

## Dynamic linkages between human pressure and stability of soil organic matter in mid-latitude mountains – A perspective review

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### ABSTRACT

Mid-latitude mountains are dynamic environments, confronted with climate change and human land-use effects. Understanding how such human pressures affect the stability of soil organic matter (SOM) is crucial for predicting SOM dynamics and mitigating climate change. To contribute to a better understanding of the determinants of SOM stability in mid-latitude mountains we propose a conceptual hierarchical framework for the spatio-temporal variability of SOM preservation. Second, we review the literature on SOM stability in various related environmental contexts, including soil types typical of different altitudinal zones as well as specific intrazonal soils such as organic soils of mountain peatlands and soils developed on calcareous parent materials. We point out the existing knowledge gaps and contradictory research results in this area. Finally, we develop a framework for understanding the link between human pressure and SOM stability, including an in-depth analysis of the effects of tree species conversion, windthrows, land use and land cover change, fires, and soil erosion. We also indicate the need for a comprehensive, holistic approach to the study of SOM stability in mid-latitude mountains, taking into account the context of soil-forming processes.

### 1. Introduction

Understanding the mechanisms of soil organic matter (SOM) stabilization and their sensitivity to human-induced disturbances and environmental change is crucial for predicting future SOM dynamics (Cotrufo and Lavelle, 2022) and thus for climate change mitigation. Moreover, the stability of SOM contributes to the overall resistance and resilience of the soil system (Yang et al., 2020a). The stability of SOM is an ecosystem property, greatly dependent on the environmental context (including climatic conditions) and soil properties (including pH, texture, aggregation, cation exchange capacity, base saturation and parent material) (Schmidt et al., 2011; Cationi et al., 2016; Soucémariadin et al., 2018; Kögel-Knabner and Amelung, 2021). Furthermore, vegetation (and thus the chemical composition of the SOM) as well as the activity and assemblage of soil micro-, meso-, and macrofauna influence SOM dynamics (Lehmann et al., 2020; Desie et al., 2021).

Many of these potential drivers of SOM stability vary naturally with

elevation. Hence, mid-latitude mountain areas are of particular relevance for understanding SOM dynamics on a landscape level (FAO, 2015). For this review, we focus on mountainous areas, as defined by Price (2010), located in mid-latitudes, i.e. between the tropics and the polar circles (Fig. 1a). Their importance for the global carbon cycle is evidenced by their spatial extent: they cover more than 23 million km<sup>2</sup> and are ca. 30 % of the Earth's land surface (Fig. 1a). Furthermore, mid-latitude mountains can have a relatively high net primary productivity (Schimel and Braswell, 2005) (Fig. 1b), which may lead to a substantial input of organic matter into the soils. Decomposition on the other hand slows down, due to the changes of climatic conditions with the elevation (Davidson and Janssens, 2006).

As such, mid-latitude mountains play a special role in soil organic carbon (SOC) sequestration and SOM stabilization (Shi et al., 2020). In addition to the polar regions where soils can store up to 200 Mg C ha<sup>-1</sup> (Tarnocai et al., 2009), mid-latitude mountains have a great SOC storage potential of up to 300 g C m<sup>-2</sup> yr<sup>-1</sup> (Sha et al., 2022) and may serve as active (still sequestering) SOC stock hotspots (Cotrufo et al., 2019;

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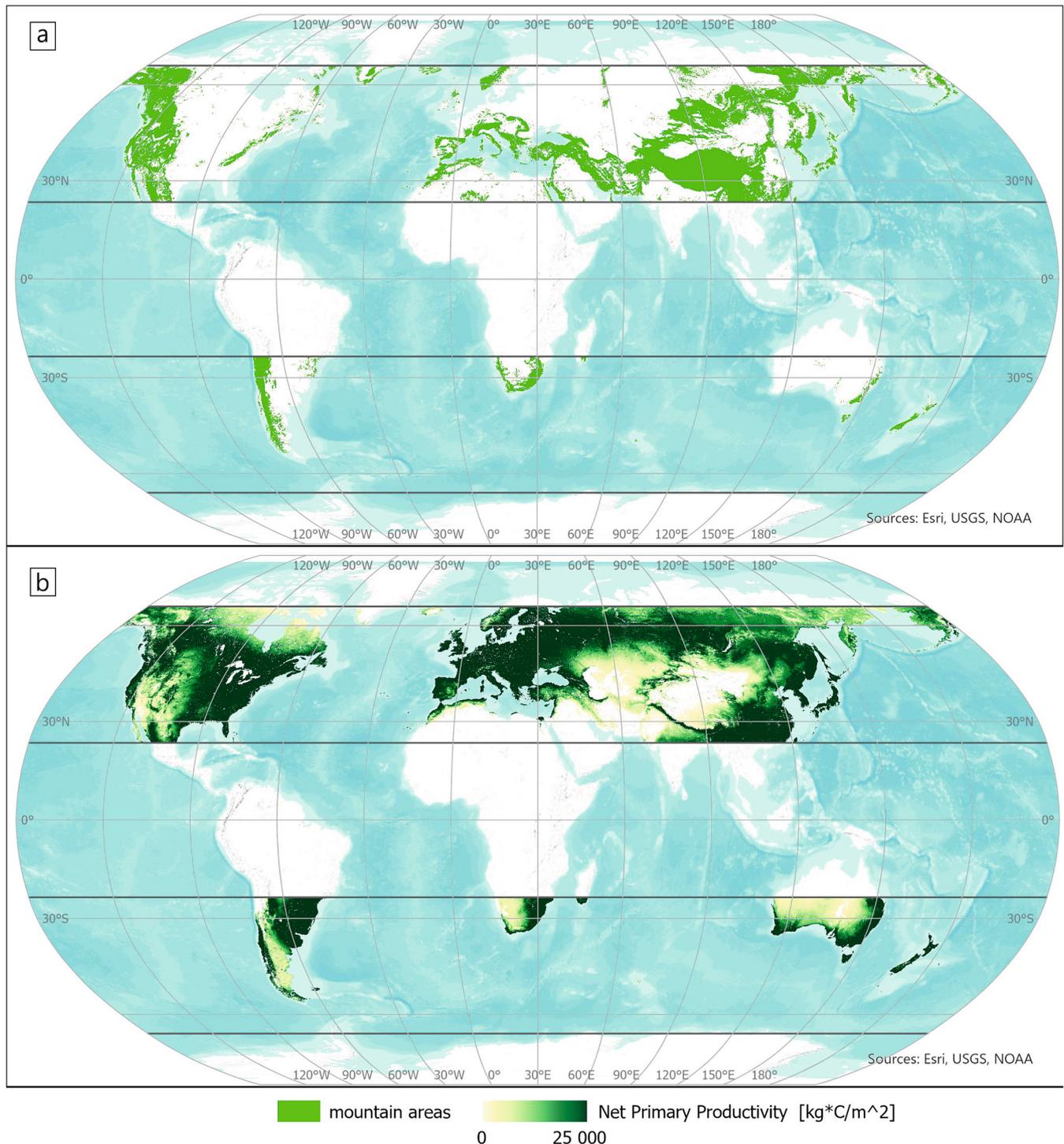
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Stanchi et al., 2021).

Soil conditions in mountainous areas also exhibit a very large local differentiation of soil properties and soil-forming processes relevant to SOM stabilization. Soils are typically younger, often shallow and may have a higher rock content as compared to soils in lower-lying elevations. The influence of the parent material is therefore high and the origin and properties of that parent material may vary substantially across the landscape. Furthermore, topo-climatic conditions and aspect as well as slope processes and erosion (Hemelryck et al., 2011) influence rates of soil formation (Egli and Poulénard, 2016) and effective

percolation (Schaetzl and Isard, 1996; Schaetzl and Rothstein, 2016). Lateral translocations of water and dissolved nutrients and colloids (including dissolved organic matter) moreover become much more evidenced than in flatter topographies (Bourgault et al., 2017).

Finally, biota in mid-latitude mountainous areas show a strong stratification according to elevation. Forests, grasslands and peatlands may be considered the main biomes, and SOC stocks between those biomes may vary considerably: in temperate mountain forests they range from 50 to 250 Mg C ha<sup>-1</sup> (Jandl et al., 2011; Bojko and Kabała, 2017; Egli and Poulénard, 2016), while soils under mountain grasslands,



**Fig. 1.** The location of mountain areas (as defined by Price et al., 2010) in temperate zones (a) and the average value of Net Primary Productivity (NPP) from 2001 to 2022 based on the MODIS sensor (b).

particularly under alpine meadows, can store up to 160 Mg C ha<sup>-1</sup> of SOC (Liu et al., 2016; Chen et al., 2017). Furthermore, there are many peatlands within mid-latitude mountains favored by the higher precipitation, and changes in topography favoring local water stagnation (Reed et al., 2023). Although mountain peatlands usually form fragmented patches, they can store on average 1500 Mg C ha<sup>-1</sup> (Hribljan et al., 2015).

Lugato et al. (2021) found that the accumulation of SOM in mid-latitude mountains occurs in large part in the form of particulate organic matter (POM) thus hypothesizing that vegetation and climate have the strongest controls on SOM persistence in those systems. POM is considered to be mainly derived of materials of plant origin that persist due to the lower temperatures and higher soil moisture contents in mountain soils, as it is not protected by sorption onto minerals like mineral-associated organic matter (MAOM; Lugato et al., 2021; Angst et al., 2023; Leuthold et al., 2023). Nevertheless, recent findings of Yu et al. (2022) indicated that a considerable portion of MAOM also consists of plant-derived SOM, especially in soils covered with forest vegetation with relatively high annual precipitation, i.e. as in the majority of soils in mid-latitude mountains. On the other hand, surprisingly rapid weathering rates in mountain soils (Egli and Poulencard, 2016) along with substantial aeolian material inputs (Mileti et al., 2017) may contribute to the formation of more MAOM. Furthermore, the decrease in average annual temperature and change in precipitation with elevation, causing an increase in SOM content, may not be the main factors affecting SOM stability: several recent papers consider that a more important role in the stabilization of SOM in mountain regions is played by nutrient availability (Tian et al., 2016; Xiao et al., 2021; Zhongsheng et al., 2023), intrinsic SOM transformations (Tian et al., 2016), SOM mineral protection (Zhongsheng et al., 2023) and the type of vegetation and its structure (Badraghi et al., 2021; Hou et al., 2021). Hence, the biogeodiversity in mid-latitude mountains leads to significant spatial differences in the potential of SOM storage as well as in SOM stability, with conditions varying dramatically over relatively small areas.

Mountains moreover are regions particularly vulnerable to global changes caused both by natural processes and various types of direct human pressures or ecological phenomena induced or affected by human activity, and climate change (Freppaz and Williams, 2015). The most important of these are: an increase in mean air temperature, an increase in frequency and severity of drought spells, a decline in snow and ice cover, a disappearance of permafrost, an upward tree line shift, catastrophic windthrows (tree uprooting), wildfires, forestation or natural forest succession caused by land abandonment, deforestation (in some regions), tree species conversion, soil acidification, soil erosion, and overgrazing (Freppaz and Williams, 2015). All these changes are reflected, to a greater or lesser extent, in soils and their ability to store and stabilize SOM. Therefore, mountains can be considered natural laboratories for empirical studies on the effects of global changes on SOM stability (Tito et al., 2020; Zhongsheng et al., 2023).

While much is known about the rapid growth of above ground biomass in mid-latitudes in recent decades (Nabuurs et al., 2013) and the increase in disturbance of terrestrial ecosystems related to global change (Seidl et al., 2017), there is still not enough information about the impact of these changes on soil properties and soil-forming processes and thus SOM stability. The large fraction of POM reported in mountain soils as described above (Lugato et al., 2021) may increase the vulnerability of their SOM: as the persistence of POM is maintained mainly by inhibiting decomposition, it can be easily released by an increase in temperature or a decrease in soil moisture while MAOM is generally considered a relatively stable and resistant fraction of SOM (Angst et al., 2023). One of the possible effects of above ground biomass accumulation on the soil system is the increase in the POM pool, while ecosystem disturbances could either increase or reduce the rate of litter decomposition. Additionally, when considering the response of soil systems, a variety of possible feedback loops affecting the stability of SOC should be taken into account. E.g. Lugato et al. (2021) predict that the soils of

some European mountains may even experience an increase in the MAOM fraction as a result of ongoing climate change.

Hence, it is still unclear to what extent different environmental variables are responsible for SOM stability in various conditions of mid-latitude mountain areas. The aim of this paper is therefore to contribute to a better understanding of the determinants of SOM stability in mid-latitude mountains and the possible effects of various human pressures on that stability. Here, we discuss (1) how SOM stability differs depending on various soil properties and soil-forming processes typical for mid-latitude mountains, and (2) how different types of human pressure and related ecological phenomena affect soils and ultimately the stability of SOM in these particular regions. To this end, we propose a conceptual hierarchical framework for SOM stability in mid-latitude mountains and we review the literature on SOM stability in different environmental contexts of these regions and, finally, on the relations between human pressure and SOM stability.

## 2. A spatial framework of SOM preservation in mountainous areas

The current paradigm of SOC sequestration and SOM stabilization centres around 3 major concepts of SOM preservation in the soil. Summarized, they include (1) the accumulation of SOM due to microbial inactivity or dormancy, (2) the spatial inaccessibility of SOM components for micro-organisms due to soil aggregation, organo-mineral interactions or SOM translocation to the subsoil and (3) the molecular diversity of the SOM compounds, and the energy return on investment for the decomposition of such compounds (Lehmann et al., 2020; Yang et al., 2020a; Kögel-Knabner and Amelung, 2021; Cotrufo and Lavallee, 2022; Angst et al., 2023).

However, spatio-temporal variability of potential drivers of such mechanisms are rarely considered. Cotrufo et al. (2021) postulated a hierarchical framework for carbon storage and nitrogen recycling on a global level, taking into account various determinants of POM and MAOM formation in topsoil and subsoil. Yet, as discussed above, controls varying with latitude on a global level vary with elevation at a landscape level in mid-latitude mountains. Hence, we focus on SOM stability and propose a reclassified hierarchical model emphasizing the spatio-temporal variability of SOM stability, adapted and applicable to a variety of conditions found in mid-latitude mountains (Fig. 2). We argue that the reclassified framework postulated in this paper represents a relevant and important improvement over the purely functional approach presented in previous work on SOM stability. By taking into account the spatio-temporal context, the proposed framework can be applied both in future research on SOM stability and to the formulation of management policies and practices in mountain areas.

We argue that firstly, on the largest spatial scale (Fig. 2), SOM preservation in mid-latitude mountains should be viewed in terms of harsh climatic conditions: in zones with low temperatures, high humidity, and oxygen deficiency on the windward side SOM decomposition and its transformation is inhibited due to the low activity of soil organisms (Cotrufo and Lavallee, 2022). Climatic conditions vary at the scale of the whole mountain range and are of key ecological importance, not only because of its broad spatial scope but also due to the extended temporal dimension. If the climate does not drastically change over time, SOM pools accumulated can remain stable for centuries (Shi et al., 2020). In zones where climatic conditions are not limiting, another medium spatial scale should be considered (Fig. 2). Plant litter quality and soil type vary at catchment to stand scale, and the interaction between soil chemistry and the chemical composition of the litter can cause an accumulation of SOM in the POM fraction (Lehmann and Kleber, 2015; Desie et al., 2020; Kögel-Knabner and Amelung, 2021; Angst et al., 2023). Vegetation changes can however happen at much faster time frames, and the persistence of POM is very variable, from months to millennia (Marschner et al., 2008; Angst et al., 2023), making it the least certain mechanism for SOM stability in terms of time. Finally,

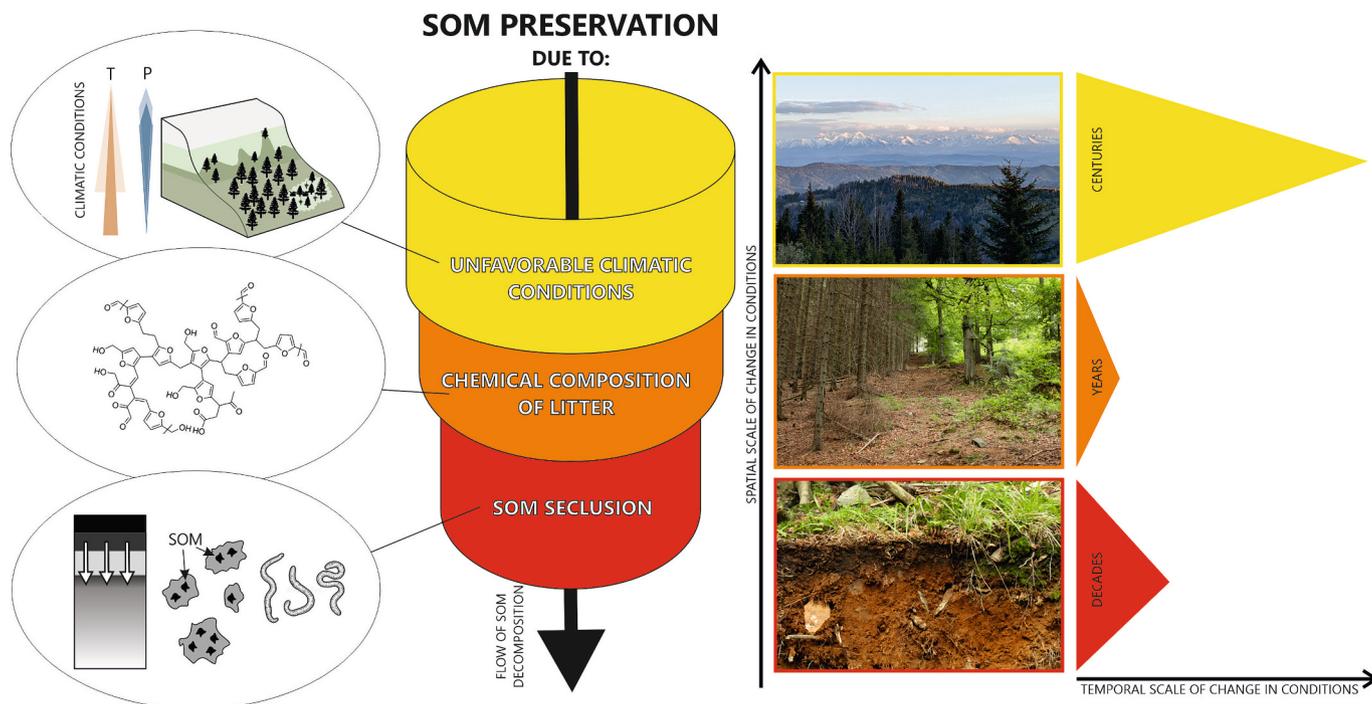


Fig. 2. A hierarchical conceptual framework for spatio-temporal variation in SOM preservation in mid-latitude mountains.

on the pedon scale (Fig. 2), SOM can be stabilized by seclusion from oxidizing agents: (i) through the distance (depth) from abundance of microbes, wildfires, etc. (Kögel-Knabner and Amelung, 2021), (ii) by physical constraints such as occlusion within soil aggregates (Six et al., 2004) or (iii) by formation of strong bonding with mineral phases (Kleber et al., 2015). The average stability of SOC in this case is estimated at decades; however, some types of SOM seclusion may persist for centuries or longer (Gaudinski et al., 2000).

### 3. Application of the framework for SOM preservation in different altitudinal zones

Many mountain areas show typical patterns of change with elevation leading to the development of distinct zones (belts) of different environmental conditions (Hemp, 2006; Hestmark, 2019; Łupikasza and Szypuła, 2019). Altitudinal variations in soil forming factors including climate (temperature, precipitation), relief (slope, aspect, erosion), organisms (vegetation), time (as in soil age) as well as geomorphic processes change along elevational gradients in the mountains, leads to the

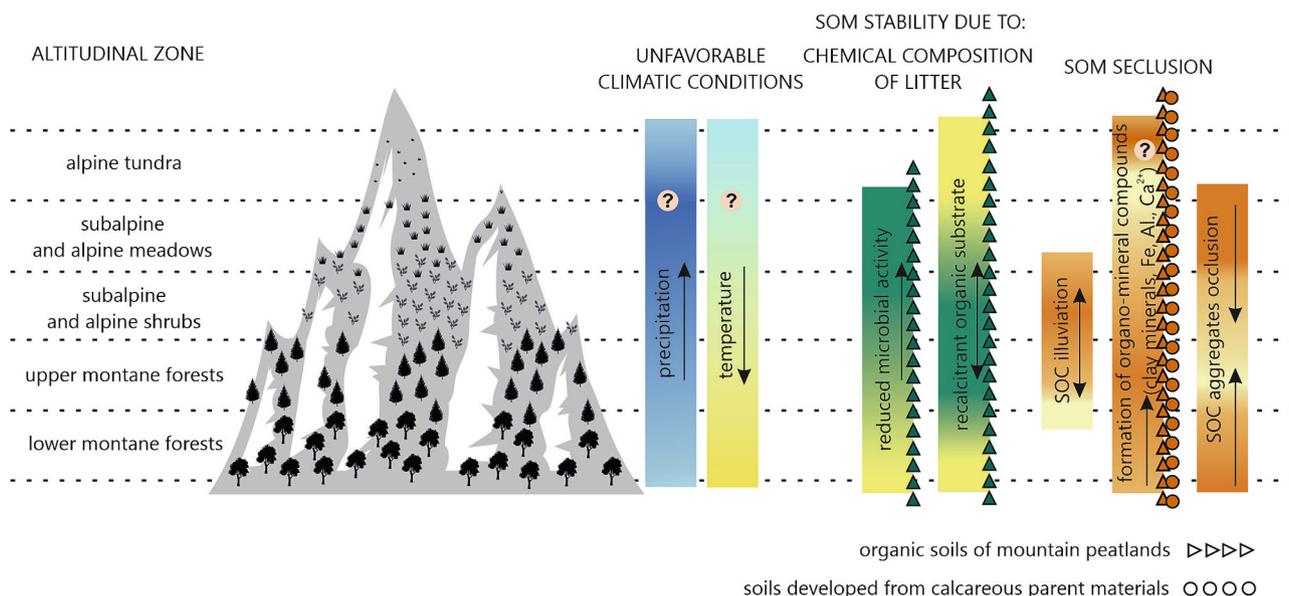


Fig. 3. Diversity of SOM stabilization mechanisms in soils of different altitudinal zones and in azonal soils typical of mid-latitude mountains. Colors with higher saturation in the elevation gradients indicate a relatively greater intensity of the discussed SOM stabilization mechanism, while the arrows show the direction in which these mechanisms change with elevation. Signatures for organic peatlands soils and soils developed from calcareous parent materials indicate relative greater SOM stability regardless of the altitudinal zone, while the question marks refer to altitudinal zones with contradictory results and/or unknown SOM stability mechanisms. See section 3 for more explanation.

development of different soil types in each belt (Skiba, 1977; Bockheim et al., 2000; Birkeland et al., 2003; Bojko and Kabala, 2016; Kramer and Chadwick, 2016; D'Amico et al., 2020). The pattern of altitudinal zonation of soils may be disturbed by changes in the soil parent material resulting from occurrence of various geological structures, local changes in topography or influence of relief-induced geomorphic processes (Alexander and DuShey, 2011; Badía et al., 2013; Waroszewski et al., 2015; Musielok et al., 2022). These factors may cause local differences in soil types to be greater than those resulting from elevational variations in climatic and vegetation conditions. Moreover, many soils in mountainous terrain with steep slopes are strongly influenced by the underlying bedrock or by slope processes. These include Leptosols with very shallow weathering profiles and Regosols exhibiting very poor soil development due to soil rejuvenation (Poulenard and Podwojewski, 2006; Egli and Poulenard, 2016; Kunchulia et al., 2018).

Fig. 3 summarizes the most common SOM stabilization mechanisms in various environmental contexts of mid-latitude mountains. The mechanisms are discussed according to the postulated hierarchical conceptual framework with distinguished groups differing in the spatio-temporal scale of SOM stability (Fig. 2). The stability of SOM is discussed in terms of zonal altitudinal diversity of soil-forming processes resulting from changes in climate and vegetation variables. However, it should be noticed that this overall characteristic pattern of soil cover differentiation in mid-latitude mountains can locally be much more complex (e.g. Catoni et al., 2016).

As mentioned before, SOM decomposition is highly dependent on soil temperature and moisture, which often translates into higher SOM content at higher elevations. However, recent studies (Tian et al., 2016; Hou et al., 2019, 2021; Zhongsheng et al., 2023) have shown that SOC stability may depend more on local variables resulting from vegetation type, parent material, etc., than on climatic conditions changing in the mountains with elevation. In Fig. 3, we therefore contrast interactions between vegetation and soil formation in different altitudinal zones.

The lower reaches of mid-latitude mountainous areas are covered mainly in forests (almost 40 % of mountains areas in the world; FAO, 2021), and as such forest floor dynamics and feedback mechanisms between plants and soils are important drivers of SOM dynamics (Frouz, 2023). In this zone, changes in parent material or bedrock primarily define pedogenic process domains (Chadwick and Chorover, 2001) or buffer ranges (Ulrich, 1991) with a profound effect on SOM dynamics, as summarized by Desie et al. (2021). Broadleaved forests, which form the potential natural vegetation in the lower montane zone, produce a leaf litter that depending on species and soil is decomposed relatively easily, which is reflected in a mull or moder humus type (Ponge, 2013). These soils typically are situated in the base cation exchange buffer domain, which corresponds to a pH-H<sub>2</sub>O higher than 4.5–5.0, and which is associated with the presence of burrowing meso- and macrofauna (Desie et al., 2020). Under such conditions, in many areas of lower montane zone in mid-latitude mountains, the main soil-forming processes are: (i) brunification leading to formation of Cambisols (Merikli et al., 2009) or (ii) melanization, which involves darkening and deepening of A horizons typical of Umbrisols and Phaeozems (Sanesi and Certini, 2005; Läßiger et al., 2008). The literature on mountain Cambisols in France (e.g. Saenger et al., 2013; Soucémariadin et al., 2018) shows that the dominant mechanism for SOM stabilization is the seclusion of SOM through the formation of organo-mineral compounds and edaphon activity, resulting in SOM occlusion within aggregates (Fig. 3). Similarly, in soils subjected to melanization, the stability of SOM depends primarily on SOM seclusion (Fig. 3). In Umbrisols, it is most probably through the formation of stable organic complexes with Al and Fe metals, as described by Turrión et al. (2009) for soils in the Sistema Central in Spain. Yang et al. (2020b), who studied Phaeozems in Andes, indicated associations of SOM with Ca<sup>2+</sup> ions as the dominant mechanism responsible for SOC stability.

In contrast, topsoils under coniferous forests – natural vegetation of upper montane zone – usually have a pH range below the pedogenic

threshold in acidity of pH-H<sub>2</sub>O 4.5, if they are not located on a calcareous substrate. The low pH implies that soil buffering properties are related to the exchange of hydroxy-Al and —Fe (Fig. 3). However, Desie et al. (2020) indicated that broadleaved forests can occur also on soils buffered by Al- and Fe- sesquioxides, depending on the parent material. Soils in the Al-buffered process domain show a decrease in the number of bacteria and burrowing earthworms and a relative increase in fungi, mites and collembola, which is reflected in moder or mor humus type and a smaller amount of SOM occluded in the aggregates (Desie et al., 2021). Moreover, coniferous litter decomposes more slowly due to its complex chemical structure and thus reduced palatability (Berger et al., 2015) (Fig. 3). More recalcitrant organic compounds occur also in humus derived from coniferous vegetation (Wasak and Drewnik, 2015). Consequently, a relatively higher share of the labile SOM pool occurs in the topsoil (Saenger et al., 2013; Soucémariadin et al., 2018). On the other hand, due to increased weathering in more acidic conditions, part of SOM can be stabilized by translocation in the form of humus-metal complexes into the subsoil as a result of illuviation in the podzolization process (Zhiyanski et al., 2017). Podzolization is a common soil-forming process in acid soils and coniferous mountain ecosystems (Chersich et al., 2015), which leads to the storage and relative stabilization of varying amounts of SOM in the lower parts of the soil (Catoni et al., 2016; Brock et al., 2020; Krettek et al., 2021). The most pronounced effects of SOM illuviation in Podzols usually occur in the upper montane zone (Fig. 3), where coniferous vegetation dominates (Kabala et al., 2012).

Nevertheless, it should be noted that the relations between vegetation, edaphon, soil properties, and soil-forming processes affecting SOM stability so far have been studied mainly in lowland forests. The validity of these relations in mid-latitude mountain areas still requires empirical verification.

At higher elevations under subalpine shrub vegetation, due to slower decomposition rates conditioned by lower temperature, moder or mor are typical humus types. Similarly to soils under montane coniferous forests those under subalpine shrubs remain in the hydroxy-Al or —Fe buffer domain and are often subjected to podzolization or andosolization (Müller et al., 2016; Van Ranst et al., 2019). The stability of SOM in these ecosystems is conditioned primarily by climatic variables, and secondly by poor litter quality (Fig. 3), associated with the supply of a substrate with a relatively complex chemical structure (Hobbie et al., 2000). In the case of Andosols, which are often associated with volcanic parent materials or parent materials relatively rich in clays and alkali compounds (Bäumler et al., 2005; Musielok et al., 2021) or showing substantial admixture of aeolian materials (Mileti et al., 2017), SOM stability also depends on pedogenic Fe-oxides and allophanes (Van Ranst et al., 2019). Furthermore, Saenger et al. (2013) reported a relatively high share of organo-mineral associations and SOM occlusion in aggregates under subalpine shrubs in French calcareous Prealps. On the other hand, Hunziker et al. (2017) in Swiss Alps noticed that most of the SOM pool under subalpine shrubs is concentrated in the topsoil in an unprotected form. In addition, SOM accumulated in the subsoil may remain in a labile form due to the transport of root exudates and detritus which increase the activity of microorganisms living in deeper parts of soil, as described by Dengzeng et al. (2022) for soils of Qinghai-Tibetan Plateau.

In comparison with subalpine shrubs, mountain grasslands – both in montane, subalpine and alpine zones – are usually the ecosystems in which the SOM pool is relatively more stable (Leifeld et al., 2009). Due to the less complex chemical structure of the tallgrass organic substrate, soil litter is relatively quickly decomposed and stored in the form of organo-mineral compounds and microaggregate occlusions as described by Leifeld et al. (2009) for soils with an acidic to neutral reaction in Swiss Alps, and Wasak and Drewnik (2015) for slightly alkaline soils in the Tatra Mountains (Poland). The abundance of available nutrients from tallgrasses leads to a relative increase in soil pH and often entails the presence of burrowing meso- and macrofauna, which in turn support

deepening of A horizons in soils (Fig. 3; Garcia-Pausas et al., 2007). Nevertheless, even under conditions that favor SOM stabilization at the surface, it was noted that subsurface layers (10–30 cm) are characterized by much higher SOM stability than the surface layers (0–10 cm) of soils, as demonstrated by Hou et al. (2021) in alpine grassland soils in Tibet. Furthermore, mountain grasslands are often areas with relatively high groundwater levels (due to reduced evapotranspiration in comparison with forests and shrubs) and, consequently, the presence of reducing conditions in the soil affecting SOM stability through changes in oxidative power and iron dynamics (Fig. 3). Recent studies conducted for mountain meadow soils in Sierra Nevada (USA) by Reed et al. (2023) indicated that site-specific soil chemical state is responsible for SOM stability determined by iron binding, regardless of parent material properties and microbial taxa composition.

Although the soils of the highest mountain zone, usually covered with alpine tundra vegetation, do not accumulate large amounts of biomass annually, in the light of recent studies they may prove crucial for understanding the concept of SOM stability in mid-latitude mountains. Pintaldi et al. (2021, 2022) found substantial amounts of SOM originating from the ancient alpine tundra in the MAOM fraction of paleosols of the late-glacial Alpine nunatak. The contemporary presence of an alpine desert in this location suggests that SOM has remained stabilized for thousands of years due to unfavorable climatic conditions (Fig. 3).

In addition, soils of some mid-latitude mountains still remaining under periglacial conditions (with permafrost) may exhibit a relatively stable SOM pool due to ongoing cryoturbation and solifluction processes that draw or bury SOM in deeper parts of soil profiles, as described for mountain soils of the Patagonian Andes (Fröjd et al., 2022). Permafrost soils investigated in the Swiss Alps by Zollinger et al. (2013) showed a high share of POM pools that are relatively more susceptible to degradation. Simultaneously, in some soils the age of the most stable SOM fraction was dated to over 10 k years BP. Wang et al. (2020) in the soils of the Qinghai–Tibetan Plateau noted significant differences in SOM stability between the active and the permafrost layer. Although the active layer was characterized by a relatively large share of both the labile fraction, related to the abundance of roots, and the heavy fraction, as a result of microbial transformation of SOM, the permafrost layers show greater SOM stability due to the interactions of SOM with clay, Fe and Al (Wang et al., 2020).

It should be noted that the altitudinal zones described above are not static but have been shifting through time, e.g. in view of shifting periglacial conditions of late Pleistocene and early Holocene, considerably affecting SOM and slope dynamics. Global analysis of SOC stability in glacier forelands (Khedim et al., 2021) showed that in the first decades of soil development SOM stocks are upbuilt with compounds of relatively high thermal stability. However, despite the increase in SOM content, its stability gradually decreases with the time of soil development after deglaciation (Khedim et al., 2021). Given the potential increased release of CO<sub>2</sub> from permafrost in mid-latitude mountains due to climate warming compared to upbuilding of SOM stocks due to vegetation shift, neither the balance nor the fate of SOM stability has yet been sufficiently verified (Fig. 3; Zollinger et al., 2013; Fröjd et al., 2022). Furthermore, according to the concept of slope cover-beds (Kleber and Terhorst, 2013) some of current subsoil (B) horizons found throughout entire mid-latitude mountain gradients were once surface (A) horizons of permafrost soils covered with tundra vegetation (e.g. Kleber, 1997; Waroszewski et al., 2013). Thus, mid-latitude mountain soils located in slope positions favorable for cover-beds preservation can store substantial amounts of ancient SOM in a secluded form for thousands of years (Figs. 2 and 3). However, this hypothesis still requires verification by radiocarbon dating of the resistant fraction of SOM accumulated in deeper parts of soils developed from slope cover-beds.

Juxtaposed on the altitudinal, zonal variations in soil forming factors described above, azonal mountain soils are also prevalent in mountains.

A first category are soils with poor soil development, such as the Leptosols and Regosols described above, which exhibit diverse SOM stabilization capabilities. Furthermore, soils developed from calcareous parent materials and organic soils of peatlands play a significant role in SOM stabilization, regardless of their position along the elevation gradient (Fig. 3).

Soils developed from calcareous parent materials, e.g. Calcaric Leptosols and Calcaric Cambisols, Phaeozems or Calcisols, are characterized by a high proportion of alkaline cations, which promotes microbial decomposition by reducing H<sup>+</sup> stress and increase the pH (Rowley et al., 2018). However, on the other, such conditions affects the stabilization of SOM within very resistant aggregates, among others, by the formation of Ca<sup>2+</sup> bridges between SOM and mineral surfaces, as described by Yang et al. (2020b) in soils of High Andes. Rowley et al. (2020), who compared carbonate-free Cambisols with adjacent carbonate-bearing Phaeozems in the subalpine zone of the Swiss Alps, showed that even small amount of carbonates in the parent material (<6.2 % CaCO<sub>3</sub>) significantly affect biogeochemistry and soil-forming processes, with consequences for SOM stability. The weathering of carbonates in a humid climate entail a relatively high soil pH and the release of a high amount of extractable Ca into the soil solution (Rowley et al., 2018). This not only stabilizes SOM through flocculation and subsequent occlusion within aggregates and/or sorption to mineral surfaces (Fig. 3), but also contributes to its higher accumulation in soils (Rowley et al., 2020). Furthermore, the authors of this study (Rowley et al., 2020) noted that the presence of carbonates in soils may affect Fe crystallization processes, which indirectly contributes to SOM seclusion (Fig. 3).

Organic soils or Histosols of peatlands are separate crucial soil type in terms of SOM stability in different altitudinal zones of the mid-latitude mountains. Anoxic conditions, conditioned by high precipitation and low evapotranspiration (Fig. 3), favor the accumulation of SOM due to lack of oxidative power to break down phenolic bounds (Wen et al., 2019). However, it is primarily the composition of the peatland vegetation that is responsible for the potential stability of SOM in terms of its palatability (Bragazza et al., 2007; Glina et al., 2019). Moreover, Wang et al. (2017) emphasized the role of iron in peat soils, which in the form of Fe(II) reduces the activity of oxidative and hydrolytic enzymes, which in turn improves the stability of SOM in an anaerobic environment, while in the oxidized form Fe(III) may increase the stability of SOM due to the formation of Fe-OM complexes.

Nevertheless, while considering SOM stabilization, it should be taken into account that ecosystem may undergo a ‘natural’ cyclic transformation involving changes in soil-forming processes, as demonstrated by Bernier and Ponge (1994) for alpine conifer forests in SE France. It can be assumed that the same pattern can apply to other types of ecosystems found in mid-latitude mountains, although human pressure can strongly disturb the functioning of all these ecosystems (see section 4). An example is the upward shift of tree lines in high mountains as a result of natural or human-induced climate warming (Cudlín et al., 2017; Cazzolla Gatti et al., 2019; Masseroli et al., 2021). It has been suggested that this process may contribute to increased SOM storage and stability at high elevations (Djukic et al., 2010) due to the expansion of vegetation with high resistance to microbial degradation (Hobbie et al., 2000). Chersich et al. (2015) pointed out that a change in a treeline often involves an upward shift in the occurrence of podzolization, which, in turn, directly affects SOM stability, while Müller et al. (2016) indicated that podzolization can slow climate-induced treeline changes. Therefore, in high mountains ecotone zones, there are many still unrecognized nonlinearities, feedback effects, and thresholds regulating SOM stability.

#### 4. Linkages between human pressure and SOM stability

Caruso et al. (2018) postulated understanding SOM stability (persistence) as a state of balance between SOM gains resulting from its

protection and SOM losses resulting from its continuous decomposition. In line with this concept, we propose a framework to explain the linkage between human pressure and SOM stability in mid-latitude mountains (Fig. 4a).

We argue that all kinds of human pressure and related or induced ecological phenomena may affect the processes operating in ecosystems through affecting the elements of environment system, such as climate, relief, vegetation, etc. The elements of the environment that can be identified with soil-forming factors (Jenny, 1941) determine the rate of weathering, biogeochemical cycles, the variation of energy flow, biomass production, and the rate of organic matter decomposition. Both soil-forming factors and processes operating in ecosystems shape soil properties, which in turn are one of the above-mentioned factors determining the occurrence and intensity of soil-forming processes (Fig. 4a). Subsequently, the soil properties can be modified as a result of the ongoing soil-forming process (Chadwick and Chorover, 2001). We argue that the type and intensity of the soil-forming process are the gateway to a correct understanding of the balance between opposing SOM fluxes, hence SOM stability (Caruso et al., 2018). Below we provide several examples of ecological phenomena induced by human pressure in mid-latitude mountains that justify considering SOM stability through the proposed framework.

One of the well-known human-aggravated ecological phenomena that significantly affects forest soils in mid-latitude mountains are windthrows (Krejci et al., 2018). Contemporary windthrows are often the result of the transformation of primary deciduous or mixed forests into coniferous monocultures in the past (Kazda and Pichler, 1998). The increased decomposition rates observed in soils after the windthrow disturbances, attributed to relatively higher soil temperature after tree canopy removal and changes in the understory vegetation, lead to a decrease in SOM stocks (Christophel et al., 2015; Mayer et al., 2017). Post-windthrow SOM losses, measured by CO<sub>2</sub> efflux, may be further enhanced by herbivore activities and associated functional changes in plant communities (Mayer et al., 2020). In addition, Mayer et al. (2023) showed that high-elevation montane forests in Swiss Alps, characterized

by relatively high SOM content accumulated in the topsoil in a more labile form, are highly susceptible to windthrow disturbances and, consequently, SOM loss. Moreover, the effects of windthrows are associated with a rapid transformation of soil microbial activity (decrease in the share of fungi in relation to bacteria), which may limit future forest restoration and rebuilding SOM stocks, as described by Wasak et al. (2020) for calcareous soils in the Western Tatras. Furthermore, in many mountain areas, windthrow disturbances are followed by salvage logging practices, which may have long-term impact on the litter layers. Hotta et al. (2020) described significantly decreased SOM stocks in soil litter layers affected by logging after the windthrow in the Ishikari Mountains on Hokkaido even after >60 years following the disturbance. On the other hand, Šamonil et al. (2010) pointed out that due to windthrows some part of the SOM may be buried below the uprooted soil material, and thus stabilized as a result of the seclusion from oxidizing factors. In addition, Don et al. (2012) in the High Tatras (Slovakia) found no significant changes in SOM stocks in topsoil mineral layers between sites with windthrow left for natural succession, with harvested windthrows, and forest reference site, indicating relative stability of SOM. However, this study showed shifts in organic and mineral topsoil layers towards more decomposed SOM as a result of windthrow disturbances (Don et al., 2012).

Among other measures to reduce the risk of wind damage, contemporary sustainable forest management practices recommend transforming conifer monoculture forests into semi-natural mixed forests (e.g. Felton et al., 2010). Galka et al. (2014) based on a comparison of SOC stocks under different tree species in the Sudety Mountains (Poland) suggested that such ecologically-oriented species conversion could result in a huge loss of SOM in montane forests. However, Achilles et al. (2021) carrying out monitoring studies of soils under converted beech forest showed that changes in the soil occurring after replacing spruces and pines with beeches lead to a stronger stabilization of SOM in a long perspective. The floors of beech forests in this study showed increased turnover rates, which led to the formation of more bioactive humus forms (mull or moder) with a higher pH than in coniferous forests.

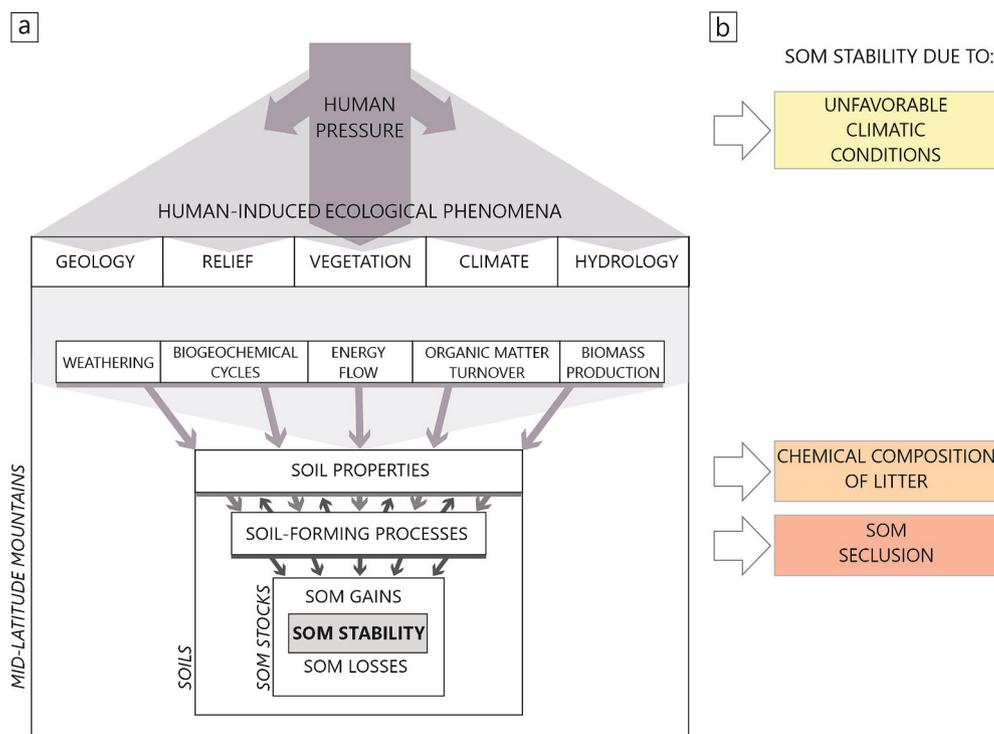


Fig. 4. A conceptual framework explaining the linkage between human pressure and SOM stability in mid-latitude mountain ecosystems (a) and its relation to spatio-temporal contexts of SOM stability (b).

Consequently, there was greater translocation of SOC to the topsoil mineral horizons, resulting in the buildup of a more stable SOM pool (Achilles et al., 2021). This issue requires further research on the time dependence of SOM stability related to tree species conversion, taking into account various variables of mid-latitude mountains (elevation, relief, and finally soil context).

Another human pressure that can have a profound impact on SOM stability in mid-latitude mountains is land-use and land-cover change (LULCC). Although the effects of various land-use changes on SOC stocks are well understood (Guo and Gifford, 2002; Deng et al., 2016; Beillouin et al., 2022), the effects on SOM stability remain a subject of intense research. In this respect, mid-latitude mountains are of particular interest because the overall land-use change trend may differ from that in many neighboring lowland regions. As a result of land abandonment, driven mainly by socio-economic and warming dynamics (Dax et al., 2021; Li et al., 2023), rapid, spontaneous forest succession and expansion of shrubs onto former croplands and grasslands have been observed in recent decades (Gehrig-Fasel et al., 2007; Palombo et al., 2013; García Criado et al., 2020). This process increases both SOC concentrations and stocks (e.g. Montane et al., 2010; Poeplau and Don, 2013; Wasak and Drewnik, 2015; Nadal-Romero et al., 2016, 2023; Sokolowska et al., 2020; Jia et al., 2022); however, the fate of SOM stability remains uncertain. Although the highest SOC stocks are typically found in mature successional forests, a much higher proportion of SOC in the stable MAOM fraction occurs in grasslands, both under humid climatic conditions, as reported for the Tatra Mountains (Wasak and Drewnik, 2015), as well as under semi-arid climate in Pyrenees (Nadal-Romero et al., 2016, 2023). These results are consistent with the findings of Poeplau and Don (2013), who showed a relative decrease in MAOM compared to POM content after the afforestation of grasslands in the European Alps. In addition, according to recent studies from the Qinghai-Tibetan Plateau (Jia et al., 2022), the expansion of shrubs over grasslands can significantly reduce SOM mineralization by delaying microbial transformation in favor of the increase in fungal necromass and thus contribute to mitigating CO<sub>2</sub> emissions from soils of alpine grasslands. In all these studies, taking into account the degree of SOM depletion due to previous erosion that may occur in grasslands as a result of grazing may be a crucial but underestimated factor (Wasak and Drewnik, 2015). Therefore, it is important to refer, whenever possible, the effects of changes in SOC stocks and their stability due to LULCC to soil properties in natural ecosystems (ancient forests or old-growth forests and intact parts of alpine meadows, respectively). The findings of Sokolowska et al. (2022), comparing the metabolic coefficient (qCO<sub>2</sub>) values between flysch-derived Cambisols under permanent meadows and old-growth forests with the same soil types under successional forests, suggest that the latter ecosystems exhibit relatively lower SOM stability. Therefore, transitional ecotone ecosystems may be more susceptible to the effects of any human pressure than stable ecosystems (regardless of their type). Moreover, the trajectories and magnitude of changes in SOC stocks and their stability due to LULCC may vary depending on the environmental context (altitudinal zone, aspect, parent material, and soil formation process).

Successional, transitional ecosystems affected by drought can become particularly susceptible to fires (Batllori et al., 2019), which can easily spread to adjacent stable ecosystems. Recent review by Pellegrini et al. (2022) highlighted the role of fire-induced changes in SOM decomposition and its stability, as processes that offset reductions in aboveground biomass. The stability of SOM is altered by fire through its direct effect on SOM composition and indirectly through changes in the post-fire environmental factors conditioning SOM decomposition; however, the specific mechanisms of SOM stability vary among ecosystem types (Pellegrini et al., 2022). Santín et al. (2008) found higher SOC content in the topsoil layers (up to 10 cm depth) of burnt sites in the acid soils of the Cantabrian Cordillera (Spain) several years after wildfires compared to unburnt sites. This difference was attributed to a decrease in SOM decomposition rates in fire-affected soils and

relatively high re-accumulation of fresh plant residues. In certain regions, the deliberate burning of vegetation may be a practice intended to maintain land for agriculture, such as for pastoralism. Armas-Herrera et al. (2016) studied the effects of prescribed burning in the Pyrenees and showed significantly decreased SOC content and reduced CO<sub>2</sub> efflux from topsoils (up to 3 cm depth) of Eutric Cambisols immediately after the fire. The total loss of SOM due to fire affected both labile and recalcitrant fractions equally. However, this disturbance changed the biochemical background for SOM decomposition, leading to a decrease in the potentially mineralizable SOM pool and relatively higher SOM stability (Armas-Herrera et al., 2016). The authors of this study also emphasized that understanding the effects of fires on SOM stability requires information on the temperature and duration of this phenomena, as well as long-term soil monitoring after the fire, including changes in SOM content, properties, and CO<sub>2</sub> efflux (Armas-Herrera et al., 2016).

Due to their steep slopes and relatively higher precipitation, mountains are inherently prone to soil erosion (Harden, 2001). All disturbances discussed above, such as windthrows (e.g. Gerber et al., 2002), LULCC (Klimek and Latocha, 2007), and fires (García-Ruiz et al., 1996) are known to accelerate surface erosion rates, which can significantly impact SOM dynamics. Recent review articles on the impact of soil erosion (Doetterl et al., 2016; De Nijs and Cammeraat, 2020) highlighted lack of consensus regarding whether this process leads to reduced or increased SOM stability. However, since most studies on erosion and SOM stability focus on soil with intensive agricultural use, mountains remain areas where these relationships still require in-depth case studies (Doetterl et al., 2016). Special attention should be directed towards the often-overlooked impact of subsurface soil erosion on SOM stability in mid-latitude mountains (Bernatek-Jakiel and Nadal-Romero, 2023).

Based on the presented examples, we postulate that the problem of human pressure on SOM stability in mid-latitude mountains should be addressed in future research through the proposed conceptual frameworks (Figs. 2 and 4a). As the determinants of SOM stability in mid-latitude mountains can be considered at different spatial scales (Fig. 2), similarly, human pressures on SOM stability can be considered in different details (Fig. 4b). When we consider the stability of SOM in mid-latitude mountains due to climatic conditions slowing down microbial decomposition, we can link it directly to various phenomena related to human pressure (Fig. 4b). Then, when referring to the stability of SOM due to the complex chemical structure of soil litter, additional information about the diversity of soil properties should be taken into account (Fig. 4b). Finally, taking into account the stability of SOM resulting from its seclusion, attention should be paid not only to soil properties but also to the specificity of soil-forming processes occurring in a given location (Fig. 4b).

## 5. Knowledge gaps and research perspectives

The presented literature review offers some new research perspectives related to existing gaps in current knowledge about SOM stability in mid-latitude mountains. One of the most fundamental questions is how climate conditions changing in elevational gradients affect SOM stability. It is necessary to research this issue within the same altitudinal vegetation zones and the same soil contexts. Another issue requiring detailed research is to determine the mutual importance of the influence of reducing conditions vs. lithology as factors determining SOM stability at the local scale. In addition, many uncertainties regarding SOM stability relate to dynamic subalpine ecotone zones. Studying the effects of upward treeline shift separately from the issue of shrubification (shrubs encroachment) and without taking into account transition of soil-forming processes between different vegetation types, parent materials, and altitudinal zones could lead to contradictory conclusions. We believe that applying the postulated context-dependent SOM stability framework would eliminate this confusion.

Considering the impact of various types of human pressures on SOM

stability in mid-latitude mountains, such as windthrows, tree species conversion, LULCC, etc., a comprehensive environmental-wide balancing of SOM gains and losses is required. Moreover, studying the effects of environmental disturbances in chronosequences may help to understand nonlinearities related to threshold mechanisms and legacy effects.

Finally, we postulate the use of the proposed conceptual frameworks in SOM stability studies and consideration of various local soil contexts. Since management policies should be nature-based, they need to be adapted to the local scale. The same environmental disturbances may have different trajectories concerning the soil context. Moreover, the diversity of soil properties should not be equated with soil-forming processes, which are crucial to understanding SOM stability.

### 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.

### Data availability

No data was used for the research described in the article.

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