpine zone (1,500 m a.s.l., red squares), and an alpine zone (2,100 m a.s.l., blue squares). On each transect and at each elevation, we defined three replicate plots ($N = 2$ regions $\times$ 2 expositions $\times$ 2 elevation zones $\times$ 3 replicates = 24 plots). The graphic shows the different variables sampled in each plot: (i) soil profile description ($n = 1$) and soil physicochemical parameters therein, (ii) soil respiration (CO_2 efflux) measures ($n = 3$), (iii) carbon degradation bioassay (EcoPlates, $n = 5$), (iv) tea bags experiment ($n = 10$ per plot and per tea type: green tea and rooibos tea).

2.2. Soil sampling and analysis

To estimate the effect of soil physicochemical parameters on litter decomposition, we analyzed physicochemical properties of the topsoils (A horizons) for each plot, since the OM content and turnover are highest in this layer. Specifically, for each plot, 5–10 soil samples were randomly collected with a soil borer (5 cm in diameter, 10–20 cm deep), homogenized, dried at 40°C, and then sieved at 2 mm.

We measured six variables: (1) pH, measured in distilled water with a Metrohm 827 pH meter (Metrohm AG, Herisa, Switzerland). (2) Soil OM, measured from the loss of ignition (Allen et al., 1974) and corrected by the ‘Howard’ correction factor (Howard and Howard, 1990). (3) Total cationic exchange capacity (CEC), determined using the ‘cobalt hexamine trichloride’ method (Ciesielski et al., 1997). (4) Total carbonates, quantified by CaCO_3 decomposition after adding HCl in CO_2 and water using the Calcimeter Bernard method (Allison and Moodie, 1965). (5) Total carbon (C) and nitrogen (N) were quantified using an elemental analyzer (FLASH 2000, Thermo Scientific, Waltham, Massachusetts, United States). (6). Soil relative humidity (Rh) was assessed after drying the soils at 105°C for 3 days.

2.3. Tea bag experiment

To determine the site-specific decomposition rate of organic material, we buried two different types of tea bags following standard procedures (Keuskamp et al., 2013). Burial took place during September and October 2020, until collection in May and June 2021 (see **Table S3.3** for precise dates of burial time). On each site, Lipton Green Tea Sencha (European Article Number (EAN No): 8714100 77,054 2, $n = 15$) and Lipton Rooibos Tea (EAN No.: 8722700 18,843 8, $n = 15$) were buried in pairwise fashion (one Green Tea and one Rooibos bag together) with 5–10 cm to each other at a soil depth of 5 cm within 15 m to the right of the plot center (**Figure 3.1B**). The burial locations were chosen as to be representative of the general vegetation of the experimental plot. After 8–9 months, tea bags were carefully excavated, wiped off adherent soil particles, and dried in paper envelopes at 40°C for at least 48 h. The decomposition rate (k – percent of weight loss per day) for both tea types was next assessed using initial weight (w_i), final weight (w_f), and burial time as follows:

$$k = \frac{\left(\frac{w_i - w_f}{w_f \times 100} \right)}{\text{Burial time}}$$

2.4. Soil microbial carbon degradation bioassay

To determine the potential of the local soil microbial community to degrade OM, we used a BIOLOG EcoPlate™ bioassay (Grządziel and Gałqzka, 2018). For this, in each plot, five randomly chosen soil subsamples (4 cm diameter × 20 cm deep) were homogenized in a plastic container and stored at 5°C in the lab for a maximum of 24 h. One gram of soil per sample was then added with 99 ml of 0.9% saline solution (NaCl), agitated at 145 rpm for 30 min at room temperature, again cooled at 4°C for 30 min, and vortexed for 15 s before pouring the supernatant (microbial suspension) into a sterile petri dish. Next, 120 µl of each microbial suspension was added to each cell of the EcoPlate. Each plate comprises 96 wells with 32 carbon sources (including blank) carbon sources in triplicates (**Figure S3. 1**). Photometric readings ($\lambda = 590$ nm) were carried out using the Biochrom Asys UVM 340 Scanning Microplate Reader and the ASYS DigiRead software. Three measurements in immediate succession were done in the morning and the evening for 8 days after the analysis started. The higher the optical density reading the more the carbon source has been used. For our study, we first analyzed the temporal dynamics of total carbon consumption in each plate (i.e., the sum of each carbon source consumed, **Figure S3. 2**), and chose the average of the two readings at day five as the maximal carbon source consumption for response variable to compare across sites.

2.5. Soil respiration

To obtain an indirect measure of potential soil biological activity (including microbial, faunal and root activity) at each site, we performed soil respiration measurements (CO₂ effluxes, n = 72) with a portable LI-8100A Automated Soil Gas Flow System (LI-COR Biosciences GmbH, Bad Homburg, Germany). In each plot, we randomly chose three measurement spots (**Figure 3. 1B**) where there was bare soil without vegetation cover in forests, and where vegetation cover was representative for the rest of the plot's vegetation in the alpine zone, avoiding shrubby vegetation or bare soil.

Before measurements, we hammered a PVC collar (20 cm Ø chamber) into the soil perpendicularly to the slope. Where the soil was too compacted or with many roots, insertion was facilitated by cutting along the collar with a pocketknife. Under sunny conditions, the setup was shaded by an umbrella to protect the detection unit from possible interference by direct UV radiation. Measurements were taken for 2 min and repeated twice (**Table S3. 4**).

We took as response variable the average of the intercept of the liner regression of the two measurements as provided by the LI-COR software.

2.6. Statistical analysis

All analyses were performed in R 4.1.1 (R Development Core Team, 2020).

Climatic variables – We visualized correlations among the climatic variables across sites using principal component analysis (PCA), calculated using the *ade4* package (Dray and Dufour, 2007). We assessed the interactive effect of elevation zone (subalpine and alpine) and exposition (north and south) using a Regularized Discriminant Analysis (RDA; Friedman, 1989) using the *vegan* package (Oksanen et al., 2013). We included the region as a blocking factor in the analysis. In addition, to estimate multivariate changes of the climatic conditions across sites (see **Figure 3. 2A**), we performed a two-way ANOVA (zone * exposition + region) on the first axis of the PCA (PCA1 in **Figure 3. 2A**).

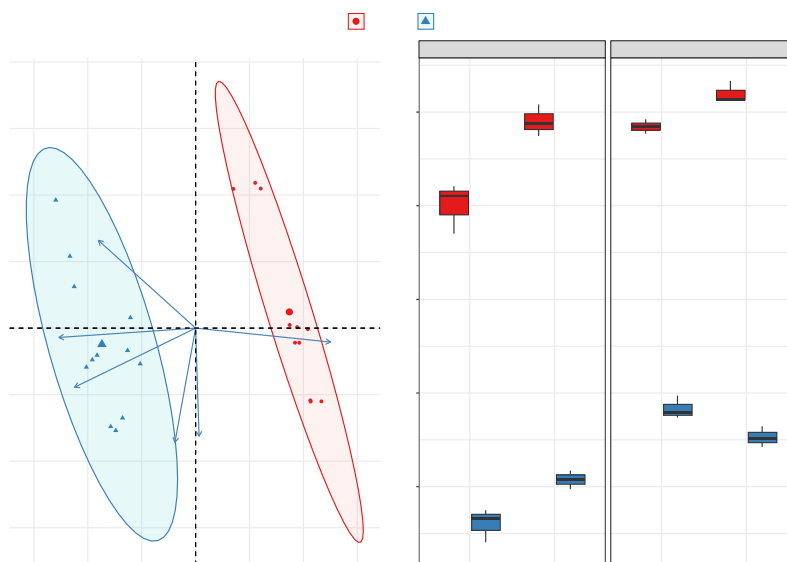


Figure 3.2 Climatic niche. Shown is (A) the principal component analysis (PCA) biplot of six climatic variables retained in the analysis: relative evapotranspiration (humidity), elevation of each site, number of frost ($<0^{\circ}\text{C}$) days during the year (frost days), annual mean precipitation (precipitation), annual mean solar radiation (radiation), average number of degree-days per year (degree days). (B) Boxplots representing average values along the first axis of the PCA separated by exposition (north versus south facing slopes), and regions (Ticino = TI, or Valais = VS). Letters above boxplots represent significant differences among main effects (Tuckey's post-hoc tests; $p < 0.05$). Red color (warm) represents the subalpine zone ($\sim 1,400$ m above sea level), and blue color (cold) represents the alpine zone (~ 2000 m above sea level).

Soil physicochemical properties – We visualized differences in the physicochemical properties of soils using principal component analysis (PCA) as described above. We assessed the effect of elevation zone on soil physicochemical properties using a Regularized Discriminant Analysis (RDA; Friedman, 1989). We included the region as a blocking factor in the analysis. To assess how the soils' multivariate space changes along the elevation gradient, we performed a two-way ANOVA (zone*exposition + region) on the first axis of the PCA (see **Figure 3.3A**).

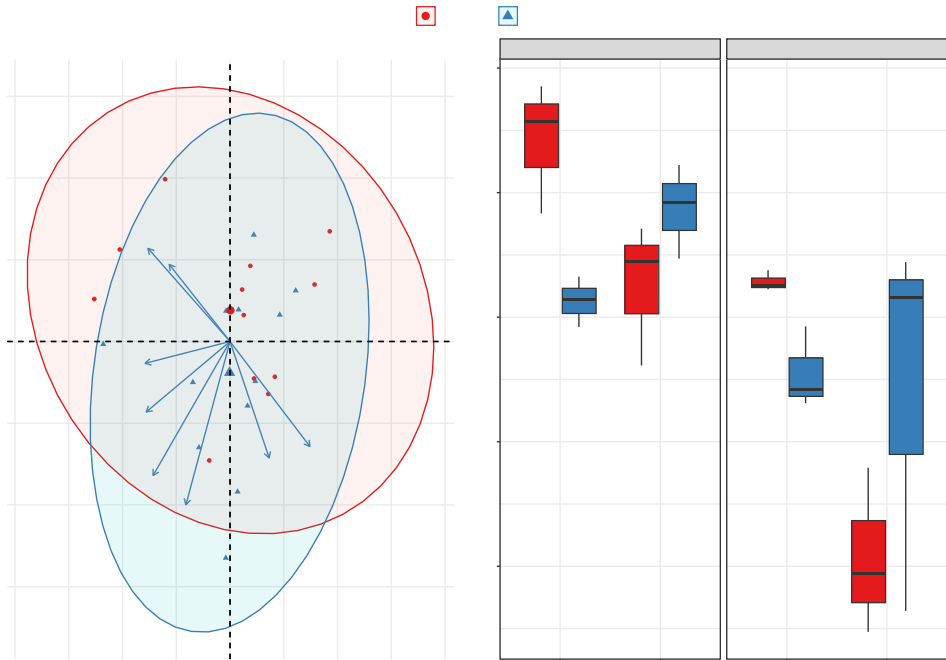


Figure 3.3 Edaphic properties. Shown is (A) the principal component analysis (PCA) biplot of eight physicochemical soil variables [pH, Cation-Exchange Capacity (CEC), total nitrogen (Ntot), total carbon (Ctot), soil OM (SOM), soil relative humidity (Rh), carbon-to-nitrogen ratio (C/N), and total carbonates (CaCO₃)]. (B) Boxplots representing average values along the first axis of the PCA separated by exposition (North versus South facing slopes), and regions (Ticino = TI, or Valais = VS). Letters above boxplots represent significant differences among main effects (Tuckey's post-hoc tests; $p < 0.05$). Red color (warm) represents the subalpine zone (~1,400 m above sea level), and blue color (cold) represents the alpine zone (~2000 m above sea level).

Tea bags degradation, soil microbial carbon degradation and soil respiration –
To analyze site differences for tea bag degradation, soil carbon degradation and soil respiration, we performed two-way ANOVAs, separately for each response variable, with elevation zone and exposition as fixed factors, and the region as blocking factor.

The relative importance of the measured variables for tea bags degradation – To finally assess the relative importance of the different explanatory variables (edaphic, climatic, soil respiration and microbial carbon degradation) on tea litter decomposition, we performed a Random Forest Regression with the *rfPermute* package in R (Archer and Archer, 2016), which allows estimating the significance of the importance of the variables for a Random Forest model by permuting the response variables and producing a null distribution of important metrics for each predictor variable.

Based on analysis of the random forest analysis results, we next performed univariate linear regressions between the explanatory variables deemed significant (see **Figure S3. 3** and **Figure S3. 4**) and the k values for green tea and rooibos tea.

3. Results

3.1. Climatic variables

Based on the ordination analyses, we confirmed that alpine zones display colder (7 times more frost days, and 40% less degree-days) and more humid conditions (6% more annual average precipitation days, and 2.3 times more humidity values) than subalpine zones (**Figure 3. 2A**; RDA analysis for elevation zone effect; $F_{1,19} = 39.01$, $p < 0.001$). North facing slopes were also colder and more humid (8% more degree-days, 26% more solar radiation, 50% less humidity, 7% more precipitations, 26% more frost days) than south-facing slopes (exposition effect; $F_{1,19} = 17.99$, $p < 0.001$). We also found a significant effect of the region ($F_{1,19} = 18.21$, $p < 0.001$), in which the Valais (VS) region displayed 3% more solar radiation, 17% more precipitation and 2.64 times less overall humidity than the Ticino (TI) region (**Figure 3. 2B**). However, the interaction between elevation and exposition was not significant ($F_{1,19} = 0.96$, $p = 0.382$), suggesting that the climatic patterns of warmer and drier conditions on the south-facing slopes were consistent across elevation zones (**Figure 3. 1B**; **Table 3. 1**).

Table 3. 1. Two-way ANOVA table for the effect of elevation zone (two levels; alpine and subalpine), exposition (two levels; north and south), region (two levels; Valais, Ticino), and interaction between zone and exposition.

Variable	Factor	Df	SSQ	F value	Pr (<F)	
PCA1 – clim	Elevation Zone (Z)	1	72.51	1187.931	<2e-16	***
	Exposition (E)	1	0.75	12.320	0.00234	**
	Region	1	2.97	48.713	1.19e-06	***
	Z * E	1	0.44	7.242	0.01446	*
	Residuals	19	1.16			
PCA1 – soil	Elevation Zone (Z)	1	0.01	0.003	0.957297	
	Exposition (E)	1	11.53	5.776	0.026617	*
	Region	1	43.01	21.537	0.000178	***
	Z * E	1	23.79	11.911	0.002675	**
	Residuals	19	37.94			
Soil respiration	Elevation Zone (Z)	1	3.838	45.257	1.98e-06	***
	Exposition (E)	1	0.004	0.049	0.826	
	Region	1	0.000	0.003	0.957	
	Z * E	1	0.102	1.199	0.287	
	Residuals	19	1.611			
C degradation	Elevation Zone (Z)	1	499.0	24.324	9.26e-05	***
	Exposition (E)	1	47.1	2.298	0.146018	
	Region	1	354.5	17.280	0.000535	***
	Z * E	1	10.2	0.498	0.489048	
	Residuals	19	389.7			
Tea bag decomposition	Elevation Zone (Z)	1	0.00895	13.151	0.00036	***
	Exposition (E)	1	0.04541	66.762	2.75e-14	***
	Region	1	0.00008	0.114	0.73646	
	Z * E	1	0.00215	3.157	0.07705	–
	Residuals	212	0.14420			

3.2. Edaphic variables

The ordination analysis highlights a non-significant effect of the elevation on soil variables, indicating that soil physicochemical properties, overall, were rather similar across the alpine and the subalpine. Yet, we found a significant effect region and exposition (**Figure 3. 3A; Table 3. 1**), meaning our soils across our 24 sites were overall quite different (**Figure 3. 3B**, and see details **Figure S3. 5, Table S3. 1**). We found that VS soils contained 1.92 times more N than the TI soils. Moreover, the total N content increases from north to south in the subalpine zone. In contrast, in the alpine zone, we found the reversed trend (see the interaction between zone and exposition in **Table S3. 1**), a trend that was mirrored for the total carbon content (C_{tot}). For carbon-to-nitrogen ratio (C/N), it was 64% higher in the TI region than in the VS region, while the residual soil humidity (Rh) was only significantly higher in the alpine soils versus the subalpine soils.

Moreover, VS soils were 2.6 times more alkaline than the TI soils, while VS soils were 1.24 times richer in OM than the TI soils.

For soil cation-exchange-capacity (CEC), we found an effect of the elevation and exposition, in which subalpine soils were 1.70 times higher in CEC than alpine soils, and south-exposed soils were 2.58 higher in CEC than north-exposed soil. Also, CEC for VS was 3.96 times higher than in TI.

For soil total carbonate content (CaCO_3), we found an effect of the elevation and exposition, in which alpine soils were 1.17 times more calcareous than subalpine soils, and north-exposed soils were 1.29 times more calcareous than south-exposed soils. We also found that TI soils were 1.42 times more calcareous than VS soils, and that carbonate content decreased from north to south in the subalpine zone. In contrast, in the alpine zone, carbonate remained similar (see the interaction between zone and exposition in **Table S3. 1**). Concerning the soil mineralogy, we found, that VS soils contained 3.66 times more clays and 1.81 more silt than the TI soils. However, TI soils were 3.08 times more sand-rich than VSs soils. Alpine soils were 1.23 times sandier than subalpine soils, and north-exposed soils were 1.28 times sandier than south-exposed soils (**Table S3. 1**).

3.3. Soil respiration, carbon degradation, and tea litter decomposition

We found that alpine soils respired 2.56 times more than subalpine soils (**Figure 3. 4A**, see elevation effect in **Table 3. 1**). However, we found a non-significant effect for exposition, region, and elevation by exposition (**Table 3. 1**). Contrary to soil respiration, the microbial carbon consumption was 16% higher in the subalpine than in the alpine elevation zones (**Figure 3. 4B; Table 3. 1**), independently of the exposition (see the non-significant effect of exposition and exposition by elevation interaction in **Table 3. 1**). Moreover, soils from the Valais region, in the northern part of the Alps, contained 13% more active microbial communities than soils from south of the Alps.

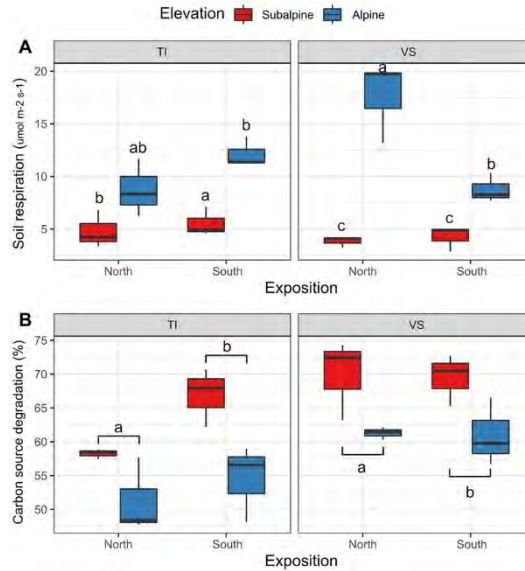


Figure 3. 4 Soil respiration and microbial activity. Shown is (A) Boxplots representing average soil respiration (Licor bioassay), and (B) average soil carbon degradation (EcoPlates bioassay) values at each site separated by exposition (North versus South facing slopes), and regions (Ticino = TI, or Valais = VS). Letters above boxplots represent significant differences among main effects (Tuckey's post-hoc tests; $p < 0.05$). Red color (warm) represents the sub-alpine zone (~1,400 m above sea level), and blue color (cold) represents the alpine zone (~2000 m above sea level). $N = 3$ plots per site.

Concerning the teabags bioassays, overall green tea degraded slightly faster in the subalpine ($k = 0.23$) than in the alpine ($k = 0.22$; **Figure 3. 5A; Table 3. 1**) and 5% more on south-facing than on north-facing slopes (**Figure 3. 5A; Table 3. 1**).

These effects were similar for the rooibos tea bags, degrading 8% faster on the subalpine than on the alpine elevation zones (**Figure 3. 5B; Table 3. 1**), and 5% faster on south-facing than on north-facing slopes (**Figure 3. 5B; Table 3. 1**).

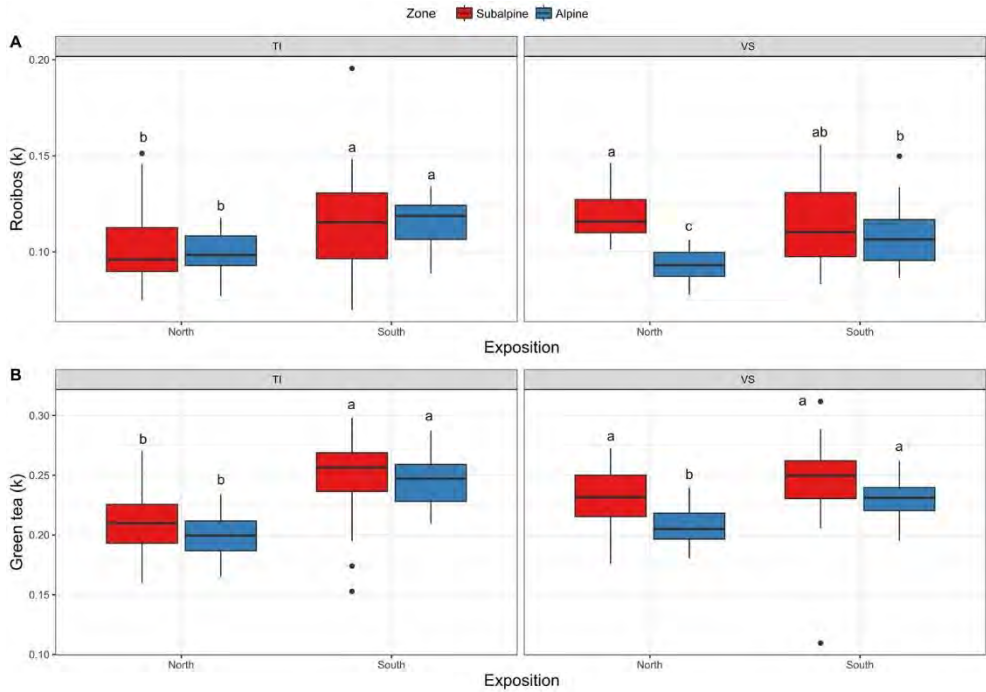


Figure 3.5 Degradation of teabags. Shown is (A) Boxplots representing rooibos degradation (k values), and (B) green tea degradation (k values) at each site separated by exposition (North versus South facing slopes), and regions (Ticino = TI, or Valais = VS). Red color (warm) represents the sub-alpine zone (~1,400 m above sea level), and blue color (cold) represents the alpine zone (~2000 m above sea level). N = 3 plots per site. The k values represent the percent of tea weight loss per day.

3.4. The relative importance of the predictor variables

The Random Forest Analysis indicated that solar radiation best explained degradation across sites for both the green tea and rooibos tea (**Figure S3. 3**, **Figure S3. 4**, respectively). The higher the average annual solar radiation the site received, the more likely the litter falling on the ground was to be degraded (for green tea, **Figure 3. 6A**, $\text{lm}; F_{1,22} = 15.98, p < 0.001$, and for rooibos tea, **Figure 3. 6B**, $F_{1,22} = 7.65, p = 0.01$). Moreover, the humidity was the second-best predictor for both tea types, followed by soil clay content (**Figure S3. 3** and **Figure S3. 4**).

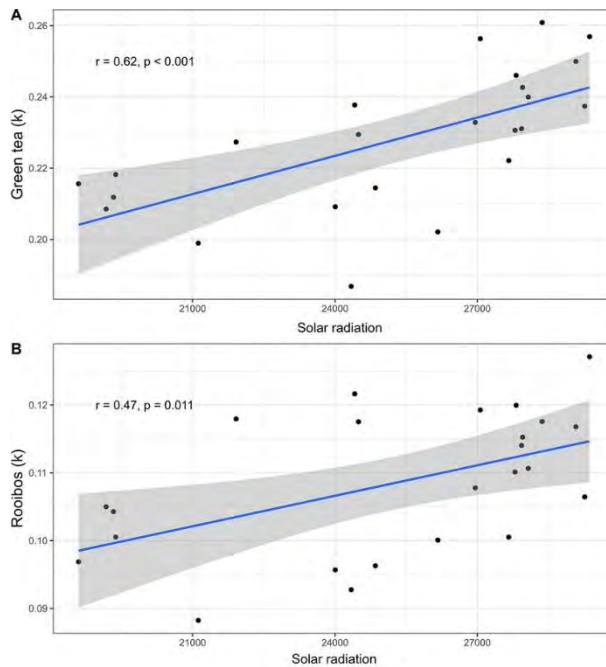


Figure 3.6 Effect of solar radiation on teabags decomposition. Scatterplots displaying liner regressions (blue lines with confidence intervals in grey) between solar radiation and k values for (A) green tea (linear regression; $n = 24$, $r = 0.62$, $p < 0.001$), and (B) rooibos tea (linear regression; $n = 24$, $r = 0.47$, $p = 0.011$).

4. Discussion

We studied the decomposition of two common litter types (green tea and rooibos tea) across 24 sites in the Alps, focusing on climatic, physicochemical soil properties, and variables related to soil microbial activity (19 in total). We found that solar radiation best captured the variation in litter degradation more so than other climatic or edaphic variables, including soil microbial activity. Below, we expand on the potential causes and consequences of the different variables affecting plant litter decomposition along large-scale ecological gradients.

4.1. The effect of climate on litter decomposition

The most stunning result of our study was to show that above all explanatory variables, variation in solar radiation across sites best-captured variation in tea bag degradation.

These results align with multiple studies showing a positive effect of light (i.e., solar radiation) on photodegradation of litter (Hussain et al., 2023). For instance, it was shown that lower levels of UV-radiations inhibited litter decomposition in a Tibetan alpine steppe ecosystem (Mao et al., 2022), or that aboveground litter decomposition was predominantly controlled by photodegradation instead of litter phytochemical composition (Austin and Vivanco, 2006; King et al., 2012). Nonetheless, Hussain et al. (2023) in their review, point out that future research should focus on studying the interactions between different ecological factors, such as the potential interaction between photodegradation, soil moisture, and microbial communities. With this study, we contribute to filling this gap. That said, “more classic” climatic variables, such as mean annual temperature or precipitation (Carter, 2020), have also been shown to control the degree of soil OM decomposition along latitude (Wang et al., 2019) or elevation (Kong et al., 2022; Mao et al., 2022). Therefore, our results should not be taken as the fact that solar radiation, alone, controls all OM degradation in the Alps, but instead, that the variation we generated using our experimental design, generated higher variance in solar radiation, which ultimately best-explained litter degradation.

Indeed, as seen in the PCA of **Figure 3. 2**, some climatic variables strongly co-varied with elevation, while others, such as solar radiation varied largely independently of elevation. Accordingly, we observed clear differences between subalpine and alpine climatic conditions across regions and south/north expositions.

Generally, alpine and north-exposed sites display colder and more humid climate conditions, while subalpine and south-exposed environments displayed higher temperatures and dryer conditions, with higher levels of solar radiation. We found a non-significant interaction between the elevation zone and the exposition, indicating that warmer and drier climatic patterns were consistent across sites (Körner, 2007). Therefore, our experimental design generated variation in solar radiation, orthogonally to the elevation axis, and independently of the temperature/humidity axis (as shown in **Figure 3. 2B**). Ultimately, this variation might have been enough to allow capturing most variation in *k* values for tea bags.

Nonetheless, our experimental design might have induced the unintended effects of vegetation cover also influencing solar radiation reaching the ground, thus indirectly affecting our results. In other words, vegetation cover might have impacted the microclimatic understory conditions, hence also indirectly impacting OM degradation.

Yet, we found that elevation zone per se did not impact the level of solar radiation (**Figure 3. 6**). In other words, we observed that the alpine and subalpine sites, overall, across the two regions received the same amount of solar radiation. Therefore, we can conclude that the observed effect of solar radiation on tea degradation was not or only partially driven by elevation differences and, therefore, not by vegetation cover differences, as the subalpine sites were always in forests, while alpine sites were always in grasslands. Perhaps, another way to understand these effects is to assume that solar radiation, here extrapolated from spatial models independent of vegetation cover, represents the amount of energy that a given ecosystem received. Hence, more energy in the system equates to faster metabolic activity and faster OM degradation (Caldwell et al., 1998). Yet, according to classical theory and widespread ecological observations, alpine habitats are where degradation of OM is slowest, likely due to inhibitory effects of low average temperatures and short growing seasons (Hartley and Ineson, 2008; Wang et al., 2019). In our study we did not find this. Instead, tea leaves generally degraded similarly across elevation zones, suggesting that variation in temperature, and also perhaps humidity, was less important for OM degradation than other variables, in our case, solar radiation. However, it also may be that the difference of about 600 m between our subalpine and alpine sites ($\sim 3.6^{\circ}\text{C}$) was not sufficient to detect an effect of elevation per se, also due to differences in vegetation cover (see discussion above).

In other words, differences in canopy cover between the subalpine forested areas and the alpine grasslands might have masked the temperature effect. Possibly, vegetation cover at the warmer subalpine level dampened high temperature on sunny days, while it increased the temperature effect disproportionately at high elevation on the same mountain slope, thereby homogenizing the real temperature effect at the soil level (i.e., for OM degradation).

Future work would thus require measuring microclimatic conditions for disentangling the canopy effect to average solar radiation effect at each site. Even more so, such effect was independent of the type of tea, although, as predicted, rooibos tea degraded slower than green tea (Keuskamp et al., 2013). Yet, the mechanisms behind these effects driven by solar radiation remain to be fully elucidated. For instance, several studies argued that solar radiation can spur litter decomposition, by indirectly facilitating soil microbial decomposition via the weakening of the tissues through photodegradation (Lin et al., 2015; Marinho et al., 2020; Méndez et al., 2022). Moreover, we could speculate that within our study sites, higher solar radiation might correspond to ideal conditions of temperature and precipitation, in which OM degradation by the local soil fauna and flora is maximal. Further experiments are therefore required to test how the overall decomposition potential varies locally with increasing elevation and solar radiation. Manipulating solar radiations (i.e., photodegradation) at each site and over extended periods (which might trigger humidity and temperature changes) could confirm these hypotheses.

4.2. The effect of soil properties on litter decomposition

Through our experimental design, we also generated significant variations in soil physicochemical properties. For instance, we found major differences in primary soil mineral composition across Valais and Ticino soils, mainly due to extensive scale processes such as glaciation. Moreover, Valais soils (situated on a calcareous bedrock) and Ticino soils (situated on a crystalline bedrock) display similar soil types at the same elevations. However, their respective topsoil horizons differed in their primary composition, thus illustrating a distinct mineral composition between regions, which should directly affect soil carbonate content, and pH (Thomas and Hargrove, 1984). Furthermore, Valais soils were more fertile (based on CEC values) and alkaline ($\text{pH} > 5$), with more significant carbon and nitrogen contents than the Ticino soils.

Several soil properties have been shown to affect litter decomposition. For instance, parental material and soil mineral composition (i.e., calcareous or acidic soils) can affect litter and soil OM decomposition (Kooijman et al., 2005).

This likely happens through parental material's mediated changes in microbial and fungal community, and their inherent functional strategies for OM degradation (Komarova et al., 2022). Along these lines, soil texture and moisture have also been shown to alter litter decomposition (Angst et al., 2021; de Godoy Fernandes et al., 2021). High clay contents, for instance, play a significant role in soil fertility as major components of clay-humus complexes (Brydon and Sowden, 1959), providing more suitable conditions for soil microbial communities to use carbon from the litter. Indeed, clays and the clay-humus complex play an essential role in providing nutrients to the soil solution (Tahir and Marschner, 2017), affect soil water dynamics (Kumari and Mohan, 2021), and in turn, create favorable conditions for bacteria or fungi communities to develop (Högberg et al., 2013). In contrast, higher relative amounts of sand contribute to greater porosity and hydraulic conductivity within soils (Usowicz and Lipiec, 2021), thereby decreasing soil fertility and likely microbial activity for efficient litter decomposition.

In sum, while multiple soil parameters have been shown to inhibit or enhance soil OM decomposition dynamics, our study highlights that among all edaphic parameters, clay content best explains teabags' degradation across sites. Therefore, future experiments that aim to manipulate soil mineral composition together with soil microbial communities and litter type could give more insights into how these different parameters interact to facilitate soil OM degradation.

4.3. The effect of microbial activity on litter decomposition

At the onset of this experiment, we predicted a general decrease in microbial functionality with increasing elevation, likely due to a rapid reduction in temperature-mediated enzymatic activity and loss of microbial biodiversity with elevation (Pellissier and Rasmann, 2018). Therefore, because microbial communities in the soil affect the carbon cycle through heterotrophic respiration (Bond-Lamberty et al., 2018), we expected that faster soil OM degradation in the subalpine versus the alpine zones, as a direct consequence of higher microbial activity in the subalpine zone. Accordingly, in our experiment, by using the EcoPlates' bioassay, we observed that microbial carbon source consumption was higher in subalpine soils than in alpine soils.

We here confirmed that microbial communities of mid-elevation can inherently degrade carbon sources faster than alpine microbial communities (Semeraro et al., 2022). Differences in soil microbial communities can be due to changes in the plant community structure and diversity (Cleveland et al., 2014), but also due to changing abiotic environmental conditions, such as temperature, humidity or solar radiations (Wei et al., 2022), or variation in soil physicochemical properties, ultimately leading to different degradation potentials. Yet, these predictions were not reflected in the tea bag experiment. While we cannot exclude that changes in soil microbial community composition and activity, as was shown previously along the same transects (Semeraro et al., 2022), could also mediate variation in OM degradation, these effects were statistically dampened by the strong effect of solar radiation and other variables measured. Yet again, photodegradation alone could not explain OM degradation without the subsequent labor of the soil microbial communities.

Thus, we suggest photodegradation facilitates the initial steps of OM degradation, which is then amplified by the bacterial and fungal community present at each site (Méndez et al., 2022).

General theory also indicates that soil microbial metabolic activity should mirror soil respiration, and therefore should increase with increasing temperatures (Johnston and Sibly, 2018). Accordingly, soil microbial communities, respiration, and temperature should be closely linked to litter decomposition processes (Joshi and Garkoti, 2020). Here, we found the opposite; alpine soils respired more than subalpine soils. Soil respiration, at least as we measured it, might also be the reflection of root respiration. Accordingly, since alpine meadows have a much higher root/soil volume ratio than forested subalpine habitats (Kergunteuil et al., 2016), our results of soil respiration were probably driven more by root-related processes than microbial activity. This observation might thus also explain why we did not detect a strong effect of soil microbial activity on teabags' degradation.

5. Conclusion

This study highlights the role of both climatic and edaphic variables in decomposition processes, and highlights that variation in OM degradation is likely mediated by variation in photodegradation, as well as soil mineral composition, which can facilitate OM decomposition through the activity of soil microbes. We showed this by measuring the decomposition of two types of teas.

While such a design allowed removing the effect of the local vegetation types, it has drawbacks: first, with this design we cannot extrapolate to how the local vegetation type – and phytochemistry therein – affects OM decomposition our experimental design. Second, we were not able to fully disentangle the effect of soil microbial activity from other ecological variables influencing OM degradation.

Nonetheless, by highlighting a predominant role of climatic conditions (solar radiation) on OM decomposition, we suggest that these dynamics are likely to change with climate and temperature change. For instance, locally, higher photoperiods, in conjunction with increases in temperature, and inherent higher microbial activity, may cause faster decomposition rates, independently of exposition or elevation, ultimately spurring faster CO₂ release in the atmosphere. Accordingly, future research manipulating solar radiation and its impacts on local soil microbial communities and decomposition should be conducted to address decomposition rates in the context of climate change.

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7. Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Humus forms and organic matter decomposition in the Swiss Alps

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Abbreviations

TNH1 to 3	Ticino North High elevation Plot n°1 to 3
TSH1 to 3	Ticino South High elevation Plot n°1 to 3
TNM1 to 3	Ticino North Mid elevation Plot n°1 to 3
TSM1 to 3	Ticino South Mid elevation Plot n°1 to 3
VNH1 to 3	Valais North High elevation Plot n°1 to 3
VSH1 to 3	Valais South High elevation Plot n°1 to 3
VNM1 to 3	Valais North Mid elevation Plot n°1 to 3
VSM1 to 3	Valais South Mid elevation Plot n°1 to 3

Keywords: elevation gradient; Parasystems; Terrosystems; Ponge the arthropod II-volume method; teabag experiment.

Abstract

Humus forms and organic matter decomposition are influenced by climate, plants and soil decomposers. Yet, whether different humus forms could be experimentally linked to litter decomposition has still to be fully assessed. To assess the link between humus systems and organic matter decomposition, we worked in two regions of the Swiss Alps (Valais and Ticino) along elevational gradients by following a north/south exposure design. We quantified humus forms macrorests proportion types by the Ponge method and measured the decomposition of green tea and rooibos tea within the Parasystems and Terrosystems. We found that Parasystems and Terrosystems differed in tea decomposition rates, with a slower decomposition in Parasystems than in Terrosystems. We also observed that elevation, and hence, vegetation type (i.e., forest in the subalpine versus grassland in the alpine), drove humus form distribution, with Parasystems found in the alpine and subalpine in Ticino, while in Valais Parasystems were only found in the alpine and Terrosystems in the subalpine levels. Further analyses are however needed to identify other variables that best correlate with variation in decomposition processes within humus systems, such as soil decomposer community composition.

1. Introduction

Nearly all primary biogeochemical cycles in terrestrial ecosystems predominantly happen within soils, particularly in the uppermost layers known as topsoil. Organic matter decomposition and integration processes primarily occur in these first soil layers (Lehmann, Bossio, et al., 2020). Topsoil layers, including the OL, OF, OH, and A horizons, form the humipedon that exhibits a high degree of organic matter accumulation and decomposition, thus constituting an interaction system and a functional transition between biotic (plant, animal, and microbe residues) and abiotic (rock weathering) components (Zanella, Berg, et al., 2018). The amount and quality of the organic matter accumulation in the humipedon are dictated by the surrounding vegetation, while the decomposition of such organic matter is under the influence of soil micro-, meso- and macrofauna (Blouin, 2018; Veen et al., 2019; Zanella, Ponge, Gobat, et al., 2018), as well as climatic conditions (Bonifacio et al., 2011; Ponge et al., 2011), resulting in the formation of a distinct sequence of layers called the humus form (Zanella, Ponge, Gobat, et al., 2018). Humus forms are thus excellent indicators of biologically mediated organic matter decomposition and integration (Ponge, 2003) because they reflect both the dynamic processes of heterotrophic decomposition driven by soil microbial and faunal activities and the stabilization of soil organic matter (Marklein et al., 2016; Ponge, 2003).

Several authors proposed simple keys to directly identify and classify humus forms in the field using morphological, biological, and physicochemical features. For this purpose, forest ecosystems were well suited to it and investigated the most as early as the nineteenth century (Baize & Girard, 2009; Brêthes et al.; Green et al., 1993; Jabiol et al., 2013; Muller, 1879, 1884) for further details, see the review of Chertov et al. (Chertov & Nadporozhskaya, 2018). Following the most recent classification, terrestrial humipedons in natural environments are principally divided into Terrosystems and Parasystems, the first being more developed, while the second is characterized by the dominance of wood and root material or the presence of mosses or lichens (Tatti et al., 2018; Zanella, Ponge, Fritz, et al., 2018). Terrosystems are further classified into five humus systems (Mull, Moder, Mor, Amphi, Tangel), which can be themselves declined into lower hierarchical levels called the humus forms (Zanella, Ponge, Gobat, et al., 2018).

The Parasystems follow the same trend as terrestrial systems (Ligno, Rhizo, Crusto, and Bryoforms) (Zanella, Ponge, Fritz, et al., 2018).

Variations in the O and A horizons' thickness and the size of the soil aggregates (miA, meA, and maA) (Zanella, Ponge, & Briones, 2018; Zanella, Ponge, Fritz, et al., 2018) are linked to organic matter decay and mixing with the mineral matrix (Golchin et al., 2018; Hellwig, Gómez-Brandón, et al., 2018; Witzgall et al., 2021). Consequently, the Mull system is more efficient in organic matter recycling than Moder, Mor, and Tangel systems (Ponge & Chevalier, 2006; Schaefer & Schauermaun, 1990), and Ponge et al. (Ponge et al.) considered it an attractor for terrestrial humus forms in forest environments. The Amphi system is a twin humus form showing both characteristics of Mull (meA and maA horizons) and Moder (presence of OH layer) due to a seasonal alternation between high and low biological activity in Alpine and Mediterranean environments (Zanella, Ponge, Gobat, et al., 2018). Except for Amphi, the accumulation in O horizons indicates a dysfunction in the process of organic matter decomposition and incorporation, which may result in a decrease in the carbon stabilization in the soil over a long time (Andreetta et al., 2011; Bayranvand et al., 2021; Ponge et al., 2010). Moreover, the soil organic carbon persistence can be explained by the functional complexity involving the molecular diversity of the organic matter, the spatial heterogeneity and temporal variability of the soil system and the biological components (Lehmann, Hansel, et al., 2020; Schmidt et al., 2011).

At the regional scale, climatic factors and parental material influence humus forms' spatial location and distribution (Marland et al., 2003; Ponge et al., 2011; van Breemen, 1993). At the local scale, the quantity and quality of litter, the biological activities, the microtopography, the micro- and meso-climatic conditions, and the physicochemical properties of the A horizon drive all the structuring of humus forms (Hellwig, Gómez-Brandón, et al., 2018), such as along elevation gradients, especially in forest ecosystems (Zanella, Bolzonella, et al., 2018; Zanella, Ponge, Fritz, et al., 2018; Zanella, Ponge, Gobat, et al., 2018). In Iran, for instance, the Mull system dominates at low elevations, and the Amphi and the Parasystems (Rhizomulls) at subalpine and alpine levels, respectively (Bayranvand et al., 2021).

These differences, including changes in the thickness and quality of the humus layers, were attributed to variations in climatic conditions along elevation, tree species composition and the inherent quality and quantity of litter that arrives in the soil. The same trend has been observed in a forest alpine tundra ecotone of the Swiss Alps: plant cover and soil organic layers are closely interrelated, and the OF layer increases in thickness depending on the exposure and the microtopography (Bednorz et al., 2000).

Focusing on soil organisms, Ascher et al. (2012) showed along an altitudinal gradient that the species richness of microannelids was higher under warmer conditions and that they were located exclusively in organic layers under colder conditions.

All the previous studies highlight the link between humus forms, pedogenesis factors, pedoclimatic conditions, biological activities and vegetation cover. However, the organic matter dynamics, i.e., its decomposition and integration in the topsoil relative to the humus system and forms, need further research. In this context, our study aims at integrating humus systems at several scales of investigation directly in the field, from a refined descriptive approach (survey, soil types and humus forms) to a functional one focused on organic matter dynamics (teabag experiment, microscopic observation of humus layers). With this holistic perspective, we aimed to compare different humus forms across a range of habitats, spread along elevation gradients, and asked if litter decomposition could be associated with varying types of humus forms, as predicted by theory (Kozlova et al., 2023; Mora et al., 2021). We hypothesized that the different proportions of macrorests would generate clusters of similar humus forms (Ponge, 1984; Zanella, Ponge, Gobat, et al., 2018). Second, we hypothesized that while mesoclimatic conditions would largely explain litter degradation, the rate of litter degradation would also be explained by the type of humus, independently of the geographic location.

2. Material and methods

2.1. Study sites

To study the relationship between standardized organic matter decomposition and different types of humus forms, we performed field surveys, in 2020-2021, in two valleys of the Swiss Alps, one in the Southern Swiss Alps, in the canton Ticino (46°27'05.052"N, 8°49'37.209"E) and one in Occidental Swiss Prealps, in the canton Valais (46°11'46.305"N, 7°00'19.319"E), see **Figure 3.7**, and **Table S3.5**. The climate in Ticino is sub-Mediterranean, while in Valais, it is tendentially more sub-continental. In each region, we studied sites placed at two elevations, the subalpine (~1500 m a.s.l.) and alpine (~2100 m a.s.l.) levels, and along two opposing facing slopes (north and south), for a total of 2 regions x 2 elevations x 2 slopes x 3 replicate plots = 24 sites. Moreover, we randomly chose three replicate plots separated by at least 100 m. Plot size varied according to the vegetation type (Semeraro et al., 2023): in the conifer forests of the subalpine zone, the plots' area was 400 m² (20 m × 20 m), whereas in the grasslands of the alpine zone, they were 25 m² (5 m × 5 m). In sum, we described humus forms in 24 sites.

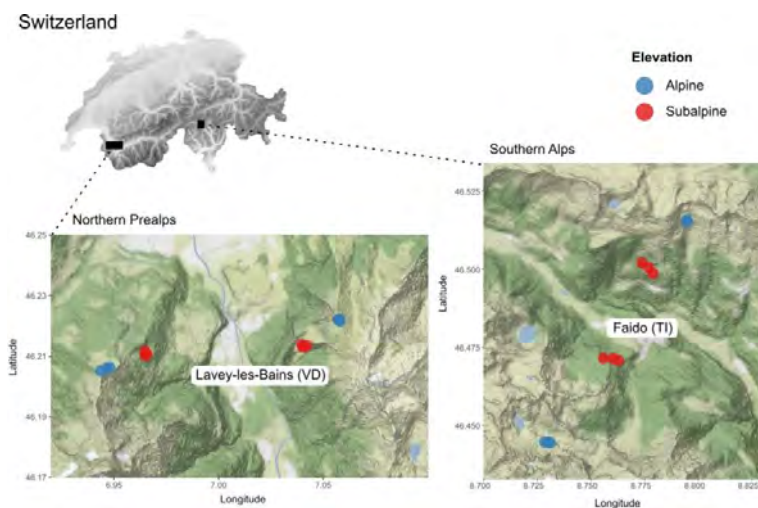


Figure 3.7 Study sites. Map of Switzerland showing the study's location; transect in the Northern Alps (Lavey-les-Bains, VD), Southern Alps (Faido, TI). The elevation transects were divided into two elevation zones; a subalpine zone (1,500 m a.s.l, red circles), and an alpine zone (2,100 m a.s.l., blue circles). In both regions, we established a north- and a south-facing altitudinal transect and at each elevation, we defined three replicate plots (N = 2 regions × 2 expositions × 2 elevation zones × 3 replicates = 24 sites); for sites coordinates see Table S1.

2.2. Humus forms and soils

In each plot, we randomly chose a 1 x 1 m² zone (ca. in the middle of the plot) to perform a soil profile description following the Référéntiel pédologique (Baize & Girard, 2009) classification system and the World Reference Base for Soil Resources (IUSS, 2022) ([Appendix B](#)). The choice of the two classifications allows the most accurate description possible regarding pedogenetic processes. We next classified the humus forms following the classification of Zanella, Ponge, Jabiol, et al. (Zanella, Ponge, Jabiol, et al., 2018).

In addition, a block of 5 x 5 x 15 cm³ was collected in the same spot using the Ponge small-volumes method (Ponge, 1984).

The material of each topsoil horizon from each block was next stored in 95% ethanol to preserve the structure of organic matter and aggregates. In the laboratory, each layer was spread gently in a Petri dish, and then covered with ethanol, taking care not to break the aggregates. The different morphological features of the O and the A layers (macrorests) were identified under a binocular lens at 40 x magnification and quantified by a point-count method (N. Bernier & J.-F. Ponge, 1994).

Then, the relative percentage of each macrorest was calculated (Jabiol & Baize, 2011; Jahn et al., 2006; Ponge, 1984). In the A, in addition to horizon depth, we visually assessed the structure, texture, pH Hellige, carbonates occurrence (HCl test), coarse elements, Munsell colors, roots abundance, and soil organisms' presence. The presence of organisms (meso- and macro-fauna) was recorded by hand when the soil pits were opened; further details are given in [Appendix B](#).

2.3. Teabag experiment

Following the recommendation of Keuskamp et al. (2013), 10 green tea and 10 rooibos tea bags were buried pairwise at a depth of 5 cm in the A layers (**Figure S3. 7**), in autumn just before the first snowfall in each plot. The burial locations were chosen to represent the general vegetation of the plot (Semeraro et al., 2023). The next spring, after 8 to 9 months, the tea bags were carefully excavated, wiping off adherent soil particles, and dried at 40°C for at least 48 h. The decomposition rate (k – percent of weight loss per day) for both tea types was next assessed using initial weight (w_i), final weight (w_f), and burial time as follows: $[k = ((w_i - w_f) / (w_i \times 100)) / \text{burial time}]$.

2.4. Statistical analysis

We performed all statistical analyses with R software, version 3.5.1 (R Core Team, 2013).

Bernier and Ponge small-volume method - To visualize macrorests proportion types and humus forms studied, we computed a descriptive visualization of the different macrorests proportion using the *geom_area* function of the package *ggplot2* (Wickham et al., 2016).

Humus systems and forms - To visualize and analyse humus systems across all plots, we used the algorithms for quantitative pedology (*aqp* package, Beaudette et al., 2013). To visualize humus systems similarities based on the determined macrorest proportions, we computed a summed, depth-segment aligned dissimilarity matrix (*profile_compare* function in the package *aqp*) at a maximum depth of 40 cm. Based on this dissimilarity matrix, we next computed a divisive hierarchical clustering *diana* in the package *cluster* (Maechler, 2019) and visualized it using the *hclust* function. To facilitate the analysis, we grouped the different types of macrorests together to obtain 11 groups representing the different types of macro tests observed (see **Table 3. 2**). Finally, we visualized differences in humus systems and correlations between macrorests using a principal component analysis (de Godoy Fernandes et al.), calculated using the *ade4* package (Dray & Dufour, 2007).

Table 3. 2 Macrorests groups. Grouping of different types of macro tests for data analysis. For more details on the different macro test groups, see Appendix A. Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1.

Group Number	Group Abbreviation	Name	Subgroup Content
1	Monocot	Monocotyledon	
2		Monocotyledon.leaf	
3		Monocotyledon.stem	
4		Monocotyledons	
5	Dicot	Dicotyledon.fragmented.leaf	
6		Dicotyledon.intact.leaf	
7		Dicotyledon.other	
8		Dicotyledon.skeletonized.leaf	
9		Dicotyledon.stem	
10		Dicotyledons	
11	NeedleCones	Fragmented.Abies.needle	
12		Fragmented.Larix.needle	
13		Fragmented.Picea.needle	
14		Fragmented.Pinus.needle	
15		Gymnosperm.cones	
16		Gymnosperm.other	
17		Gymnosperm.twig	
18		Intact.Abies.needle	
19		Intact.Larix.needle	
20		Intact.Picea.needle	
21		Intact.Pinus.needle	
22	Roots	Roots [>2 mm]	
23		Roots [0–2 mm]	
24	Wood	Wood	
25	Bryophyte	Bryophyte	
26	Holorganic	Holorganic	
27	Organomin	Organomin	
28	Mineral	Mineral	
29	Mycelium	Mycelium	
30	Other	Fauna, feces and undetermined holorganic matter	

Tea litter decomposition (mean k value change) in humus systems and forms - To analyze the relationship between humus forms and tea litter degradation, we organized the humus macroaggregates across the different sites using non-metric multidimensional scaling (NMDS), onto which we fitted a smooth surface of the k values for both tea types separately (package *vegan*, (Oksanen, 2010)). Next, since we highlighted two major humus types across all sites (Parasystem and Terrossystem), we were able to assess the interactive effect of soil type and humus types on k values using a two-way ANOVA.

3. Results

3.1. Soils

In Ticino, soils at the alpine level were classified according to the Référentiel Pédologique and the World Reference Base for Soil Resources, respectively, as Organosols Insaturés; Umbrisols (TNH1, TNH2 and TNH3) and Colluviosols; Colluvic Regosols (TSH1, TSH2 and TSH3) for north-exposed and south-exposed sites, respectively. At the subalpine level soils were classified as Organosols Holorganiques; Histosols (TNM1, TNM2) and a Régosol; Leptosol (TNM3) for north-exposed sites, and Organosols Insaturés; Umbrisols (TSM1 and TSM3) and one Régosol; Leptosol (TSM2) for south-exposed sites. In Valais, soils were Brunisols Dystriques; Cambisols (VSM1, VNM1, VNM2, VNM3, VNH3, VSH1, VSH2, VSH3) and Alocriisols (VNH1 and VNH2). Cambisols dominate at the alpine and subalpine levels for both expositions, except for two Peyrosols; Leptosols (VSM2 and VSM3). Overall, all our soils were observed on crystalline substrates except for two soils (VSM2 and VSM3) that were found to be on a calcareous substrate.

3.2. Terrosystems and Parasystems distribution

Combining field description and macrorests analysis, we found two Terrosystems (Mulls and one Mor) and two types of Parasystem (Rhizoforms and Lignoforms) (**Figure 3.8**).

The Mulls were only found in the Valais, while Mors and Lignoforms restrict themselves to Ticino, except for VSM3. The Rhizoforms were always found at the alpine level.

The pairwise dissimilarity tree groups the humus systems relative to the organic matter dynamics revealed by the horizons sequences: Rhizoforms on the left, Lignoforms with one Mor on the right, and Mulls are spread more or less everywhere (**Figure 3. 8**). All Mulls were less than 15 cm in depth except for VSM2, VNM2 and VSM3, and the thickest humus forms (> 22 cm) were two Rhizoforms (TSH1, TSH3), two Lignoforms (TNM1, TSM1) and one Mull (VSM3). The Lignoforms are strongly linked to the organic layers' thickness and, not surprisingly, to the proportion of wood decay debris and the presence of mycelium (**Figure 3. 9**). The high ratios of cones and needles favour the Mors. The well-structured A layer (meA and maA) drives the identification of Mulls, while the roots, as expected, explain the Rhizoforms (**Figure 3. 9**). Moreover, our results suggest that the humus forms distribution (**Figure 3. 10**) varies across elevation (**Figure S3. 8**) and exposition (**Figure S3. 9**).

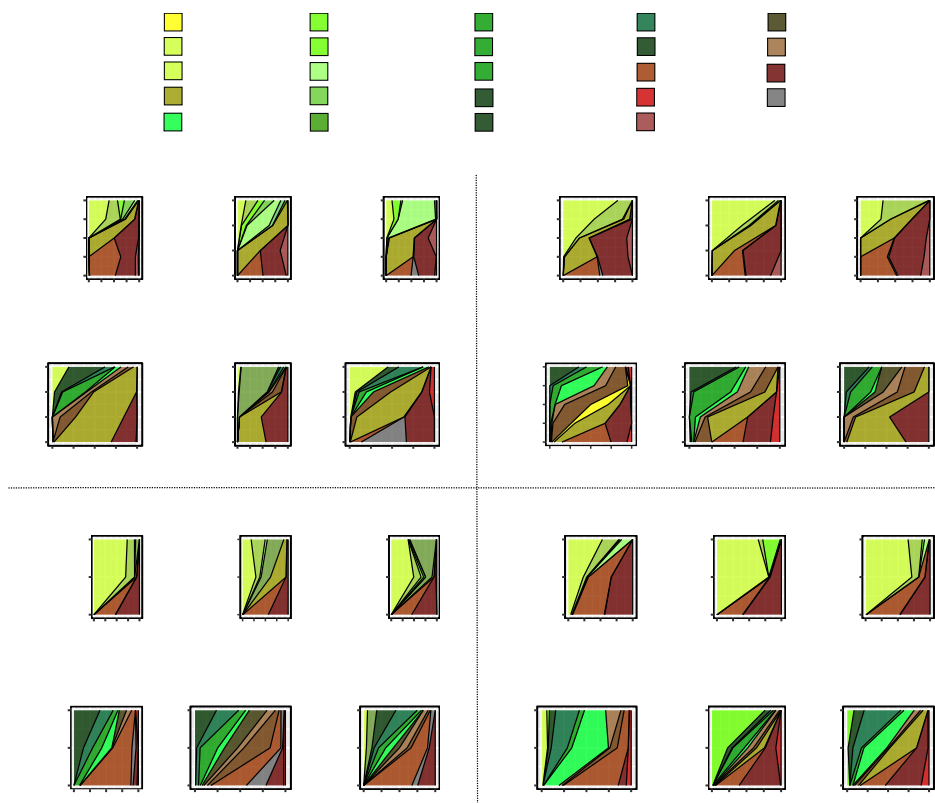


Figure 3.8 Illustration of all different humus forms “macrorests” types of proportions for each region and each replicate plot using the the arthropod II-volume method (Ponge 1984). The Ticino region (T): alpine north-exposed (TNH 1 to 3) and south-exposed (TSH 1 to 3) sites, subalpine north-exposed (TNM 1 to 3) and south-exposed (TSM 1 to 3). The Valais region (V): alpine north-exposed (VNH 1 to 3) and south-exposed (VSH 1 to 3), subalpine north-exposed (VNM 1 to 3) and south-exposed sites (VSM 1 to 3). Groups are based on the 11 macrorest types of the Ponge the arthropod II-volume method, including Monocotyledon leaves and stem (Monocot), Dicotyledon fragmented leaf, intact leaf, skeletonized leaf, dicotyledon stem (Dicot), fragmented and intact *Abies* sp., *Larix* sp., *Picea* sp., *Pinus* sp. needle, gymnosperm cones and twig (Needle and Cones), Roots from 0 to 2 mm and >2 mm (Roots), Wood (Wood), Bryophytes, holorganic, mineral, mycelium, organomineral layers, and other (fauna, feces, and undetermined holorganic matter). Colors indicate the different groups of macrorests.

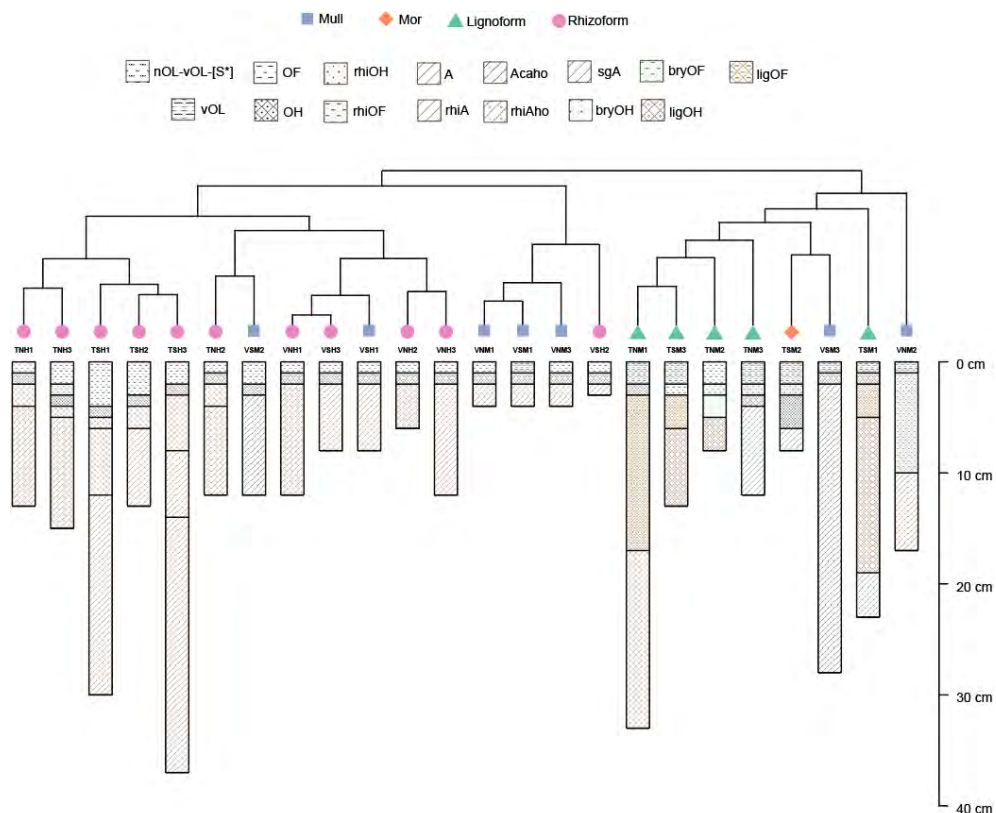


Figure 3.9 Divisive hierarchical clustering of 24 humus forms based on the 11 macrorest groups of the Ponge the arthropod II-volume method, including Monocotyledon leaves and stem (Monocot), Dicotyledon fragmented leaf, intact leaf, skeletonized leaf, dicotyledon stem (Dicot), fragmented and intact *Abies* sp., *Larix* sp., *Picea* sp., *Pinus* sp. needle, gymnosperm cones and twig (Needle and Cones), Roots from 0 to 2 mm and >2 mm (Roots), Wood (Wood), Bryophytes, holorganic, mineral, mycelium, organomineral layers, and other. Colored circles indicate the humus systems: mulls (purple squares), mors (orange diamonds), lignoforms (green triangles), and rhizoforms (pink circles).

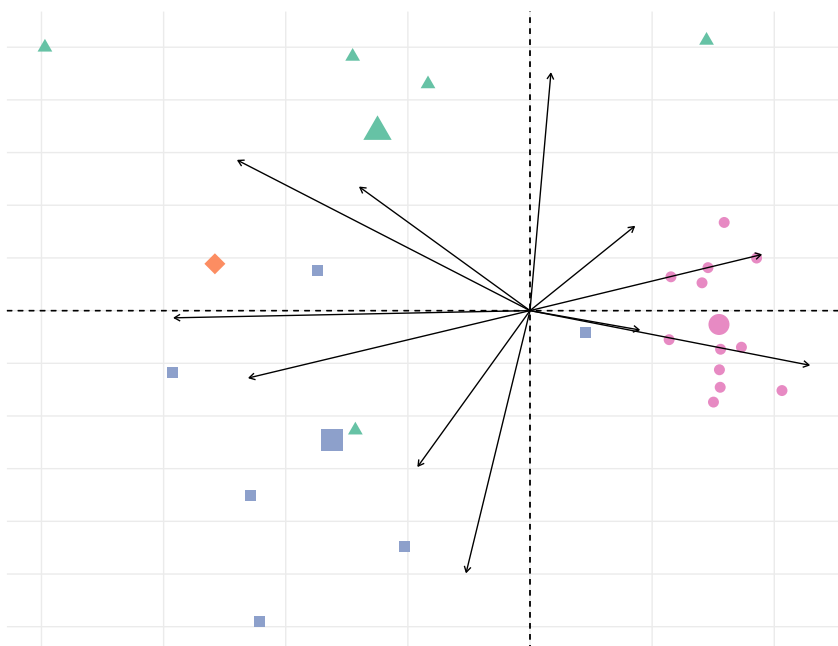


Figure 3. 10 Humus system and Ponge macrorest analysis. Principal Components Analysis Biplot (PCA-Biplot) illustrates described humus systems as a function of Ponge macrorests' proportions variables (weighted means). All humus systems are grouped along a recalcitrance gradient from woody and fungal macrorests and mineral components to more organic components. The PCA shows the aggregation and distribution of humus systems along the macrorests' proportion gradient. Colors indicate the different humus systems: lignoforms (green triangles), mors (orange diamonds), mulls (purple squares), and rhizoforms (pink circles).

3.3. Humus forms and their morphological features across regions

In Ticino, we observed 11 Parasystems, including Rhizomodors (n=6), Lignomodors (n=2), Lignomors (n= 3), and 1 Terrossystem with a Humimor. At the alpine level, across both slopes, the dominant humus forms were Rhizomodors (TNH1, TNH2, TNH3, and TSH1, TSH2 and TSH3), coupled with a higher proportion of monocotyledons, holorganic matter and roots for south-facing sites (**Figure 3. 8, Appendix B**). Rhizoform horizons identified were nOL, vOL, OF, rhiOF, rhiOH, and the rhiA comprised mesoaggregates (meA). Generally, the O horizons were thicker in the south (5 to 8 cm) than the north exposure (4 to 5 cm).

At the subalpine level, Parasystems dominate with 3 Lignomors (TNM1, TNM2, and TNM3), 2 Lignomodors (TSM1 and TSM3), and one Terrossystem (TSM2), a Humimor. All humus forms at the subalpine level contain high proportions of needles, gymnosperms, fine holorganic matter, wood, and root debris (**Figure 3. 8, Appendix B**). The horizons identified were vOL, OF, OH, ligOF, ligOH, and the A horizon was always single grain (sgA). As observed at the alpine level, the O horizons are generally thicker in the south (4 to 21 cm) than in the north (3 to 24 cm). In Valais, the biological activities and the organic matter types (no wood debris) lead to more efficient humus forms in terms of organic matter integration and decomposition. Whether north- or south-facing, the humus forms are 6 Parasystems with Rhizomulls (n=4) and Rhizomodors (n=2) at the alpine level. Only Terrossystem, with 6 Mulls, were described at the subalpine level with Dysmulls (n=3), one Oligomull (n=1) and Mesomulls (n=2), highlighting an increase in organic matter dynamics. Thus, at the alpine level, the predominant system is Parasystems with Rhizomulls (VNH3, VSH1, WSH2 and WSH3) and Rhizomodors only in the north-exposed sites (VNH1 and VNH2). All Rhizoforms have a higher proportion of Monocotyledons debris, but south-exposed sites show a higher proportion of organomineral material (Zanella, Ponge, & Briones, 2018) and roots (**Figure 3. 8, Appendix B**). The horizons identified were nOL, vOL, OF, and the A horizon comprised mesoaggregates. In addition, the thickness of O horizons was similar in the south and the north (0.5 to 1.5 cm), which reveals that the organic matter integrates better in Valais than in Ticino. At the subalpine level, only Terrossystem with Mulls were recovered in the forests with an Oligomull (VSM1), two Mesomulls (VNM1 and VNM3), and three Dysmulls (VNM2, VSM2 and VSM3). They all have large proportions of needles and roots (**Figure 3. 8, Appendix B**). The horizons identified were vOL, OF, and the A horizon was well-structured and comprised macroaggregates (maA). The O horizons are generally thicker in the south (1 to 3 cm) than in the north (1 to 2 cm), but the difference is tiny.

3.4. Tea litter decomposition

Using NMDS and smooth fitting, we observed that k values decreased when moving from the subalpine to the alpine zone, independently of region and exposition (**Figure 3. 11A and B**).

Moreover, we found a significant effect of the tea type (**Figure 6**, tea type effect; $F_{1,44} = 753.068$, $p < 0.001$), in which green teas degraded on average 18 times faster than rooibos tea, and that decomposition rate was 7 % higher in Terrosystems than in Parasys-tems (**Figure 3. 12**, Humus type effect; $F_{1,44} = 6.136$, $p = 0.017$), independently of the tea type (interaction effect; $F_{1,44} = 0.108$, $p = 0.744$).

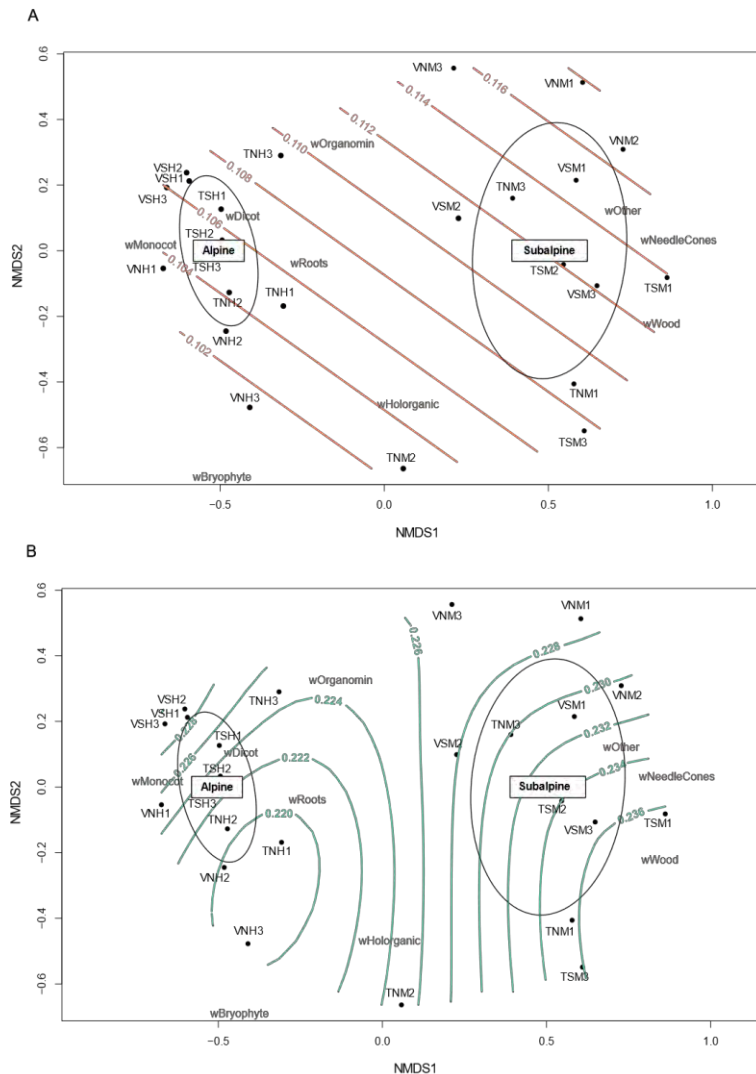


Figure 3. 11 Nonmetric multidimensional scaling (NMDS) of teabag decomposition. NMDS ordination with fitted environmental vectors and regression surfaces. The surfaces show smooth trends of the relationship between the (A) rooibos decomposition mean k value and (B) green tea decomposition mean k value for each site. The mean k values represent the mean percent of daily tea weight loss.

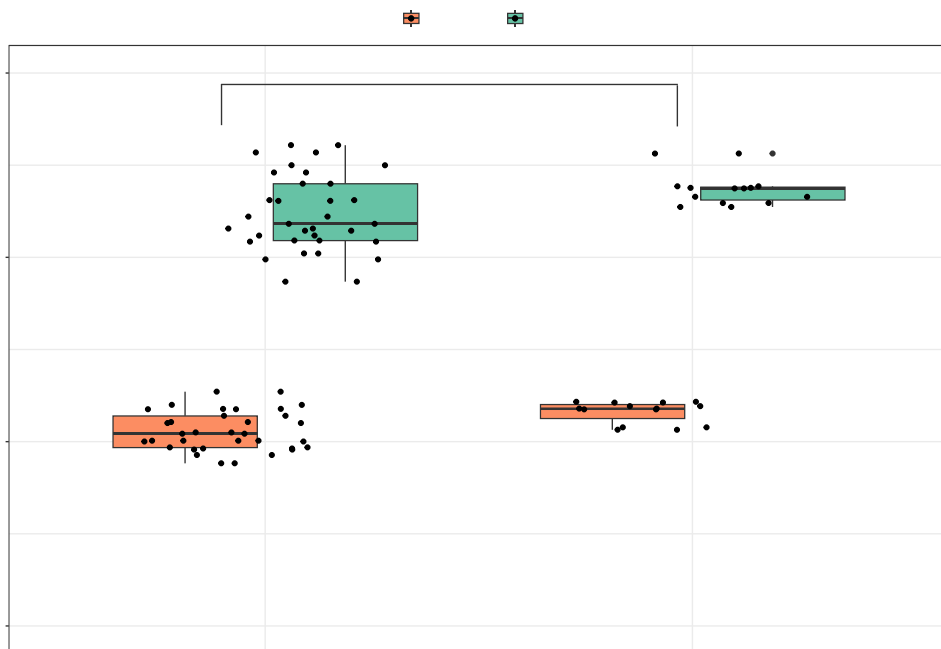


Figure 3. 12 Tea litter degradation according to humus forms. Boxplots represent mean degradation rates (k values) for the two tea types: rooibos (orange) and green tea (green), according to Parasystems and Terrosystems. Letters and stars (***) indicate a significant difference between boxplots (Tukey's HSD; $p < 0.05$). Boxplots represent, from bottom to top, minimum, first quartile, median, third quartile and maximum, and black dots represent the outliers.

4. Discussion

Based on an ecosystemic approach, we studied the diversity of humus systems in alpine meadows and subalpine forests at several scales by integrating descriptive tools (vegetation survey, soil types, humus forms) and functional ones (teabag experiment, macrorests). Except for Rhizoforms, the humus forms reflect the soil evolution processes relative to the geology, the pH and the soil biota activity. In addition, elevation determines the humus system, and exposure influences the diversity of humus forms, likely mediated by different vegetation types. Moreover, teas degraded faster at the subalpine level but generally quicker in the Terrosystems than in the Parasystems.

4.1. Humus forms and soil pedogenetic processes

Soils and humus forms result from the parent material transformation occurring in a circumscribed time under the climate and the biota action (Chersich, 2018). It is well known that the humus O and A layers form under the control of soil organisms (bacteria, fungi, pedofauna).

At the same time, the deeper horizons are mainly related to physicochemical processes (Duchaufour, 1977; Weil & Brady, 2017). In our study, we observed a relationship between the pedogenetic domain and humus forms, as previously highlighted by Chersich (Chersich, 2018).

In Valais, the Mull systems correspond to Brunisols (Cambisols) or Peyrosols (Leptosols) at the subalpine level, and earthworm activities were observed everywhere.

The brunification process in Brunisols is indeed often associated with an A layer (biostructured and mediated by earthworms, with clay-iron-humic complexes) and an S layer (subangular aggregates due to non-biological clay-iron complexes) (Baize & Girard, 2009; Duchaufour, 1977; Weil & Brady, 2017). The higher soil pH in the two Peyrosols (Calcaric Leptosols) compared to the other soils on an acidic substrate (schists, loess, sandstone) also improve earthworm activity and, consequently, the formation of soil aggregates and the A horizon thickness (11 and 26 cm for VSM2 and VSM3, respectively). Moreover, the occurrence of high biological activities in soil pockets in the stony horizons (Xpcaho) leading to meso- and macroaggregate formation is often observed in Peyrosols, especially on calcareous substrates (clay-calcium-humic complexes (Gobat & Guenat, 2019)). In Ticino, the bedrock was composed exclusively of gneiss leading to low soil pH (< 5; see [Appendix B](#)). Such acidic conditions, enhanced by the massive amount of woody litter, are unsuitable for endogeic and anecic earthworms (Edwards et al., 2022). Organosols (Umbrisols and Histosols) and Lignoforms result from this organic matter accumulation that limits the pedogenesis evolution with only O and A layers (Baize & Girard, 2009). Focusing on the Rhizoforms at the alpine level, they were found independently of the location (Valais and Ticino) on Brunisols and Alocriisols (Cambisols), Colluviosols (Regosols), Organosols (Umbrisols) and Régosol (Leptosol). Earthworms were present only in Valais, confirming their dependence on geology and pH.

We assume that the Rhizoforms seem more related to the vegetation cover than the pedogenetic processes. The proportion of Monocotyledons at the alpine level seems to be negatively correlated with biological activity, while the litter from *Larix* sp. and *Abies* sp. seems to be beneficial to earthworms' presence and their bioturbation activity (more organomineral components) at the subalpine level.

4.2. Alpine meadows: humus homogeneity and organic matter accumulation

We observed Parasystems at the alpine level in both regions. In the alpine meadows of Ticino, the decomposers' activity seems microfauna oriented in Rhizomodors, with arthropods such as mites and springtails observed in the field. Earthworms were absent in both *Carici curvulae*-Nardetum and *Rhododendro ferruginei*-*Vaccinetum* associations for all north-exposed sites (TNH1, TNH2 and TNH3; for more details, see **Table S3. 6, Appendix C**).

The same trend was observed for south-exposed sites under the *Hypochoerido*-Nardetum association (TSH1, TSH2 and TSH3), probably due to the high root density and the soil's thickness. Indeed, the soil instability (Colluviosol; Leptosol), coarse elements (pebbles, sand) and low temperatures of more than half-year probably favour roots instead of earthworms. In contrast, in Valais, the biota activity was mainly macro- and mesofauna-oriented in Rhizomulls and Rhizomodors, with arthropods and earthworms observed under the *Geomontani*-Nardetum association for all north-exposed sites (VNH1, VNH2 and VNH3 ; for more details see **Table S3. 6, Appendix C**). On the other hand, on south-exposed sites under *Hypochoerido*-Nardetum vegetation, only a few arthropods were observed, while earthworms were very abundant (VSH2 and VSH3); for more details, see **Table S3. 6, Appendix C**. Plant litter is often considered to decompose better in its original environment due to the adaptation of decomposer communities to the phytochemical composition (Veen et al., 2015; Wallenstein et al., 2013), but other studies suggest a different outcome as there is a multitude of interactions between plants, decomposers, and climate (Austin et al., 2014). Furthermore, Lin et al. (Lin et al., 2021) found that both aboveground tree species richness and leaves litter composition play a role in litter decomposition regulation (Lin et al., 2021). Rosenfield et al. (2020) observed that green leaf traits – and not leaves litter traits – accurately predicted litter decomposition.

Exposure also impacts biological activity and organic matter mineralization, with thicker rhiOF and rhiOH horizons in the north-exposed sites. Such an accumulation of organic matter directly affects edaphic factors such as soil pH by releasing organic acids and decreasing soil pH with increasing elevation (Badía-Villas & Girona-García, 2018). Zhu et al. (Zhu et al., 2013) showed that the litter decomposition rate positively correlates with mean soil temperature during the plant growing season and the number of freeze-thaw cycles during the winter. In addition,

Ascher et al. (2012) showed that thermal differences might affect soil biological properties and that microbial biomass was higher at higher elevations. Indeed, soil moisture influences microbial community activities and soil organic matter dynamics (Bian et al., 2022).

Also, Matteodo et al. (2018) showed that organic matter dynamics diverge with depth, with each soil layer having a different organic matter thermal stability, but also that in litter horizons, organic matter quality (lability) was the most important (Matteodo et al., 2018). The Rhizoforms observed at high altitudes in our study have thick rhi-layers that might better retain water and favour enzyme activities (A'Bear et al., 2014). The high root density provides also food and habitat for earthworms as they were present in almost all Rhizoforms in the Valais.

The teabag experiment helped us compare a standardized litter decomposition rate along elevation gradients (Keuskamp et al., 2013). Previous studies confirmed the suitability of this approach in terms of the representativeness of experimental comparisons of local litter with teabag decomposition dynamics (Didion et al., 2016; Duddigan et al., 2020). As previously demonstrated by Didion et al. (Didion et al., 2016), we confirmed the slowest decomposition rate at the alpine level, and also that rooibos tea degraded slower than green tea (Semeraro et al., 2023). In alpine environments, microtopography can play a decisive role in the spatial distribution of different humus systems and forms (Hellwig, Tatti, et al., 2018; Zhu et al., 2019). Indeed, in our study, we also observe microtopography and plant communities being decisive factors driving humus forms distribution in the alpine environment, which was also highlighted by the study of Hellwig et al. (Hellwig, Tatti, et al., 2018).

4.3. Subalpine forests: the organic matter dynamics vary according to the vegetation

Overall, the forest ecosystems at the subalpine levels showed a different trend than the alpine meadows. In Ticino, the large amounts of wood debris on the soil surface favour the presence of fungi in the Lignoforms and the Humimor. The soil humidity of the north-exposed sites (TNM1, TNM2 and TNM3) and the forest associations of Larici Piceetum and Homogyno-Piceetum allow not only the presence of fungi but also lots of mesofauna. On the south-exposed sites (TSM1, TSM2 and TSM3, for more details see **Table S3. 6, Appendix C**) under Calluno-Pinetum forest, the mycelium was still abundant, like mesofauna, but without earthworms (for more details see **Table S3. 6, Appendix B and C**).

The wood decay fungi are some of the most important decomposers in the forest ecosystem (Hyde et al., 2016; Riley et al., 2014).

Fukasawa et al. (2021) studied fungal community assemblies and substrate quality in different stages of wood decay (Fukasawa & Matsukura, 2021). They showed that changes in fungal communities and wood quality during wood decomposition affect the fungal diversity–decomposition relationship.

These results align with Hellwig, Gómez-Brandón, et al. (2018) that highlight humus forms having a high potential to indicate soil microbiological properties in a high mountain forest.

In Valais, earthworms act as the primary ecosystem engineers at the subalpine level. The forest canopy and the quality of the litter mediate the distribution of humus forms and systems, in particular by providing favourable conditions for decomposers such as earthworms and arthropods (Desie et al., 2020; Lindahl et al., 2010; Salmon, 2018). The palatability of the litter from Abieti-Fagetum favours the presence of earthworms and mesofauna in the south-exposed sites (VSM1 to 3, for more details see **Table S3. 6, Appendix C**). In the north-facing areas (VNM1 to 3), Adenostylo-Abietum creates a cool and fresh local climate ideal for earthworm activities (for more details see **Table S3. 6, Appendix B and Appendix C**). Of all the humus forms we described, the Mulls we observed in the Valais highlight the better organic matter decomposition and integration in soil macro aggregates. Building soil macroaggregates influences humus forms' functioning (Terrosystems with Oligo-Meso- and Dysmulls) (Yudina & Kuzyakov, 2023).

The teabag experiment confirms the decomposition processes compared to the alpine meadows. However, further investigation is needed on how different soil communities affect organic matter decomposition in Parasystems and Terrosystems.

5. Conclusion

Being at the interface of vegetation and bedrock, the humipedon reflects the overall soil evolution processes and varies according to elevation and exposure. Our study confirms that the humipedon is also a good index of ecosystem functions such as organic matter decomposition and integration in the soil. The variations in organic matter decomposition (teabag experiment) can be explained by different biotic and abiotic factors, such as the soil decomposers' community, but also the impact of their selective feeding behaviour on either rooibos or green tea. It would suggest specialization of organisms for the primary degradation of recalcitrant or labile organic matter, respectively (Daebeler et al., 2022), but also soil temperature and edaphic properties. Also, a variation in tree species composition due to climate change may drastically affect belowground communities and humus forms. Accordingly, future research is needed to investigate the humipedon impact on organic matter decomposition dynamics in the context of climate change.

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7. Conflicts of Interest

The authors declare no conflict of interest.

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Phytochemical variation and decomposition of leaves and roots in mountain environments

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Abstract

Plant specialized metabolites (PSMs) are diverse chemical compounds produced by plants to cope with biotic and abiotic stresses but also play crucial roles in emergent ecosystem processes, such as the decomposition of organic matter. Yet, it is unclear whether site-specific community-level phytochemical variation drives variation in decomposition rates and provides home-field advantage (HFA) effects. We conducted a reciprocal litter transfer experiment across subalpine and alpine ecosystems, following a north-south slope gradient. Utilizing advances in untargeted metabolomics, we integrated high-resolution mass spectrometry data of leaves and roots with assessments of litter degradation, as well as local climatic and edaphic conditions. We observed significant differences in phytochemical composition across sites, as evidenced by notable shifts in phytochemical beta diversity when moving from subalpine to alpine environments. These changes in diversity were associated with a general reduction in the production of several metabolite superclasses in alpine regions. Additionally, while we detected significant variability in litter decomposition rates, these effects were only weakly associated with elevation or the HFA effect. Instead, decomposition rates were correlated with the phytochemical diversity of both roots and leaves across different elevations. We concluded that both community-wide root and shoot phytochemical composition, modulated by elevation sites, impacts litter decomposition. Moreover, the general decline in phytochemical diversity at high elevation was not associated with an HFA, show that PSMs affect decomposition rates across environments, but these effects are further controlled by local climatic and edaphic conditions. The general lack of HFA effect, highlights a combinatorial framework including edaphic factors, climate and soil biota in explaining variation driven by phytochemical composition in organic matter decomposition in soils.

1. Introduction

Decomposition is a fundamental ecological process that recycles nutrients and organic matter within ecosystems. It involves the breakdown of complex organic molecules into simpler compounds, facilitated by a variety of microorganisms and environmental conditions (Aerts, 1997; Bradford et al., 2014). The rate and extent of decomposition are influenced by multiple factors, including the diversity of the local soil biota; micro- and mesofauna, and especially the microbial communities of bacteria and fungi, which in turn are affected by temperature and moisture, as well as the chemical composition of the decomposing material (Swift et al., 1979). Indeed, plant-specialized metabolites (PSM) have been shown to significantly impact decomposition processes across a range of ecosystems (Chomel, Guitttonny-Larchevêque, et al., 2016; Goga et al., 2018).

Plant secondary metabolites (PSMs) are a diverse array of chemicals produced by most plant species to address biotic and abiotic stresses. These include alkaloids, phenolic compounds, and terpenes, with thousands of unique compounds identified (Sharma et al., 2022). Phenolic compounds, for instance, provide defense and structural support in plant tissues, and in litter decomposition, they can inhibit microbial activity, slowing decomposition and impacting nutrient release and soil fertility. Overall, PSMs play crucial roles in plant interactions with both abiotic and biotic factors, influencing plant-plant, plant-microbe, and plant-animal interactions (Khare et al., 2020; Wang et al., 2021; Yang et al., 2018). PSMs enter ecosystems through four primary pathways: (i) volatilization and diffusion from plant tissues, (ii) leaching from above-ground plant material, (iii) exudation from plant roots, and (iv) litter decomposition. The three latter pathways release significant amounts of PSMs into the soil, influencing various soil processes crucial for ecosystem functioning (Berg, 2014; Berg et al., 2000; Berg et al., 2004; Hättenschwiler & Vitousek, 2000; Horner et al., 1988). Therefore, the nature and diversity of PSMs produced by leaves and roots have been hypothesized to impact key ecosystem processes such as organic matter decomposition and nutrient cycling, ultimately shaping the structure and function of ecosystems (Aber & Melillo, 1982; Chomel, Guitttonny-Larchevêque, et al., 2016; Moore et al., 2014; Moore et al., 2011; Reich et al., 2010).

At the local scale, both the rate and extent of decomposition are shaped by the chemical variability and composition of the plant species within the specific environment or habitat. For instance, tannins can bind proteins and inhibit microbial activity, thereby increasing litter recalcitrance and slowing decomposition rates (Moore et al., 2011).

Higher nitrogen concentrations and lower lignin concentrations generally correlate with faster decomposition rates (Ntonta et al., 2024; Talbot & Treseder, 2012). At broader scales, PSMs can explain the unique effects of litter mixtures on decomposition rates and the adaptation/selection of soil organisms, leading to a 'home-field advantage' (HFA), where litter decomposes faster in its native environment (Fanin et al., 2021; Perez et al., 2013; Rúa et al., 2016; Geertje F. Veen et al., 2015). This advantage is attributed to factors such as microbial adaptation, environmental conditions, and competitive interactions (Austin et al., 2014; Ayres, Steltzer, Simmons, et al., 2009; Van der Putten et al., 2013; Wardle, 2006). Local microbial communities are adapted to the chemical and physical properties of native plant litter, facilitating more efficient decomposition compared to foreign litter (Ayres, Steltzer, Berg, et al., 2009; G. F. Veen et al., 2015).

In this study, we examine how elevation gradients, particularly transitions from below to above the tree line—a significant ecotone—affect phytochemical diversity and its impact on leaf and root litter decomposition. Elevation gradients, which typically ranges from warmer temperatures at lower elevations to colder and more humid climates in the alpine, influences a range of ecological factors including soil chemistry, vegetation types, and microbial activity (Hernández-Cáceres et al., 2022; Ivashchenko et al., 2021). Accordingly, it is assumed that litter at high elevation degrades more slowly than at low elevation, mostly due to slower pace of microbial activity (Nottingham et al., 2015). Yet, it is unclear how community-level phytochemical diversity varies from across the tree line ecotone, and how this variation impacts rates of litter degradation.

Our aims were, first, to assess community-wide phytochemical diversity along elevation gradients. And second to test the HFA related to chemical variability. We hypothesize that plant communities at high and low elevations exhibit distinct phytochemical profiles, influenced by local climatic and edaphic conditions.

Based on previous research, we predicted higher levels of phytochemical diversity at the subalpine than in the alpine elevations (Defosse et al., 2021).

Second, we hypothesized that litter would decompose differently based on the specific chemical mixtures present in local plant communities.

Specifically, we predicted litter to decompose more slowly in its non-native environment due to mismatched phytochemical-soil biota mixtures. Accordingly, when plant litter containing specific phytochemicals decomposes in its native environment, microorganisms and fungi adapted to those chemicals break down the litter efficiently. However, when this litter is introduced into a non-native environment where the resident microbial community may not be adapted to these phytochemicals, decomposition rates can decrease (Lu et al., 2017).

This mismatch can hinder the ability of local decomposers to recognize and metabolize the litter effectively, thereby slowing down the overall decomposition process. We also anticipate that the HFA effect will be more pronounced at higher elevations, where plants produce more recalcitrant litter (Ayres, Steltzer, Simmons, et al., 2009; Wallenstein et al., 2013). To address our aims, we conducted a reciprocal litter transfer experiment in subalpine and alpine ecosystems in the Swiss Alps. Leveraging advances in untargeted metabolomics, we characterized phytochemical diversity using high-resolution mass spectrometry and applied bioinformatics tools to analyze complex metabolite mixtures (Walker et al., 2022; Walker et al., 2023). This approach allowed us to study the relationship between phytochemical composition and litter decomposition under different environmental conditions.

2. Materials and methods

2.1 Study sites and sampling

To characterize the role of phytochemicals in litter decomposition, we performed a litter reciprocal transfer experiment in the Swiss Prealps (**Figure 3. 13a**). The study took place within the alpine valleys of two regions of Switzerland: one in the canton Ticino (TI), located on the southern side of the Swiss Alps with a sub-Mediterranean climate, and one in canton Valais (VS), located in the Western Prealps, with a sub-continental climate (for details, see **Table S3. 31**).

For each region, we selected four sites: two on the north-facing and two on the south-facing slopes of the valley, one at the subalpine (about 1500 meters above sea level (m a.s.l.), and one at the alpine level (about 2000 m a.s.l.) each (**Figure 3.13a**). At each site, we randomly selected three plots (c. 50 m apart) characteristic of the local environment within each site. Subalpine sites were located in coniferous forests, while alpine sites were located in alpine meadows. Each plot consisted of a 20 x 20-meter area at the subalpine level. In contrast, at the alpine level, each plot consisted of a 5 x 5-meter area, according to classical vegetation survey recommendations for forest and grassland inventories (Braun-Blanquet, 1932; Mueller-Dombois & Ellenberg, 1974). In each plot, all plant species were determined to the species level according to the Swiss Flora (Aeschimann & Burdet, 1989; Braun-Blanquet, 1932; Braun-Blanquet & Pavillard, 1925; Eggenberg & Möhl, 2013), and all species abundance-dominance values were estimated following Braun-Blanquet & Pavillard (1925). See supplementary materials for detailed methods of vegetation sampling. Finally, roots and leaves were collected for the 10 most abundant species at each site (**Table S3.32**), we produced a reduced species list of the collected leaves and roots of the 10 most abundant species at each site for phytochemical analysis (**Table S3.33**).

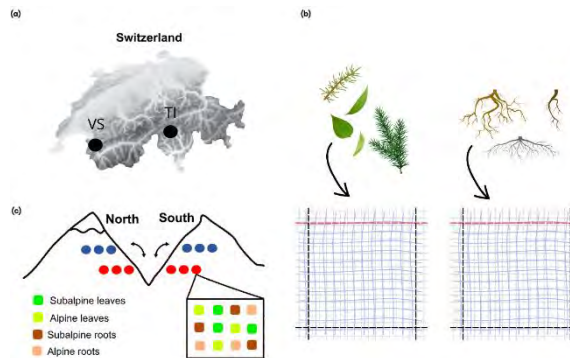


Figure 3.13 Experimental design. Map of Switzerland (a) showing the locations of plant collection sites: Valais-Vaud (VS) in the Northern Alps and Ticino (TI) in the Southern Alps. Two-sided mesh litter bags used for the study, containing leaves and roots (b). Litter bags were reciprocally transferred (black arrows) between subalpine and alpine levels, with three replications at each elevation for each transect. In each region (12 plots), litter bags containing subalpine leaves ($n = 3$), alpine leaves ($n = 3$), subalpine roots ($n = 3$), and alpine roots ($n = 3$) were randomly buried at 5 cm depth and spaced 1.5 meters apart. This procedure was repeated three times at each site. In total, 288 litter bags were deployed (c).

2.2 Litter bags transfer experiment

The 10 most abundant plants at each site were sampled during the summer 2020, by collecting the youngest fully expanded, and healthy leaves of several (2 to 3) individuals per species.

Root material was sampled by excavating several individuals per species, and carefully removing soil attached to roots with tap water. When possible, roots < 2mm were harvested. Leaf and root material were dried at 40°C for 7 days before being cut into small pieces for the preparation of the litter bags. The content of each litter bag consisted of the same mass of each of the ten most abundant species collected at each site (0.2 g ± 0.005g per species for a total of 2 g per litter bag for roots and shoots). With this procedure, we aimed to capture the most representative phytochemical composition of each site by focusing on the dominant plant species entering the soil.

To achieve this, we used litterbags (10 x 19 cm, **Figure S3. 10**) constructed with two types of meshes: a bottom fiberglass mesh with 1 mm openings to prevent litter loss, and a top nylon mesh with 4 mm openings to allow macrofauna passage (Tresch et al., 2019).

At each site we buried a total of N = 6 replicates * 2 elevations of origin (i.e., plant tissue from the 'home' site and from the opposite elevation within the same slope and transect) * 3 plots * 2 organs (roots and shoots) = 36 litter bags, for an overall total of 36 litter bags per site * 2 elevations * 2 expositions * 2 regions = 288 litter bags (**Figure 3. 13**). Litter bags were placed about 5 cm under the humus layer for 32 weeks (until May 2022), and 36 weeks (until June 2022), at the subalpine and the alpine level, respectively, following (Graça et al., 2005; Karberg et al., 2008). At the end of the experiment, the remaining biomass in each litter bag was air-dried at 40°C for 7 days. Litter mass loss (k) was determined using the following formula (Bray et al., 2012; Graça et al., 2005; Wieder & Lang, 1982):

$$k = \ln \left(\frac{\frac{m_1}{m_{0.1}}}{-t} \right)$$

With: m_0 = mass before decomposition,
 m_1 = mass after decomposition, and
 t = decomposition time in days

2.3 Phytochemical analysis

To estimate the effect of phytochemical diversity and quality on litter decomposition, we analyzed leaves and roots chemical compounds by Ultra-High-Pressure Liquid Chromatography coupled to mass spectrometry (UHPLC-MS). For this, leaves and roots for the most abundant species were collected separately in paper envelopes containing silica gel beads and stored in sealed plastic bags to avoid excess moisture during transfer to the laboratory (Chase & Hills, 1991; Esteban et al., 2009). Then, all leaves and roots samples were dried at 40°C for three days, and ground to powder using a ball mill for 5 to 10 minutes at 30 Hz (MM 400, Retsch, ME, Germany). Phytochemical extraction was done by adding 1ml MeOH:miliQ H₂O: formic acid solution (80:20:0.5) to 20±1mg of ground plant tissue (roots or leaves of each plant species), and by homogenizing the mixture for 3min at 30 Hz with a ball mill and centrifuged for 3 minutes at 14,000 rpm. Finally, a 2.5µl volume of the supernatant was injected into an Acquity UPLC C18 column (50 mm × 2.1 mm, 1.7µm; Waters, MA, USA). We analyzed the samples via UHPLC quadrupole time-of-flight mass spectrometry (QTOFMS) with an Acquity UPLCTM coupled to a Synapt XS IMS (Waters, MA, USA) by using a binary solvent system (H₂O and acetonitrile supplemented with 0.05% formic acid). See Supplementary Methods for details of the chromatographic analysis.

2.4 Soil analyses

We analyzed several physiochemical properties of an aggregated soil sample (~200 g of soil randomly collected within each site) of the first organo-mineral horizon, including; total carbon, and total nitrogen, which were measured with an elemental analyzer (FLASH 2000, Thermo Fisher Scientific, MA, USA). Residual humidity (RH) was determined after drying the soils at 105°C. Organic matter content was measured using the loss of ignition (LOI) method (Howard, 1965), which was assessed by calcination of the RH samples at 450°C (Nabertherm L9/C6, Gerber instruments, ZH, Switzerland). Soil total cationic exchange capacity (CEC) was quantified with cobalt-hexamine trichloride (Ciesielski et al., 1997) by Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES; Optima 2100 DV, PerkinElmer, MA, USA).

Soil pH was determined with a BlueLine electrode (SI Analytics, Thermo Fisher Scientific, MA, USA) and a Metrohm 827 pH meter in distilled water (Metrohm, AG, Switzerland). Soil properties across the subalpine and alpine regions were visualized using a principal component analysis (PCA) (**Figure S3. 11**).

2.5 Climate

For each site, we extracted climate data as interpolated values from meteorological stations from 1981 to 2010 for degree days, radiation, frost growing days, evapotranspiration, and precipitation, following Zimmermann & Kienast (1999). Furthermore, specific sites' ground temperature was measured hourly from October 2020 to mid-May 2021 with 2 Hobo probes buried at 5cm depth in each site (Hobo UA-001-64 Pendant, Onset Computer Corporation, MA, USA). The average monthly temperature and the average total temperature were calculated by averaging the temperature measurements of each month and all months, respectively. The winter period was estimated by summing the days with a mean ground temperature $\leq 1^{\circ}\text{C}$ (Baptist et al., 2010). Climate across the subalpine and alpine regions was visualized using a principal component analysis (PCA) (**Figure S3. 12**).

2.6 Statistical analyses

Statistical analyses were performed in R, version 4.1.1, using RStudio, version 1.4.1717 (Team, 2021). Graphical representations were done with the ggplot2 (Wickham et al., 2016), and the ggfortify packages (Tang et al., 2016).

Phytochemical diversity along elevation – To estimate the level of phytochemical variation across sites, roots, and shoots, we performed a three-way permutational analysis of variance (PERMANOVA) with the Hellinger-transformed chemical dataset as response variable, and with elevation, exposition, and organ as fixed factors, and with plant species, and regions as blocking factors (adonis2 function in the vegan package, (Oksanen, 2010). Data were then visualized using non-metric multidimensional scaling (NMDS) plots (metaMDS function from the vegan package. Both the PERMANOVA and the NMDS were estimated using Bray-Curtis distance matrices.

A total of 379 plant samples were analyzed using ultra-high-performance liquid chromatography-quadrupole time-of-flight mass spectrometry (UHPLC-QTOFMS) with an Acquity UPLC™ I-Class and Synapt XS system. Mass spectrometry was performed in negative electrospray ionization mode with data-dependent acquisition (DDA), and quality control samples were analyzed throughout the batch. Data analysis using MZmine involved feature detection, chromatogram deconvolution, and isotope peak grouping with specific parameters.

Feature annotation was performed with CSI and CANOPUS, focusing on (M+H)⁺ and (M+Na)⁺ ions and allowing for molecular formula computation with selected elements (for more details, see in the supplementary materials). We next visualized the dataset at the superclass level. For this, the initial annotation dataset was filtered for retaining only those compounds annotated to the superclass level with a probability score > 0.7, ultimately retrieving 57 superclasses of metabolites. We build heatmaps using the pheatmap package (Kolde & Kolde, 2015), for visualizing the hierarchical clustering of superclasses' relative abundance across sampling sites. We tested for the effect of elevation (alpine versus subalpine) on each of the 57 superclasses at the community level using linear models with elevation as fixed factor. We next focused on highly expressed superclasses and the effect of elevation on phenol-based compounds superclasses (hereafter named phenolics).

For this, we summed the intensity of all compounds present in the following superclasses: alkylresorcinols, coumarins, diarylheptanoids, flavonoids, isoflavonoids, lignans, phenolic acids (C6-C1), phenylethanoids (C6-C2), phenylpropanoids (C6-C3), and xanthones.

We then performed a two-way ANOVA to test for the interactive effect of elevation (alpine versus subalpine) and organ (roots versus shoots) on phenolics. For then dissecting the effect of elevation per se from the local climatic and edaphic factors driving variation of superclasses, we performed a fourth corner analysis with all climatic and edaphic variables and the superclasses which showed a significant variation across elevation.

The fourth-corner statistic (Dray & Legendre, 2008; Legendre et al., 1997) links the three tables of species abundances at each site sites, of environmental variables, and of trait values (superclasses' abundances in our case), for correlating environmental variables with community-weighted means of traits.

Litterbags decomposition experiment – We performed two mixed-model analyses of variance (ANOVA, lmer test in the lme4 package (Bates et al., 2015)) to assess the effect of origin (local versus foreign), elevation (alpine versus subalpine), exposition (north versus south), and their interactions on the degradation of leaf and root litters, separately (N = 144 for both leaves and roots). The two elevation transects situated in two regions of Switzerland were set as random factors in the model.

We tested the HFA advantage effect by calculating effect sizes between local versus foreign litter across the eight sites studied. We calculated effect sizes using Cohen's d statistics (cohens_d function in the effectsize package, (Ben-Shachar et al., 2021)). In our case, positive values indicate that the local litter degrades faster than the foreign litter, hence indicating a HFA advantage effect. To assess if phytochemistry from the subalpine versus the alpine levels shows different decomposition patterns, we fitted the k vectors on the NMDS chemical ordinations as described above, for roots and leaves separately (envfit function from the vegan package (Oksanen et al., 2013)). The significance of the fitted models was assessed using a permutation test with 999 permutations.

3. Results

3.1 Phytochemical diversity along elevation gradients

From the 49 selected species of the litterbag experiment, the chemical analysis pipeline retained 15'289 unique molecular features that were used to explore phytochemical diversity variation, with a maximum value of 9753 features in *Calamagrostis varia* and a minimum of 7744 features in *Adenostyles alliariae*. Overall, we found an effect of practically all main factors and their interactions on the entire phytochemistry of the different species of plants, except a non-significant effect of elevation by exposition (**Table 3.3**).

In order of importance, besides plant species themselves explaining the highest fraction of the phytochemical diversity, organ (roots versus shoots), and elevation (alpine versus subalpine), were the factors with the highest explanation score (**Figure 3. 14**, and **Table 3. 3**).

Table 3. 3 Three-way permutational analysis of variance (PERMANOVA) for measuring the effect of elevation, organs, and exposition on community-level phytochemical diversity. Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘’ 1.

	Df	SumOfSqs	R2	F	Pr(>F)	
Elevation (Ele)	1	2.605	0.04714	12.9847	0.001	***
Exposition (Exp)	1	0.647	0.0117	3.2238	0.001	***
Organ (O)	1	4.328	0.07832	21.5715	0.001	***
Region (R)	1	0.767	0.01387	3.8209	0.001	***
Species (S)	48	24.357	0.4408	2.5294	0.001	***
Ele x Exp	1	0.126	0.00228	0.6276	0.994	
Ele x O	1	1.077	0.0195	5.3699	0.001	***
Exp x O	1	0.37	0.0067	1.8458	0.006	**
Ele x Exp X O	1	0.316	0.00572	1.5755	0.026	*
Residual	103	20.663	0.37396			
Total	159	55.255	1			

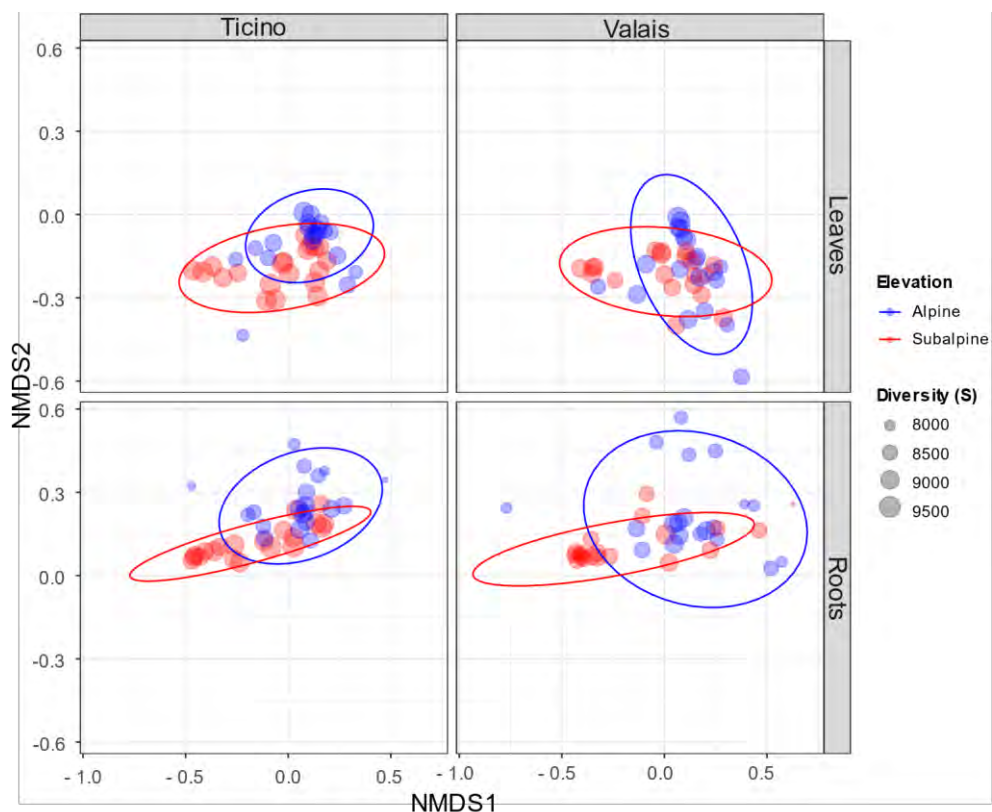


Figure 3.14 Chemical diversity of leaves and roots of alpine and subalpine plant communities. Shown is a non-metric multidimensional scaling (NMDS) ordination plot illustrating the chemical diversity of leaves and roots from the 10 most abundant species in Alpine and subalpine plant communities. Points are colored to differentiate plant material from subalpine (red) and alpine (blue) sites. The size of each dot represents the number of unique chemical features identified in the corresponding sample, with larger dots indicating a higher chemical diversity. This plot illustrates the variation in chemical profiles among plant samples collected from different elevations in the Alps.

3.2 Environmental effects at the superclass level

Overall, our findings reveal distinct differences in superclass diversity and abundance between leaves and roots of plants inhabiting alpine and subalpine environments. Notably, the abundance of metabolite superclasses in leaves (

Figure 3.15A) showed significant variation, with particularly pronounced differences between subalpine and alpine leaves in both the Ticino and Valais regions. Exposure also to influenced plants' metabolite abundance at low and high altitudes, where the highest variability in highly abundant metabolites was observed in the south-facing subalpine plants of Ticino.

Superclasses such as apocarotenoids, diterpenoids, eicosanoids, isoflavonoids, meroterpenoids, octadecanoids, sesquiterpenoids, sphingolipids, and triterpenoids were particularly prominent. In contrast, the Valais region showed a high abundance of different superclasses, including aminosugars and aminoglycosides, anthranilic acid alkaloids, histidine alkaloids, linear polyketides, lysine alkaloids, mycosporine derivatives, ornithine alkaloids, polyols, saccharides, and tryptophan alkaloids. Overall, the leaf metabolite profiles across both regions were more diverse at the subalpine level, especially in south-exposed plants, while other sites exhibited less diversity and metabolite abundance.

In the roots (

Figure 3. 15B), our results indicate a greater diversity and abundance of metabolites in Ticino, particularly in south-facing subalpine plants and north-facing subalpine plants in Valais.

Overall, the alpine sites in both Valais and Ticino exhibited much lower abundance and diversity than the subalpine sites. Notably, the south-facing alpine site in Valais showed a significant abundance of guanidine alkaloids. In contrast, the alpine site in Ticino had a significant abundance of polycyclic aromatic polyketides and serine alkaloids. Statistical analyses confirmed substantial variability in superclass abundance across these environments. ANOVA tests revealed statistically significant differences ($p < 0.05$) in superclass composition between sampling sites in alpine and subalpine environments for both leaves and roots (**Figure 3. 16**). Similarly, we found 57% more phenol-based compounds in the subalpine versus alpine (

Figure S3. 13, Table S3. 34), and overall, 2.3 times more in leaves than in roots (

Figure S3. 13, Table S3. 34), with no interaction between elevation and organs. These findings highlight the presence of distinct root metabolic profiles associated with altitude, which were mostly related to climatic conditions rather than to edaphic conditions, as shown by the fourth-corner analysis (**Figure S3. 14**). While we still found clear negative correlations with elevation (in turn positive with degree days and negative with humidity values), the only strong edaphic characteristics, mostly correlated with root chemistry, were all positively related to CEC (**Figure S3. 14**).

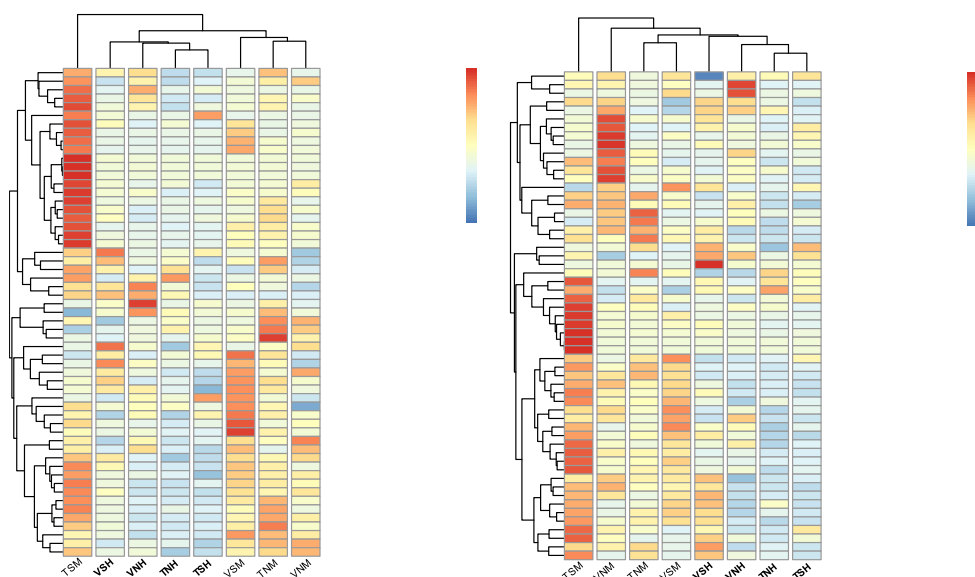


Figure 3. 15 Distribution of metabolite superclasses across sites by plant organ. Heatmap depicting the metabolomic superclasses of (A) leaves and (B) roots. Columns represent different sampling sites, with Alpine sites highlighted in bold and subalpine sites listed in regular font. Each row corresponds to a metabolomic superclass, and the color intensity within each cell indicates the relative abundance of chemicals. Darker colors represent higher relative abundance, while lighter colors indicate lower abundance. This heatmap visualizes the variation in metabolomic profiles across sampling sites.

3.3 Litterbags decomposition experiment

Overall, we found variability in how litter is decomposed across sites, organs, and elevations (**Figure 3. 16, Table 3. 4**). First, we observed that leaves degraded 2.9 times faster than roots, and that litter in Valais degraded 30% faster than litter in Ticino (**Figure 3. 16**). For leaves, we found an effect of elevation, with leaf material degrading 16% faster in the subalpine than in the alpine level (**Figure 3. 16A**). Yet, this effect was dependent on the origin of plant material (**Table 3. 4**). For roots, we found a significant three-way interaction ($p < 0.001$, **Table 3. 4**), and while root litter from the northern sites was degrading 28% times faster than on southern slopes, most effects were idiosyncratic across elevation and origin of litter (**Figure 3. 16B**).

Table 3.4 Mixed-model analysis of variance (ANOVA) table to assess the effect of origin (local versus foreign), elevation (alpine versus subalpine), exposition (north versus south), and their interactions on the degradation of leaf and root litters (N = 144 for both leaves and roots). The two elevation transects placed in two regions of Switzerland were set as random factors in the model. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Organ	Factor	Chisq	Df	Pr(>Chisq)
Roots	Origin (O)	0.0459	1	0.830
	Elevation (Ele)	0.6536	1	0.419
	Exposition (Exp)	20.3413	1	< 0.001 ***
	O x Ele	7.1249	1	0.008 **
	O x Exp	0.3176	1	0.573
	Ele x Exp	0.5421	1	0.461
	O x Ele x Exp	22.3038	1	< 0.001 ***
Leaves	Origin (O)	1.0491	1	0.306
	Elevation (Ele)	5.6312	1	0.018 *
	Exposition (Exp)	2.5131	1	0.113
	O x Ele	4.4093	1	0.036 *
	O x Exp	0.4619	1	0.497
	Ele x Exp	0.0429	1	0.836
	O x Ele x Exp	0.0363	1	0.849

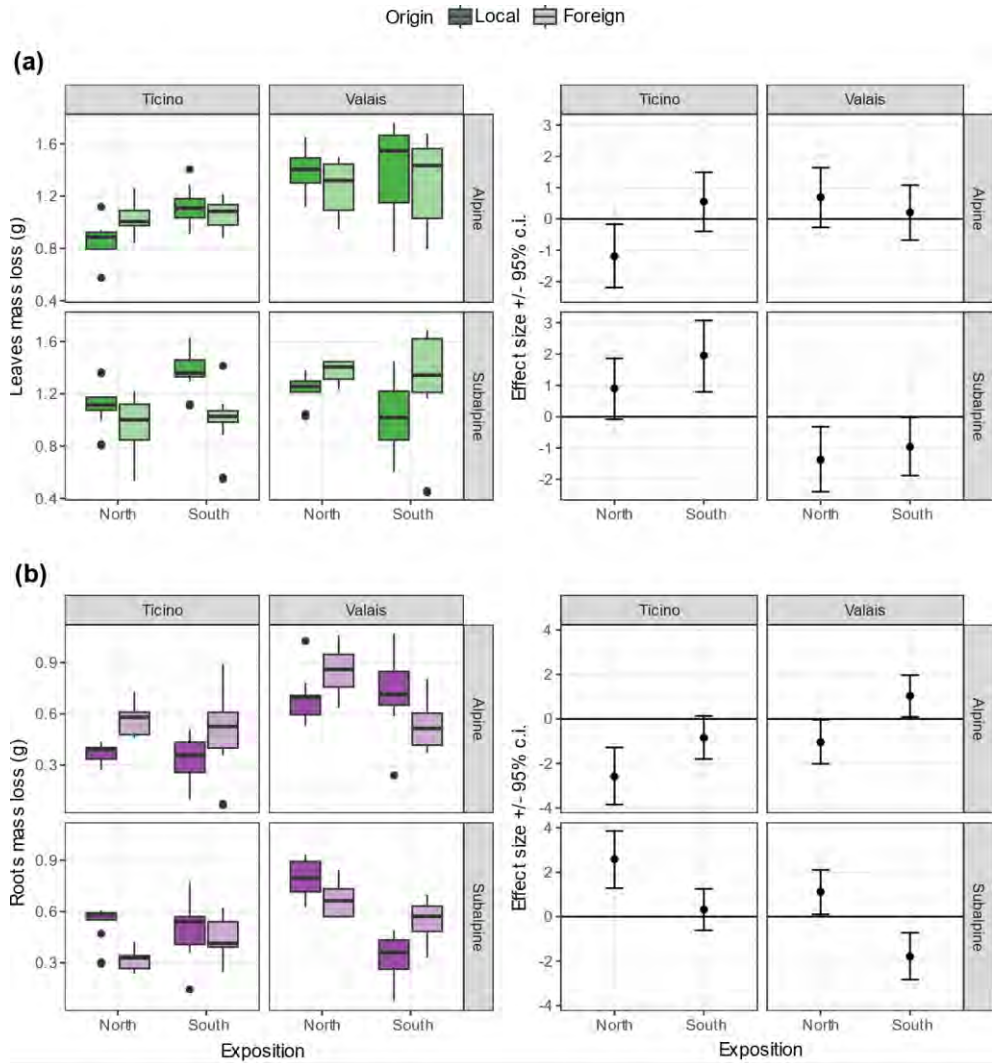


Figure 3.16 Decomposition of local and foreign leaves and roots litter. The boxplots on the left illustrate the median and range of mass loss (k values) for (A) leaves (green) and (B) roots (purple) of the 10 most abundant plant species in litterbags from two Alpine regions: The Cantons of Ticino and Valais. The experiment was conducted at two elevations (subalpine and alpine) and on two valley flanks (north- and south-facing). Within each mountain flank, material was reciprocally transferred between subalpine and alpine plant communities, creating local (dark colors) versus foreign (light colors) treatments within each elevation. The right panels display the mean effect sizes with 95% confidence intervals, comparing local versus foreign effects. Positive effect sizes indicate faster degradation of litter locally.

We found a weak indication of the HFA advantage effect (**Figure 3. 16**). In fact, we only observed two significant positive effects, one for leaf litter material placed on the south-facing (**Figure 3. 16A**), and one for the roots on the north-facing (**Figure 3. 16B**) subalpine sites of Ticino. Instead, we observed negative and no effects, distributed idiosyncratically across sites (**Figure 3. 16**).

Finally, when combining the chemistry of plants and the decomposition experiment (**Table S3. 33**) together in an ordination, we observed that for both leaves (**Figure 3. 17A**) and roots (**Figure 3. 17B**), k values were significantly associated with chemical variation, at the community level, between the alpine and the subalpine elevations.

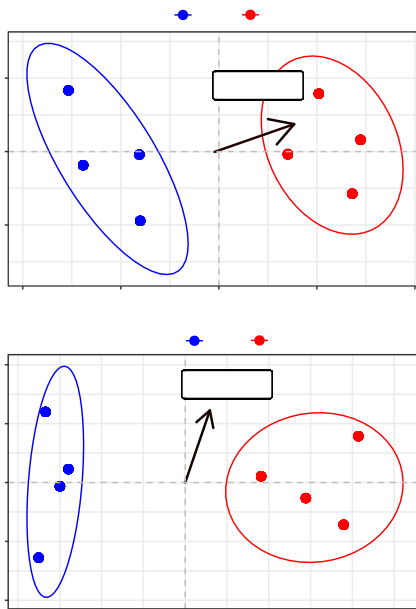


Figure 3. 17 Environmental fitting of decomposition on chemical composition. The NMDS ordination plots illustrate the compositional similarity of samples based on their chemical profiles: (A) for leaves and (B) for roots. Each point represents an individual sample, with proximity indicating higher chemical similarity. The arrows indicate correlations between chemical composition and decomposition stages, with direction pointing towards increasing decomposition, and length representing the strength of the correlation. Longer arrows denote stronger associations. Significant vectors ($p < 0.05$) highlight key relationships between decomposition stages (k_{ln}) and the chemical composition of leaves and roots. Colored ellipses for leaves and for roots show different elevation ranges, highlighting the influence of alpine elevation (blue) and subalpine elevation (red) on community composition.

4. Discussion

We used a reciprocal transplant experiment for measuring phytochemical effects on plant litter decomposition at different elevations. We found significant variation in the phytochemistry of leaves and roots phytochemical composition between elevations, which was reflected in a strong increase in phytochemical beta diversity when moving from the subalpine to the alpine environment. These changes in chemical profiles were associated with a general decrease in the production of several metabolite superclasses when transitioning from the subalpine level to the alpine level.

Moreover, we found strong variability in litter decomposition rates, which were unrelated to elevation, nor the home-advantage effects. Instead, decomposition rates were related to the phytochemical diversity of both roots and leaves across elevation.

4.1 Environmental influence on phytochemical profiles

The phytochemical profiles of plant species varied notably between subalpine and alpine environments. Such variation likely reflects on plants' adaptations to local climatic and edaphic conditions, as was shown for several species (Böhm, 2009; Calvo-Irabién et al., 2014; Karimi et al., 2020; Le Roux et al., 2017; Ouerghemmi et al., 2021)

or entire plant communities (Defosse et al., 2021). Environmental factors such as temperature, moisture, and soil composition, as well as plant-consumer interaction (Glassmire et al., 2016), are known to significantly influence PSM production in plants (Hunter, 2016; Richards et al., 2016; Zhang et al., 2024). For example, in our study, the elevated metabolite diversity in the subalpine regions could be attributed to more favorable growing conditions, as well as more intensity in biotic interaction (Fernandez-Conradi et al., 2022), which would support a wider range of chemical defenses and interactions, as was previously shown (Defosse et al., 2021). Additionally, exposure to sunlight on south-facing slopes could enhance the synthesis of certain secondary metabolites, further contributing to the observed differences between south- and north-facing slopes (Mishra et al., 2024). Interestingly, these effects were also true for phenol-based compounds, such as tannins phenolics acids, and flavonoids, which we could have predicted to increase with elevation.

This prediction arises from the observation that alpine plant communities tend to be mostly composed of slow-growing species, with conservative strategies, according to the leaf economics spectrum theory (Wright et al., 2004), to withstand harsher environmental conditions (Rasmann et al., 2014). Hence, alpine plants should invest in producing more carbon-based molecules, such as phenolics. We speculate that these effects were instead driven by major functional changes from the subalpine forested sites, where pine trees and other woody species dominate, to the alpine grasslands, where grasses dominate the sites (**Table S3. 32**, and **Table S3. 33**).

Accordingly, major ecosystems shift along the treeline ecotone impose major phytochemical reshuffling at the entire plant community levels. By utilizing a fourth-corner analysis we could highlight that this phytochemical variation was more associated with climatic than to edaphic variable. Moreover, we found a significant association between the climatic and the soil matrices across all sites, coinertia test; $r = 0.25$, $p = 0.014$) (Aqeel et al., 2024). Therefore, disentangling the relative role of different ecological factors driving phytochemical beta diversity along elevation gradients would require studying selection and evolutionary processes using experimental manipulations (Nomoto et al., 2024; Wetzel & Whitehead, 2020). Nonetheless, our study provides evidence for the role the environment plays in the diversity of plant specialized metabolites (PSMs), in turn influencing decomposition processes across elevation gradients.

4.2 Phytochemical diversity and decomposition dynamics

We observed that phytochemical variation between subalpine and alpine sites is linked to litter decomposition rates and, consequently, nutrient cycling and ecosystem functioning. Previous research has highlighted that PSMs, including alkaloids, phenolics, and terpenes, can either enhance or inhibit microbial activity and enzyme functions involved in decomposition (Chomel, Guittonny-Larchevêque, et al., 2016; Goga et al., 2018). For instance, certain phenolic compounds can bind to proteins, making them resistant to microbial degradation and thus slowing down the decomposition process (Hättenschwiler & Vitousek, 2000). Yet, other factors intervene in the process of litter degradation.

For instance, we observed that leaf litter decomposed faster than root litter, consistent with previous studies (e.g., Talbot & Treseder, 2012), potentially due to the higher nitrogen and lower lignin content in leaves (indeed we measured a total C to total N ratio for leaves = 32.9, and for roots = 45.2).

Moreover, the faster decomposition rates observed in Valais compared to Ticino could be attributed to regional climatic differences, such as temperature and precipitation patterns, which influence microbial activity and litter breakdown (Austin et al., 2014; Couëteaux et al., 1995). This recalcitrance can hinder microbial activity, leading to slower decomposition rates, as supported by our findings and previous research (Ayres, Steltzer, Simmons, et al., 2009). Moreover, the chemical composition of litter, particularly the presence of PSMs that inhibit microbial enzymes, can further slowdown decomposition in these environments (Moore et al., 2005).

4.3 Home-Field Advantage (HFA) Effect

The concept of HFA, where litter decomposes faster in its native environment, was weakly supported in our study. We observed significant positive effects only in specific sites, suggesting that local adaptation of microbial communities to the native litter may not always result in a measurable HFA effect. This idiosyncratic pattern could be due to various factors, including the specific chemical composition of the litter and the adaptability of the local decomposer communities (Griffiths & Philippot, 2013; Wardle, 2006). The lack of a consistent HFA effect across sites may also indicate that other factors, such as the chemical complexity of PSMs and the specific interactions between plant-derived compounds and microbial enzymes, play a more critical role in determining decomposition rates. For example, Veen et al., observed that litter with high concentrations of certain phenolics or terpenoids might inhibit decomposer activity even if the microbial community is well adapted to the local environment (G. F. Veen et al., 2015; Geertje F. Veen et al., 2015). This complexity highlights the need for further research to disentangle the mechanisms driving decomposition in different environmental contexts.

4.4 Implications for ecosystem functioning

Understanding the role of PSMs in litter decomposition is crucial for predicting how environmental changes, such as climate change, will impact ecosystem processes. The differential decomposition rates and phytochemical profiles along elevation gradients provide insights into how nutrient cycling and soil fertility may shift with changing climatic conditions (Liu et al., 2024; Xiong et al., 2023). Our findings emphasize the importance of considering both biotic and abiotic factors in ecological studies to develop comprehensive models of ecosystem dynamics.

In conclusion, our study sheds light on the intricate relationships between plant chemistry, environment, and decomposition processes. By elucidating the role of PSMs in these interactions, we contribute to a deeper understanding of ecosystem functioning and resilience, particularly in mountainous regions experiencing rapid environmental changes (Chan et al., 2024). Future research should focus on exploring these dynamics across broader spatial and temporal scales to inform conservation and management strategies aimed at preserving ecosystem health and stability. Additionally, understanding the potential feedback mechanisms between plant chemistry, environmental conditions, and microbial adaptation will be essential for predicting long-term soil organic matter responses to global environmental change.

5. Acknowledgments

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6. Competing interests

The authors declare no competing interest.

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Thematic 4: Soil diversity and community composition

Soil arthropods along elevation gradients: biological and functional diversity linked to soil quality

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Abstract

Soil microarthropods, primarily detritivores, play a pivotal role in organic matter degradation and nutrient cycling but are frequently underutilized to establish soil quality along elevation gradients (i.e. from deciduous forest, through thorn forest to alpine meadows). This study employs the QBS-Ar index (Biological Quality of Soil) to evaluate diverse ecological indices of soil microarthropods and proposes an application of the QBS method to assess the biological quality of soils along an altitude gradient and north and south facing transects. Traditional soil quality assessments often rely on abiotic indicators such as bulk density, aggregate stability, and chemical metrics particularly in the agricultural context which, while being useful, provide a limited perspective on soil quality in a more natural context. To gain a more comprehensive understanding of soil biodiversity, particularly in the context of global climate change, the need of incorporating biological monitoring is crucial. Here, we examine how soil microarthropod communities vary along climatic gradients in the Swiss Alps experiencing significant shifts towards warmer, drier conditions. Our findings reveal that climatic factors, particularly degree days and humidity, significantly influence soil microarthropods community's composition, with a high proportion and abundance of Acari individuals across habitats. By applying the QBS-Ar method to natural soil along an altitude gradient to determine soil quality using the threshold value of 100, soil quality was found to be generally poor except for north-exposed mountain forests. Overall, the study confirmed the potential of soil microarthropods as valuable biological indicators of soil quality in natural environments but highlighted but it also highlights the problem of threshold values, which are taken as reference values to determine whether the soil is of good or poor quality. We propose new perspectives for the creation of a new reference soil value applicable to natural environments. Understanding the dynamics of soil microarthropod communities in response to climate change is essential for developing effective soil management strategies and improving soil health assessments in a natural context.

1. Introduction

Traditional methods for evaluating soil quality and productivity often focus on abiotic indicators such as bulk density, aggregate stability, organic matter content, and various other physico-chemical parameters. While these metrics provide important insights into soil structure and nutrient content, they offer a somewhat limited perspective on overall soil health. To gain a more comprehensive understanding of soil degradation and potential risks, incorporating biological monitoring is essential (Layke et al., 2012; Parisi et al., 2005; Rosenberg et al., 2023). Biological indicators, which reflect the living components of soil, such as microorganisms and invertebrates, are crucial as they play a significant role in soil processes. For instance, the presence and activity of soil microflora and microfauna are recognized as key indicators of soil quality due to their contributions to nutrient cycling, organic matter decomposition, and overall soil functionality (García-Palacios et al., 2016; Velasquez & Lavelle, 2019). However, utilizing biological indicators can be complex due to several factors. First, the diversity and abundance of soil organisms can vary widely across different soil types and environmental conditions, making it challenging to establish universal benchmarks for soil quality (Anthony et al., 2023; Philippot et al., 2024). Second, the interactions between various soil organisms and their responses to changes in soil management practices can be intricate and not always straightforward to interpret. Moreover, biological indicators often require specialized and time-consuming methodologies for assessment, such as soil microbial community analysis or invertebrate population surveys (Davidson et al., 2024). These complexities can make it difficult to standardize biological monitoring practices and integrate them effectively with traditional soil evaluation methods.

In response to these challenges, researchers have increasingly focused on alternative, biodiversity-based, more practical indicators, such as by studying soil arthropods. This group of soil organisms, mostly including mites and springtails, is now acknowledged for its significant roles in influencing soil properties. Soil arthropods contribute to soil health by affecting soil structure, aggregation, and fertility.

They facilitate decomposition processes and nutrient cycling by breaking down plant and animal debris, which sustains the complex food webs of soil ecosystems (Petersen & Luxton, 1982).

Additionally, the activity of soil arthropods has been shown to enhance soil porosity, water retention, and root penetration, thereby preventing surface crust formation and erosion, and facilitating soil fertility (Culliney, 2013).

Moreover, given that soil arthropods represent a substantial portion of the soil fauna, especially within the meso- and macrofauna categories, and the fact that they are relatively easy to capture compared to larger soil organisms (Van Straalen, 2004; van Straalen et al., 1988), soil arthropods represent valuable candidates for assessing soil quality alongside traditional microflora and microfauna metrics. Soil organic carbon (SOC) plays a crucial role in sustaining soil arthropod populations by providing essential food sources, creating favorable habitats, and enhancing soil structure and health. Consequently, reductions in SOC can lead to diminished arthropod populations and reduced community diversity, reflecting a decline in overall soil quality.

Studying the interaction between soil fauna and soil quality has been often advocated via the assessment of the presence and abundance of key taxa (Cluzeau et al., 2012; Menta & Remelli, 2020; Rousseau et al., 2013). Yet, studying the abundance, or the functional role of individual species can represent a somewhat limited approach, as studies using single species are often prone to high levels of context dependency (Mauro et al., 2022), and might not reflect indirect effects mediated by community changes (Tobisch et al., 2023). Moreover, evaluating a single taxon can offer insights into specific aspects of ecosystem health but may not fully address questions related to organic matter renewal and plant nutrient availability (Venturo et al., 2024). Hence, comprehensive assessments of entire soil arthropod communities, and understanding their ecological functions are crucial, as indicated by a surge of research in this domain (Doelman & Eijsackers, 2004; Madej et al., 2011; Paoletti et al., 1996; Ritz et al., 2009; Van Straalen, 2004). One such endeavor is represented by the “Biological Quality of Soil” (QBS-Ar) index (Parisi et al., 2005).

The QBS-Ar index focuses on the concept of morphospecies richness and the adaptations of arthropods to soil life, thereby indicating biodiversity and vulnerability while simplifying the assessment process by avoiding the need to perform detailed taxonomic identification of all taxa sampled.

Accordingly, in addition to taxonomic assessments, evaluating the functional traits of soil arthropods can yield deeper insights into their roles within the soil ecosystem.

Functional traits—such as morphology, feeding habits, life history, physiology, and behavior—affect how species interact with their environment and contribute to ecological processes (De Bello et al., 2010). A functional approach helps explain changes in community structure and their impact on ecosystem functions (Farská et al., 2013; Makkonen et al., 2011; Zhou et al., 2020).

However, categorizing traits and understanding their implications can be complex, particularly given soil arthropods' behavioral responses and movement patterns to environmental changes (Moretti et al., 2017). Instead, the QBS-ar methodology, which is based on a life-form approach, obviates the need to calculate either the quantity or quality of microarthropod communities in soils and is thus practical to implement, even for non-taxonomic experts, while retaining the functional narrative of soil arthropods (Galli, 2020).

To date, most research using the QBS-Ar index focused on describing soil quality within an applied context, such as in agricultural fields (Elmqvist et al., 2023; Kurniawan et al., 2023; Reilly et al., 2023), natural parks (Fusco et al., 2023), or in urban soils (Tóth et al., 2023), leaving open the question of whether the QBS-Ar index could be used, alongside classic biodiversity measures of soil arthropods community changes, to assess soil quality along large-scale ecological gradients. To fill this gap, we here compared several diversity metrics of a wide range of arthropod taxa using functional traits such as trophic diet, hunting guild, and body size. Specifically, we investigated how arthropod communities vary along steep elevation gradients of the Swiss Alps, and whether these variations in community assemblages correlate with soil quality.

By using the QBS-Ar index to assess functional diversity across three elevations, we hypothesized higher elevation sites to exhibit lower arthropod biodiversity and functional diversity, reflected by lower QBS-Ar values and potentially reduced soil organic carbon content. With this work, we thus explore the potential of utilizing “easy-to-use” methods for assessing soil health in natural ecosystems spread along ecological gradients.

2. Materials and methods

2.1. Study area and design

To investigate the relative importance of arthropods' functional trait diversity on soil quality and organic matter decomposition, we sampled soil arthropods in the Swiss Alps during summer 2022, by following a north-south-facing slope model including two transects situated along an elevation gradient to include variation in both abiotic and biotic factors (

Figure S4. 1). On each transect, three sites were chosen: at the alpine (~2000 m a.s.l), subalpine (~1500 m a.s.l), and mountain (~1000 m a.s.l) level. Mountain sites were under deciduous mixed forests and shifted, while the subalpine sites were characterized by conifer-dominated mixed forests. Instead, alpine sites, above the tree line, were characterized by alpine grasslands.

At each site, we sampled three replicated plots, and each plot within a given site was separated from another by at least 100 m to avoid a maximum of spatial autocorrelation. Soil arthropods were sampled from soil cores, which were collected in each plot according to a 3-point dice representation, with 1 core in the upper and lower corner of the plot and one in the center. Plot size varied from 20 x 20 m plots in forests to 5 m x 5 m in pastures. To provide a more comprehensive representation of arthropod communities and mitigate the effects of drought soil cores were collected twice, in May and October 2022 for mountain and subalpine sites and in July and September 2022 for alpine sites. The temporal difference accounts for persistent snow at high altitudes, especially on north-facing slopes with less annual sunshine, resulting in more extreme ground surface temperature. In total we sampled; $N = 2 \text{ expositions} \times 3 \text{ elevations} \times 3 \text{ plots} \times 3 \text{ soil cores} \times 2 \text{ collection time} = 108 \text{ samples}$.

2.2. Climate

To describe sites climatically, in addition to elevation, we extracted degree-days with 3°C threshold limits), humidity (monthly moisture index), radiation (daily average of global potential shortwave radiation per month), precipitation days (number of precipitation days per growing season), annual average from 1961 to 1990. Values for degree-days, precipitation, and moisture, and humidity were calculated from meteorological stations using a Digital Elevation Model (DEM) at 100 m resolution and interpolated following (Zimmermann & Kienast) (1999). We estimated solar radiation values using the tool implemented in ArcGIS 10.

2.4. Arthropod sampling and extraction

We used a soil core extractor made from a PVC tube (15 cm high, 10 cm diameter) to calibrate the soil quantity collected for each soil core. Each soil core extractor was filled to the cylinder's maximum capacity, although soil thickness varied in some disturbed sites, resulting in the arthropod smaller samples. Immediately after collection, all soil cores were wrapped in aluminium foil, stored in a cool box for a maximum of three days, before proceeding with the extraction. Specifically, soil arthropods were extracted with a MacFadyen extractor (MacFadyen, High-Gradient-Extractor, EcoTech Umwelt-Messsysteme GmbH, Bonn, Germany). The MacFadyen device heats the soil samples from above with hot air while slightly cooling and humidifying them from below with fresh, moist air. As the soil cores dries on top, the microarthropods migrate toward the cooler zone until they fall into the collection containers beneath the extractor (Macfadyen, 1961).

Each soil core was left five days in the MacFadyen extractor, with temperatures gradually increasing from 25°C on the first day to 60°C on the final day, with a 7°C temperature increase per day. Arthropods migrating from the samples were collected in a screw-top jar containing 70% ethanol, which preserved the membranous structures of the microarthropods and ensured long-term preservation of the samples. After extraction, all individuals were identified under a Leica-2035 binocular magnifying glass (**Table S4. 1**). The identification process was conducted at the order or class level to facilitate a broader understanding of community structure and dynamics following the Nowak identification key (Nowak, 2014).

2.5 The QBS-Ar Index

We assigned an Ecological Morphological Index (EMI) to all arthropod individuals to quantify their level of adaptation to soil environments, following the methodology of Parisi et al. (2005). EMI values range from 1 to 20, where 1 indicates no adaptation to soil and 20 represents perfect soil adaptation. Arthropod groups exhibiting a diversity of morphotypes or feeding habits received EMI values within ranges such as 1 to 5, 1 to 20, or 10 to 20, depending on their degree of adaptation. Specifically, edaphic forms were given an EMI score of 20, hemi-edaphic forms received EMI values between 5 and 15 based on their soil adaptation level, and epigeous forms were assigned an EMI value of 1.

The QBS-Ar index, calculated as the sum of all EMI values, enables the comparison of soil adaptation levels among different microarthropod communities. This index enhances our understanding of the ecological roles these communities play within soil environments.

2.3. Statistical analysis

All statistical analyses were conducted using R version 4.1.1 (Team, 2020).

We assessed the multivariate climatic niche of each site by performing a Principal Component Analysis (PCA) on all climatic variables collected. The PCA was performed with the *ade4* package (Dray & Dufour, 2007). We next correlated the entire arthropod matrix with the climate matrix using a coinertia analysis (*coin* function in the *vegan* package (Oksanen, 2010)).

For soil microarthropod data, we first assessed the effect of elevation (fixed factor, three levels; mountain, subalpine, alpine) on the entire arthropod matrix using a permutational analysis of variance (PERMANOVA; *adonis2* function in *vegan*) and visualized the ordination using non-metric multidimensional scaling (*metaMDS* in *vegan*). For both the PERMANOVA and the nMDS, a distance matrix based on Bray-Curtis dissimilarity was calculated.

Next, we calculated several ecological indices from both abundance and presence-absence data, including (morpho)species richness (S), Shannon's diversity index (H), and Piélou's evenness index (J).

Species richness was computed using the *specnumber* function from the *vegan* package, while Shannon's diversity index was derived with the *diversity* function. Pielou's evenness index was calculated by dividing H by the $\log$ of S . To avoid biases in Shannon's index from rare species, we excluded taxa with fewer than 20 individuals, specifically Coleoptera, Psocoptera, Hymenoptera, and Isopoda. The effect of elevation on the three diversity indices and the QBS-Ar index was calculated using an analysis of variance (ANOVA). Finally, we performed an analysis of covariance (ANCOVA), with the QBS-Ar index as response variable and the C:N as explanatory variable, and elevation (mountain, subalpine, and alpine) as fixed factor.

3. Results

3.1 Climate

The coinertia analysis, illustrated in **Figure 4. 1**, investigates the relationship between climatic variables and arthropod diversity using two datasets: climatic factors (radiation, elevation, degree days, humidity, precipitation, and frost days) and arthropod diversity groups (e.g., Acari, Araneae, Chilopoda). This analysis produced two canonical dimensions that effectively summarize the associations between these datasets. The Monte-Carlo test was highly significant ($p < 0.001$), showing the robustness of the observed relationships and confirming that the association between climatic conditions and arthropod diversity is statistically significant. **Figure 4. 1A** displays the climatic canonical weights, revealed that radiation and degree days strongly influence the first canonical axis. **Figure 4. 1B** shows the arthropod canonical weights, illustrating how various arthropod groups align with these climatic variables.

Specifically, Araneae, Psocoptera, and Coleoptera were associated with colder, more humid environments, while Chilopoda, Isopoda, Collembola, Pauropoda, and other holometabolous adults were linked to warmer, drier conditions. Other arthropod groups exhibit a distribution ranging from cold, humid to warm, dry environments, typical of mid and low elevations.

Furthermore, principal component analysis (PCA) of climatic variables (**Figure 4. 1A**) identified radiation and degree days as major contributors to the first canonical axis.

This axis differentiates climatic conditions with high temperatures and low moisture, aligning Chilopoda and Collembola with hotter, drier environments, and Araneae, Psocoptera, and Coleoptera with warmer, more humid conditions. These findings highlight the significant associations captured by the coinertia analysis and reinforce the relationship between climatic variables and arthropod diversity.

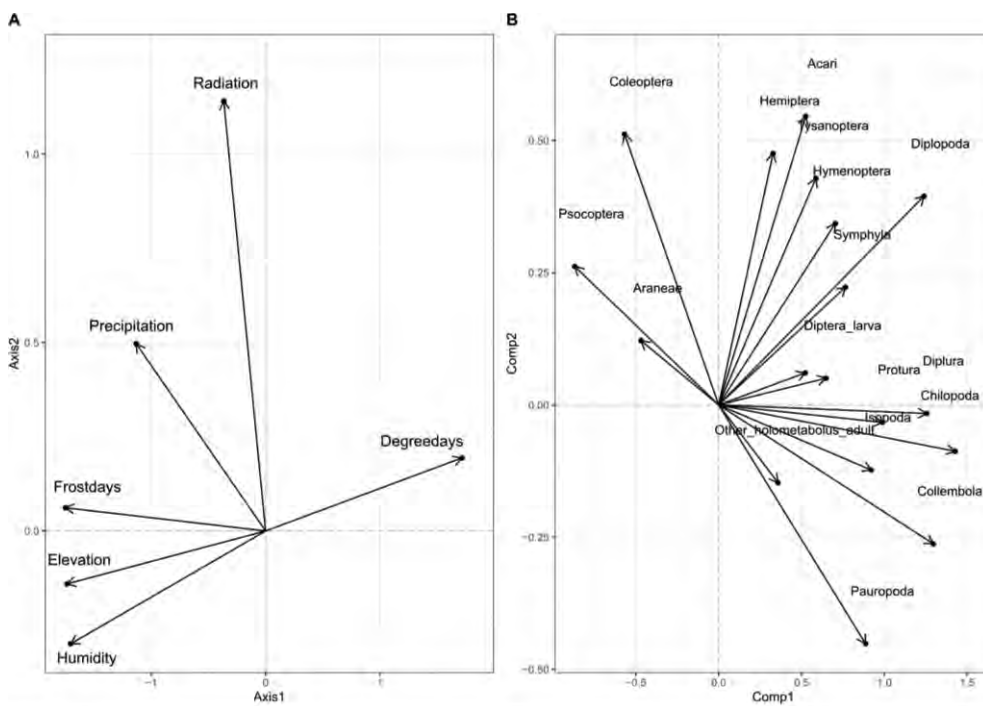


Figure 4.1 Site-specific climatic niche. The co-inertia analysis shows the association between climatic conditions and arthropod diversity. The ten site-specific climatic properties are: average number of degree-days per year (degree days), annual mean solar radiation (radiation), annual mean precipitation (precipitation), relative evapotranspiration (humidity), the elevation of each site (elevation), and the number of frost ($<0^{\circ}\text{C}$) days during the year (frost days).

3.2 Arthropods

Among the 23,076 arthropod individuals sampled (**Figure 4. 2**), Acari emerged as the most dominant group, constituting over 70% of the total population.

Collembola followed, making up more than 20%, while Hemiptera accounted for approximately 3.5%. These findings underscore the predominance of Acari within the arthropod community (**Figure S4. 1**).

The distribution of Acari varied significantly across different environments. Specifically, the lowest proportions of Acari were recorded in north-exposed subalpine forest sites, ranging from 39% to 54%, while the highest proportions were found in north-exposed alpine grasslands, ranging from 65% to 88%. Conversely, the abundance of Collembola showed an inverse relationship with Acari abundance. Collembola were more prevalent in plots where Acari constituted less than 50% of the total arthropod population.



Figure 4.2 Arthropod community composition. Images of soil microarthropods found in this study. (A) Aranea, (B) Tysanoptera, (C) Symphyla, (D) Chilopoda, (E) Protura, (F) Diplopoda, (G) Pauropoda, (H) Acari, (I) Collembola, (J) Hemiptera, (K) Other holometabolous larvae, (L) Other holometabolous adults, (M) Diptera larvae, (N) Psocoptera, (O) Diplura, (P) Coleoptera, (Q) Isopoda, and Heteroptera. The white arrow shows the individual illustrated when several individuals are present in the image. All images were obtained with a Leica-2035 binocular magnifying glass by (© N.Rytz).

The NMDS ordination (**Figure 4.3**) effectively represents the data in a two-dimensional space, indicating a robust ordination. The PERMANOVA analysis

revealed significant effects of elevation ($F = 5.417$, $p = 0.003$) and the interaction between elevation and exposition ($F = 5.950$, $p = 0.004$) on the composition of arthropod communities. In contrast, exposition alone did not significantly affect community composition ($F = 2.185$, $p = 0.113$). These findings highlight the importance of elevation and its interaction with exposition in shaping soil arthropod community structures. Further insights were gained from distance-based redundancy analysis (dbRDA), which explored the relationships between community data and environmental variables.

The dbRDA confirmed that elevation has a significant impact on community structure ($F = 4.558$, $p = 0.006$), while exposition alone had a marginal effect ($F = 2.143$, $p = 0.091$). The interaction term between elevation and exposition was also significant ($F = 4.981$, $p = 0.001$), underscoring the intricate interactions between these environmental factors. Overall, the combination of NMDS and dbRDA analyses, reinforced by PERMANOVA, provided a thorough understanding of how elevation and its interaction with exposition influence the diversity and composition of soil arthropod communities.

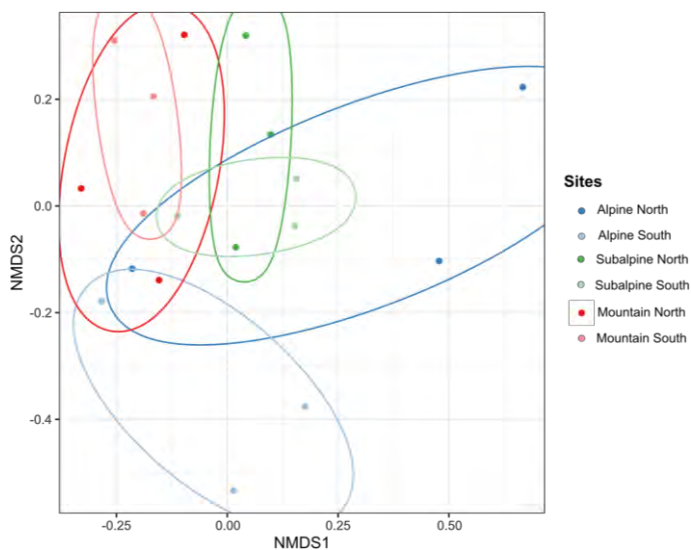


Figure 4. 3 NMDS of soil arthropod communities. The NMDS ordination plots illustrate the compositional dissimilarity of arthropods communities according to site elevation and exposure. Each point represents an individual sample, with proximity indicating higher chemical similarity. Colored ellipses show different elevation ranges: mountain north-exposed sites (red), mountain south-exposed

sites (light red), subalpine north-exposed sites (green), subalpine south-exposed sites (light green), alpine north-exposed sites (blue), alpine south-exposed sites (light blue), on community composition.

Overall, our findings provide a comprehensive view of how elevation affects different aspects of species diversity and soil quality. **Figure 4. 4** and **Figure S4. 2** illustrate the impact of elevation on various metrics of species diversity and abundance. **Figure 4. 4A** indicates that species diversity (H) remains relatively stable across different elevations, as there is no significant variation detected ($F = 2.829$, $p = 0.091$). Conversely, **Figure 4. 4B** shows that species richness (S) is significantly influenced by elevation ($F = 5.244$, $p = 0.019$), highlighting substantial changes in species count with varying elevation levels. **Figure 4. 4C** reveals that species abundance (J) does not show a significant relationship with elevation ($F = 1.13$, $p = 0.349$), suggesting consistent levels of species abundance across elevations. Finally, **Figure 4. 4D** demonstrates a significant variation in the QBS-Ar index with elevation ($F = 9.652$, $p = 0.002$), indicating notable shifts in soil quality in relation to different elevation levels.

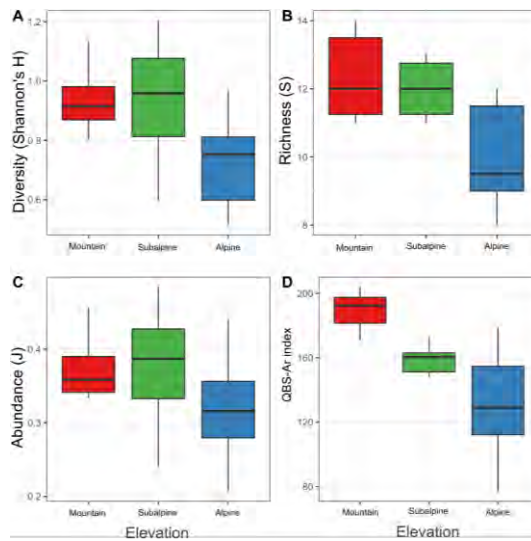


Figure 4. 4 Arthropod ecological indices. Boxplots represent the arthropod diversity (A), richness (B), abundance (C), and the QBS-Ar index (D) for each site elevation. The colors show the environmental groups, with mountain forest (red), subalpine forest sites (green), and alpine grassland sites (blue).

Additionally, the scatter plot of the QBS-Ar index against the first coinertia axis reveals a positive relationship, as illustrated in **Figure 4. 5**. A linear regression

analysis further supports this finding, with the analysis yielding a significant result ($p < 0.05$).

This model accounts for approximately 48% of the variance in the coinertia scores, highlighting a significant association between the QBS-Ar index and the environmental variables represented by the coinertia analysis.

Specifically, the results suggest that as elevation increases and conditions become colder and more humid, the QBS-Ar index tends to decrease. This implies that the QBS-Ar index is implicitly linked to the environmental gradients captured by the coinertia analysis, reflecting how arthropod diversity changes with varying environmental conditions.

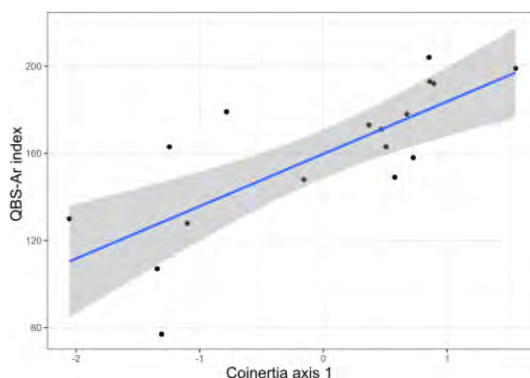


Figure 4.5 Scatter plot illustrating the relationship between the QBS index and the first coinertia axis.

The plot reveals a positive correlation between the QBS index and the coinertia scores, supported by a linear regression analysis ($p < 0.05$).

4. Discussion

Understanding the interactions between soil biota and soil processes is essential for comprehending ecosystem functioning and quality. Soil arthropods, through their functional traits and community composition, significantly influence decomposition and nutrient cycling. Given their role in affecting soil properties and nutrient availability, variations in arthropod diversity and abundance can be closely linked to changes in the carbon-to-nitrogen ratio in the soil. This correlation emphasizes the importance of soil arthropods in maintaining soil quality and ecosystem stability.

4.1 Environmental effects on soil microarthropods

Our sampling revealed that certain arthropod groups, such as isopods, beetles, psocopters, and hymenoptera (especially ants), were underrepresented. This underrepresentation is likely due to their high mobility and the constraints of our sampling methods (Dauber et al., 2005).

Additionally, low humidity and elevated temperatures may have driven some arthropods deeper into the soil in search of more favorable conditions (SØMme, 1989; Tsiafouli et al., 2005; Villani et al., 1999). Consistent with previous studies (Barnett & Johnson, 2013; Franken et al., 2018), our findings indicate that climatic variables exert a stronger influence on arthropod diversity than temperature alone. We observed a reduction in arthropod richness towards the end of the growing season at sites affected by elevated temperatures and altered precipitation patterns (**Figure S4.3**), aligning with Fernandez-Conradi et al. (2022) and (Gebert et al. (2024).

Predation also played a role, with sites containing spiders showing reduced numbers of Diptera, Holometabola larvae, and adult Diptera. Furthermore, higher arthropod abundance and species richness were found in mountain and subalpine sites compared to alpine sites, supporting the notion that structural heterogeneity within forest ecosystems promotes biodiversity across arthropod taxa (Harmon et al., 1986; Sulkava & Huhta, 1998). However, climatic conditions significantly shape microarthropod abundance and diversity, as reflected in the QBS-Ar index values. Alpine grassland sites, characterized by harsher temperature fluctuations and lower precipitation, exhibited reduced arthropod diversity and lower QBS-Ar values compared to forest sites. Cold temperatures and dry conditions appear to limit arthropod survival and diversity, potentially slowing decomposition and nutrient cycling. The short growing season in alpine sites may further restrict biological activity, impacting the QBS-Ar index. In contrast, mountain and subalpine forest sites benefit from more moderate temperatures, consistent precipitation, and richer organic matter due to dense vegetation, fostering a more abundant and diverse arthropod community and resulting in higher QBS-Ar values. Thus, while the QBS-Ar index offers insights into

soil quality and ecosystem functionality, it is important to interpret the results within the context of the study's design and environmental conditions.

When assessing QBS-Ar values at the site level, the indices often fall below the threshold of 100, suggesting good soil quality (**Table S4. 3**). However, analyzing each plot independently reveals variability, with only one plot falling below the threshold. This highlights the importance of contextualizing QBS-Ar results, particularly in natural environments with minimal human impact. Proper experimental design can still yield meaningful conclusions despite these variations.

4.2 Functional role of arthropods

Arthropod communities are integral to terrestrial ecosystems, playing essential roles in nutrient cycling, soil structure, and overall ecosystem functioning (Coleman et al., 2024; Siepel, 1994). Different arthropod groups fulfill specific ecological functions: predators such as spiders (Araneae), predatory mites (Acari), centipedes (Chilopoda), and predatory beetles (Coleoptera) help regulate other soil organisms, maintaining ecological balance. Decomposers, including millipedes (Diplopoda), Symphyla, Protura, Pauropoda, springtails (Collembola), and Diptera larvae, break down organic matter, recycling nutrients and supporting soil fertility.

Herbivores and fungivores, such as thrips (Tysanoptera), Hemiptera, booklice and barklice (Psocoptera), Diplura, and woodlice (Isopoda), contribute to decomposition and nutrient cycling by feeding on plants, fungi, and decaying matter. Omnivores, including various holometabolous larvae and adults, perform multiple ecological functions. Sap-sucking pests like Hemiptera and Heteroptera influence plant-soil interactions by extracting plant sap. These complex interactions sustain soil quality and productivity. Despite some groups being underrepresented due to sampling limitations and environmental factors, our study highlights their critical roles in maintaining soil structure and ecological balance. For instance, centipedes and spiders significantly regulate arthropod communities, although their effects can be complex. Seasonal variations in arthropod abundance reveal dynamic shifts across exposure and elevation gradients, potentially affecting community structure and function (Botham et al., 2020; Koltz et al., 2018).

Mite populations, remaining stable despite drought conditions, demonstrate adaptability to environmental changes (Xu et al., 2012). Our findings also underscore the importance of effective forest management practices, such as preserving dead wood, which enhances decomposer communities and enriches soil nutrients critical for plant colonization (Tomao et al., 2020).

The lower QBS-Ar index values in alpine grasslands compared to mountain and subalpine forests reflect differences in community composition, with more diverse functional groups (i.e., predators, decomposers, herbivores, and omnivores) in forest sites.

However, these results must be interpreted within the context of the different ecosystems studied—forests versus grasslands—to fully understand their functional dynamics. The combination of litter inputs and environmental pressures affects the soil matrix, arthropod functional groups, and soil quality, with QBS-Ar values indicating ecosystem functionality and potential impacts on soil organic matter decomposition and nutrient cycling. Higher QBS-Ar values in subalpine and mountain forest sites highlight the benefits of forest conditions and management practices for supporting diverse and healthy soil arthropod communities. Overall, arthropods are crucial for soil food webs, serving as primary food sources for higher trophic-level organisms and contributing to ecosystem stability, resilience, and productivity. Their abundance and diversity are essential for maintaining ecological balance.

4.3 Soil Quality Assessment

Arthropod community activities—such as feeding, excretion, and movement—play a significant role in the breakdown and transformation of organic matter (David, 2014; Soong & Nielsen, 2016). Predatory arthropods, including spiders and beetles, help regulate microbial populations by preying on microbes and other soil organisms, preventing dominance by any single microbial group and promoting balanced decomposition (Bernardin et al., 2024; Heinen et al., 2024). Decomposers like millipedes and springtails fragment organic matter, enhancing microbial access and accelerating decomposition. Their activities influence microbial respiration rates, leading to CO₂ release.

Herbivores and fungivores, which feed on plant material and fungi, further integrate organic matter into the soil, facilitating nutrient recycling and carbon flow (Gloria et al., 2024; Maboreke et al., 2017; Sanders et al., 2024). This continuous flow supports essential soil functions, with microarthropod communities contributing to soil structure, nutrient cycling, and carbon dynamics. The diversity and abundance of arthropods are crucial for modulating soil biota and maintaining soil quality. Indicators such as the carbon-to-nitrogen (C:N) ratio and the QBS-Ar index are valuable for assessing soil quality (Bertolotto et al., 2016). An optimal C:N ratio suggests balanced decomposition and nutrient cycling (Nicolardot et al., 2001; Prescott, 2010).

Extreme C:N ratios can indicate issues with nutrient availability and organic matter decomposition (Schimel et al., 1994). The QBS-Ar index measures soil microarthropod diversity and abundance, with higher values indicating a healthier, more biologically active soil ecosystem.

Together, a balanced C:N ratio and high QBS-Ar index reflect good soil quality by signaling robust biological activity and efficient nutrient cycling.

Conversely, imbalanced C:N ratios and low QBS-Ar indices might suggest poor soil conditions, highlighting the need for management interventions to improve soil functionality and sustainability.

5. Conclusion

This study offers valuable insights into the interplay between environmental variables, arthropod communities, and soil quality across alpine ecosystems. Our findings highlight the pivotal role of climatic conditions—such as temperature and humidity—in shaping arthropod diversity and community composition.

The coinertia analysis highlighted significant associations between climatic variables and arthropod diversity, with radiation and degree days strongly influencing these relationships. Specifically, Araneae, Psocoptera, and Coleoptera were linked to colder, more humid environments, while Chilopoda, Isopoda, Collembola, Pauropoda, and other holometabolous adults were associated with warmer, drier conditions.

We demonstrated that elevation and its interaction with exposition significantly affect arthropod community structure, while exposition alone had a marginal effect.

Further analysis confirmed the impact of elevation on community structure and illustrated the complex interactions between elevation and exposition and these results were reflected in the species diversity metrics, where species richness varied significantly with elevation, while species abundance remained stable. The QBS-Ar index also showed notable variation with elevation, indicating shifts in soil quality from higher values in forested environments to lower values in harsher alpine conditions. The analysis of the carbon-to-nitrogen (C:N) ratio revealed the influence of elevation on the C:N ratio and highlights substantial variation across different elevation zones.

Overall, the study reinforces the crucial role of arthropods in maintaining soil structure, nutrient cycling, and ecosystem functionality. Despite some limitations in sampling—such as the underrepresentation of certain arthropod groups — our results emphasize the importance of preserving diverse and healthy arthropod communities for sustaining soil quality and ecosystem resilience.

Effective forest management practices, such as maintaining dead wood and considering climatic effects, are essential for supporting rich arthropod communities and ensuring soil quality.

Integrating the QBS-Ar index with other soil quality indicators, like the C:N ratio, provides a comprehensive approach to assessing soil quality. Future research should continue to explore these relationships in various environmental contexts and refine methodologies to capture the full spectrum of arthropod diversity and its implications for soil quality.

6. Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

7. Data availability

Data will be made available on request

8. Acknowledgments

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Discussion

Soil-forming factors—weather, parent material, climate, topography, and biological activity—are particularly significant when studied together, especially within the context of climate change. Climate change increasingly impacts terrestrial ecosystems, a challenge further compounded by accelerating environmental degradation (Malhi et al., 2020; Warner, Hamza, Oliver-Smith, Renaud, & Julca, 2010). Understanding soil-forming processes can mitigate these effects in this context by enhancing our knowledge of how soils interact with the atmosphere, particularly in carbon sequestration and decomposition dynamics. Through pedogenesis, especially soil organic matter (SOM) dynamics, soils exhibit resilience to environmental stressors (Eswaran et al., 2019; Harden et al., 2018). Investigating how soil evolution, organic matter composition, and decomposition influence soil functions is critical for developing effective land management and conservation strategies. These processes are intrinsically linked to ecosystem services, such as carbon storage and soil fertility, which underpin ecosystem sustainability (Smith et al., 2021; Deng et al., 2022). Thus, a comprehensive understanding of soil-forming factors—examined holistically—offers valuable insights into the interconnected roles of soils within the atmosphere, biosphere, and lithosphere, supporting global climate mitigation efforts. Our research investigates how soil-forming factors drive soil development and organic matter dynamics. By adopting both synchronic and diachronic approaches, we examine soils across temporal and spatial dimensions, including studies along altitudinal gradients to assess the impact of elevation on soil properties. Field analyses and detailed laboratory investigations enable a robust characterization of soil processes across diverse Swiss environments.

The research is structured around four thematic areas:

Thematic 1: A 37-year analysis of soil changes across Switzerland, revealing significant shifts in the C:N ratio linked to climate, with distinct soil types exhibiting unique characteristics shaped by local geomorphology.

Thematic 2: An exploration of soil evolution using X-ray diffraction (XRD), highlighting mineralogical changes and identifying opportunities for future research through expanded techniques.

Thematic 3: An investigation into the influence of roots and shoots phytochemical composition on litter decomposition across elevation gradients, emphasizing the critical role of plant organic matter in nutrient cycling.

Thematic 4: A study of soil microarthropods, elucidating the effects of climate and ecological interactions on soil biodiversity and quality. This theme links soil communities to soil quality, evaluated through the Quality Index for Soil (QBS), demonstrating how microarthropod activity enhances soil quality.

These four thematic areas collectively underscore the intricate relationships between soil-forming factors—climate, geology, topography, soil organisms, and time—and their combined influence on soil development and SOM dynamics. This integrated perspective highlights the necessity of considering multifactorial interactions to fully grasp soil formation processes and their implications for ecosystem health, particularly amidst rapid environmental change. My dissertation adopts an interdisciplinary approach to address critical knowledge gaps in soil organic carbon (SOC) dynamics and climate change. By integrating ecosystem functioning and pedogenesis across the heterogeneous Swiss landscape, the study synthesizes findings from the four thematic areas to advance our understanding of soil dynamics, mineralogy, litter decomposition, and the ecological roles of soil microarthropods (**Figure VI**). This work provides a comprehensive framework for assessing the interactions between soil processes and ecosystem sustainability in a changing climate.

The study synthesizes insights from four thematic areas to comprehensively understand soil dynamics, soil mineralogy, litter decomposition, and the role of soil microarthropods (**Figure VI**).

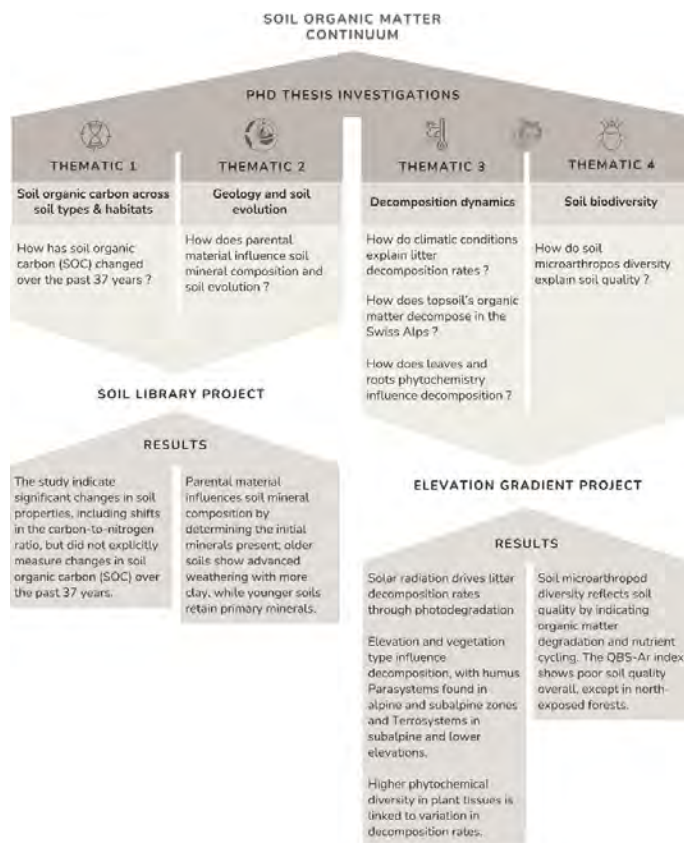


Figure VI. Conceptual figure of the five soil formation factors studied in this dissertation. Figure VI illustrates the five key soil formation factors studied in this dissertation: time, parental material, climate, topography, and biological activity and the results found. The thematic areas of the research correspond to these factors, providing a comprehensive understanding of their roles in soil dynamics. Thematic 1 on how soil properties evolved over a 37-year period. This investigation into the time factor revealed significant variations in soil physicochemical properties and nutrient dynamics, showing how soil profiles change predictably with time and climate. Thematic 2 examined the impact of parental material on soil mineralogy through X-ray diffraction (XRD). O revealed how different mineralogical compositions, influenced by the geological substrates, reflect various soil formation processes and environmental conditions. Thematic 3 addressed the role of climate in soil organic matter decomposition. Solar radiation emerged as the primary driver of decomposition rates, highlighting how climatic factors, like UV radiations, influence litter decomposition processes and soil carbon cycling. Thematic 3 also investigated topography by studying how elevation gradients and slope aspects affect decomposition rates. The research showed that topographical variations influence solar radiation exposure and thus impact the decomposition dynamics of plant litter. Thematic 4 focused on biological activity by analyzing soil microarthropods and their role in decomposition. This thematic area demonstrated how climate affects microarthropod populations and soil quality, illustrating the complex interactions between soil biology and environmental factors.

The 37-year-old soil library served as a historical benchmark, revealing long-term trends and shifts in SOC, pedogenesis, and nutrient cycling. It helped track soil property evolution in response to climatic and anthropogenic changes, though it had limitations, such as gaps in spatial coverage and potential inconsistencies with modern sampling standards. **Elevation gradients** revealed how soil properties and processes varied across different altitudinal zones, providing insights into how temperature and precipitation influenced soil formation and soil organic carbon (SOC) dynamics. This approach identified altitude-related patterns and interactions between soil properties and ecological processes, offering a detailed view of how soils responded to environmental conditions. **North-south facing slope models** explored how slope orientation affected soil development by examining variations in solar radiation, temperature, and moisture. This method assessed how microclimate differences impacted soil characteristics and functions, enhancing our understanding of spatial heterogeneity within the landscape. **Reciprocal transfer experiments** examined how plant materials, such as leaves and roots, decomposed when moved between different environments. This approach isolated the effects of specific environmental factors on decomposition processes, offering insights into how soil systems might have adapted to changing climatic conditions. Integrating these methods provided a holistic view of soil dynamics.

From a general perspective, the soil library offered historical context, elevation gradients, and slope models revealed spatial variability, and reciprocal transplants provided insights into decomposition and environmental interactions. This comprehensive framework highlighted the need for continued research to address limitations, such as potential biases in historical data and the need for broader spatial coverage. Future research could build on this design by incorporating additional variables, expanding geographical coverage, and refining methodologies to better capture soil and ecosystem processes. Integrating findings from these diverse components will be crucial for developing comprehensive models that inform sustainable soil management and conservation strategies amidst ongoing climate change and environmental pressures.

Soil dynamics and transformation in the central European Alps

Thematic 1 shed light on SOC dynamics across Swiss landscapes but faces limitations in generalizability. Although the study captured a broad range of pedogenetic processes and soil diversity, limitations include the restricted generalizability of findings beyond the Swiss context.

The focus on specific soil types and environments limits the extrapolation of results to regions with different soil characteristics.

The study's focus on Switzerland's diverse soils, characterized by specific geological and climatic conditions, may restrict the applicability of its findings to other regions with different soil types, such as agricultural fields, natural soils, or urban soils. This limitation is due to these areas' unique environmental histories and soil properties. Additionally, methodological challenges arise from collecting data across varied and remote landscapes, and disentangling the complex interactions between biotic and abiotic factors remains a significant difficulty. Long-term monitoring is crucial to capture dynamic changes in soil organic carbon (SOC) storage and turnover rates, particularly given the accelerated climate change and increasing anthropogenic pressures. To address these challenges, several key Swiss institutions are actively engaged in relevant research. The Swiss Federal Office for the Environment (OFEV) is involved in monitoring biodiversity and developing climate scenarios, which help inform strategies for environmental adaptation. The Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) conducts long-term studies on forest ecosystems and alpine environments, focusing on how climate change impacts forest dynamics and soil processes. The Swiss Soil Science Society (SSSS) oversees the Swiss Soil Monitoring Network (NABO), which tracks soil quality and organic carbon levels, alongside dedicated projects on soil carbon research. Additionally, local universities such as ETH Zurich, the University of Bern, and the University of Basel contribute through projects investigating ecosystem services, mountain soils, and soil-microbe interactions.

Together, these efforts provide a comprehensive understanding of soil dynamics and guide effective land management and climate mitigation strategies. Methodological constraints in data collection and the complexity of biotic and abiotic interactions further challenge the full understanding of SOC dynamics.

Future research should prioritize both long-term and short-term soil monitoring across various geographical settings and employ diverse analytical methods to accurately capture changes in SOC storage (Han et al., 2024; Le Noë et al., 2023) and turnover rates (De Rosa et al., 2024).

This approach is crucial for understanding the impacts of accelerated climate change and increasing anthropogenic pressures on soil health and functionality. Collaborative efforts with national and international partners, such as the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), the European Soil Data Centre (ESDAC), and global organizations like the Food and Agriculture Organization (FAO), will be essential in advancing our knowledge and developing effective strategies for soil conservation and carbon management.

Soil mineralogical changes and pedogenesis

The influence of geological substrates on soil formation and mineralogical changes was explored in **Thematic 2** but has spatial coverage constraints. The reliance on Swiss soil archives and limited sample size affects the representativeness of soil mineralogy across different geological units. Integrating X-ray diffraction (XRD) data with field observations and experimental data poses challenges in interpreting the causal relationships between geology and soil properties (Hughes, Moore, & Glass, 1994; Omran, 2017). Future research should focus on longitudinal studies with broader geographical and spatial scales, incorporating advanced geospatial technologies to simulate soil evolution under changing climatic conditions. This approach is essential for understanding the dynamic interactions between soil properties and environmental factors. While this approach provided valuable insights into mineralogical changes and soil formation processes, limitations include the study's restricted geographical and temporal scope. The reliance on Swiss soil archives, limited spatial coverage, and poor number of soil horizons investigated may only partially represent soil development processes in other regions with different geological histories.

Future research should incorporate broader geographical scales and advanced geospatial technologies (Dash, 2024; Kumari, Vimal, Rai, Paswan, & Misra, 2024) to simulate soil mineralogical evolution under changing climatic conditions and use broader geographical scales coupled to advanced technologies, like scanning electron microscopy (SEM) and inductively coupled plasma mass spectrometry (ICP-MS), to better simulate soil evolution under diverse climatic conditions and enhance our understanding of soil resilience to environmental stressors (Chaudhary, Yadav, & Dutta, 2024; Moor, Lymberopoulou, & Dietrich, 2001; Zacháry et al., 2024). Addressing these gaps will enhance our understanding of soil formation processes.

Litter decomposition dynamics in alpine environments

Then, litter decomposition dynamics were investigated in **Thematic 3**, highlighting the significant role of solar radiation but also facing methodological limitations. Using standardized organic matter sources like tea bags simplifies the complexity of natural litter inputs and faunal feeding preferences, potentially overlooking variations from diverse vegetation types and feeding activity (Blume-Werry et al., 2021; Mori, Ono, & Sakai, 2021). Disentangling solar radiation effects from other environmental factors, including microbial activity and community composition, remains challenging. Expanding research to include diverse soil types and climatic regimes and advanced analytical techniques, such as molecular biology tools, could provide deeper insights into the mechanisms driving SOC decomposition ((Lorenz, Lal, Preston, & Nierop, 2007; Schmidt et al., 2011; Van Hees, Jones, Finlay, Godbold, & Lundström, 2005).

Long-term studies are crucial for understanding how future climate scenarios may alter decomposition dynamics and carbon cycling processes. The study's use of standardized organic matter sources like tea bags simplified decomposition dynamics but may not fully capture the complexities of natural ecosystems. Methodological challenges in isolating the effects of solar radiation from other environmental factors and microbial activity introduce uncertainties. The next step would be to use advanced analytical techniques, such as molecular biology tools for microbial community analysis and mesocosms experiments (Riggs & Hobbie, 2016), which might provide deeper insights into SOM decomposition's mechanisms.

The role of soil microarthropods in decomposition processes

Finally, the role of soil microarthropods in decomposition processes was examined in **Thematic 4** but was limited by coarse taxonomic resolution and sampling methods. The focus on broad taxonomic groups may overlook finer-scale variations in community composition and functional diversity. The QBS-Ar index, while useful for measuring microarthropod contributions, may only partially capture spatial variability in densities and species distributions. Enhancing taxonomic analyses, incorporating molecular tools for species identification and functional trait assessments, and setting up mesocosm experiments could significantly improve our understanding of arthropod responses to environmental variability.

Also, as macrofauna, earthworms play a crucial role in the soil ecosystem by influencing soil food webs and soil organic matter (SOM) dynamics.

Their activities—such as burrowing, feeding, and excreting—affect soil structure, nutrient cycling, and the decomposition of organic materials (Barot, Ugolini, & Brikci, 2007). We are conducting a preliminary field campaign to assess earthworm diversity and abundance along an elevation gradient to better understand their role. This research aims to uncover how earthworm populations, as essential ecosystem engineers, vary with altitude and environmental conditions. Earthworms enhance soil structure by creating burrows that improve aeration and water infiltration, contribute to nutrient cycling by consuming organic matter and excreting nutrient-rich castings, and accelerate organic matter decomposition through their feeding activities (Sharma, Tomar, & Chakraborty, 2017). By examining these factors across different elevations, we seek to gain insights into earthworm adaptability and their impact on soil quality, enriching our understanding of soil biodiversity and the functional roles of earthworms in maintaining soil ecosystem functionality. Overall, challenges include the complexity of data collection across varied landscapes and the difficulty of disentangling biotic and abiotic interactions.

Long-term monitoring and inclusion of diverse geographical settings are essential for capturing dynamic changes in SOC storage and turnover, especially in the face of accelerated climate change and increasing anthropogenic pressures.

Future research should focus on these aspects to enhance our knowledge of SOC dynamics and improve applicability to broader contexts.

Relevance

This study offers valuable insights into SOC dynamics, pedogenesis, litter decomposition across the Swiss landscape, and the roles of soil microarthropods. It provides a detailed and nuanced understanding of how these processes interact within specific soil types and environmental contexts, contributing to a comprehensive view of soil and ecosystem functioning. The integration of long-term data, elevation gradients, slope models, and reciprocal transplant experiments enhances the robustness of the findings and allows for a multifaceted analysis of soil dynamics. However, the research has limitations, particularly in its applicability beyond the Swiss context. While the study offers in-depth insights into SOC dynamics within Switzerland, the findings may not extend to regions with different soil characteristics or environmental histories.

The specific focus on Swiss soil types and conditions may limit the generalizability of the results to other geographical areas with varying climatic and soil conditions.

Our multifaceted experimental design integrated various approaches to provide a comprehensive understanding of SOC dynamics, pedogenesis, and related processes. Each method offered unique insights and complemented the others, creating a robust framework for analysis.

Our research offers substantial contributions to the field of soil science by synthesizing insights across four critical thematic areas: SOC dynamics, soil mineralogy, litter decomposition processes, and soil microarthropod roles, all within the diverse landscapes of Switzerland. By examining these aspects, my study provides a holistic understanding of key soil processes and ecosystem functioning under varying environmental conditions.

Integrating advanced analytical techniques and comprehensive field studies has enabled a nuanced exploration of how different factors—from pedogenesis and soil mineral composition to climatic influences and microbial activity—interact to shape soil health and carbon dynamics.

The relevance of our research extends beyond academic inquiry, addressing pressing global challenges such as the impacts of climate change on soil health and resilience. Understanding SOC dynamics and the role of various soil processes in carbon sequestration is crucial for predicting how ecosystems will respond to ongoing environmental changes.

The findings highlight the sensitivity of mountain regions to climate change, which can act as an early warning system for broader environmental shifts. These regions exhibit heightened vulnerability and offer potential solutions through adaptive management practices and targeted conservation strategies. Integrating interdisciplinary approaches and leveraging insights from our research are essential for advancing soil science and supporting sustainable soil stewardship practices globally. By addressing current knowledge gaps and enhancing predictive capabilities, my study aids in developing informed policies and practices that promote soil conservation and biodiversity. The findings underscore the importance of mountain ecosystems as indicators and solutions to climate change impacts, emphasizing the need for ongoing research and adaptive management strategies to ensure soil health and ecosystem stability in a rapidly changing world.

Conclusion

My research revealed that over a 37-year period, soil properties in Switzerland showed significant changes driven by time, with distinct soil types reflecting variations in parental material, while climate and topography influenced litter decomposition rates, and biological activity, particularly soil microarthropods, played a crucial role in nutrient dynamics and soil quality. This dissertation comprehensively explores critical soil processes across Swiss landscapes, integrating insights from organic carbon dynamics, mineralogy, litter decomposition, and soil microarthropods. By examining these interconnected factors, the study advances our comprehension of how soil systems respond to environmental gradients and climate change. Key findings reveal that soil stability and transformations, as observed through long-term studies, underscore soil profile resilience and slow evolution. The analysis of mineralogical changes over decades highlights how geological substrates influence soil development, while insights into litter decomposition emphasize the significant role of climatic variables, particularly solar radiation, in organic matter breakdown. In addition, we shed light on the intricate relationship between environmental conditions and soil biodiversity, showcasing how varying climates and habitats impact arthropod communities and soil quality. Overall, this work highlights the importance of integrating advanced analytical methods with field-based observations to capture the complexities of soil processes. It emphasizes the critical role of mountain ecosystems in signaling and potentially mitigating the effects of climate change on soil carbon and health. By synthesizing these findings, the study provides valuable guidance for developing effective soil management and conservation strategies, which are crucial for addressing global environmental challenges. Continued interdisciplinary research is essential to further unravel the dynamics of soil systems, enhance predictive models, and support sustainable practices that safeguard soil ecosystem resilience in a changing climate.



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