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Tracing hotspots of soil erosion in high mountain environments: how forensic science based on plant eDNA can lead the way – an opinion

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Abstract

High mountain environments are among the most fragile on Earth. Due to anthropogenic disturbances and the exposure to extreme weather events, the rates of soil erosion have recently been accelerating, resulting in ecological degradation and geological hazards. Ecological restoration of mountains and an improved understanding of nature-based solutions to mitigate land degradation is therefore of utmost urgency. Identifying hotspots of soil erosion is a first step towards improving mitigation strategies. A promising methodology to identify erosion hotspots is sediment source fingerprinting, that differentiates the properties of soil from different sources, using signatures such as elemental geochemistry or radionuclides. However, in areas with complex lithologies or shallow and poorly developed soils, geochemical fingerprints allow only a rough distinction between erosion hotspots. In this opinion paper, we explore the relevance of environmental DNA (eDNA) that originates from plant litter and fixes onto fine soil particles, as a targeted sediment fingerprinting method sensitive to vegetation that could potentially allow the identification of erosion hotspots and their relative importance from sedimentary deposits. Pioneering studies indicate that eDNA allows not only the detection of specific vegetation communities, but also the identification of individual plant species. Supported by the increasing availability and quality of vegetation maps and eDNA reference libraries, we argue that sediment source fingerprinting using eDNA from plant litter, will evolve into a valuable method to identify hotspots of soil erosion and allow stakeholders to prioritize areas where ecological restoration is necessary in high mountain environments.

Keywords: alpine, erosion, landslide, sedDNA, sediment source fingerprinting, soil and water bioengineering, vegetation

Introduction

High mountain regions are characterised by "rugged terrain, a low-temperature climate regime, steep slopes, and institutional and spatial remoteness" (Hock et al 2019). These fragile environments are much valued as they provide many ecosystem services, such as habitats for endemic plant and animal populations, diverse living and recreational opportunities, and forest and agricultural production (Mao et al., 2021). Pressure on these mountainous environments is particularly high (Le Roux et al. 2016), especially when they are flanked by densely populated regions. Being the source areas of major rivers, mountains are also important for providing water and modulating runoff and sediment regimes. However, anthropogenic activities in recent decades have drastically accelerated land degradation at high elevations, leading to ecosystems that are slow to recover (Liu et al. 2021). Road-building, overgrazing, heavy logging, tourism and wildfires have all been shown to increase the occurrence of landslides or cause significant water erosion (e.g., Sidle et al., 2014; Bajard et al. 2020; Hendrickx et al. 2020; Keiler et al. 2010; Salesa & Cerdà, 2020). In many regions, these processes are exacerbated by the increased frequency and magnitude of extreme weather events (Seneviratne et al. 2012), driven by climate change. As a result, high energy hydrogeomorphological regimes cause flash floods that negatively affect both human communities and the environment across multiple spatial scales (e.g. Serrano-Muela et al. 2015) (**Fig. 1**), as well as becoming increasingly fatal (Haque et al. 2016).

Fig. 1 *Example of a highly connected mountain sediment cascade showing the effects of high-energy hydrogeomorphological regimes propagating along the river course (Central Pyrenees, France). A) shows landslides mobilising soil on an overgrazed slope high in the mountains; B) shows landsliding in the valley bottom on a forested slope. C) shows sediment deposition in the valley bottom. Note the significant infrastructural damage on B and C. Photographs reproduced with kind permission from A) Eco-Altitude, France, B) J. Acquier, C) J. Guyot).*

The urgent need to mitigate severe water erosion and landsliding, especially in the current context of a changing climate and biodiversity loss, calls for an improved understanding of nature-based solutions and their efficacy in restoring disturbed heterogeneous landscapes in mountainous regions (Nelson et al. 2020). Determining the hotspots of soil erosion is a first step towards improving mitigation strategies and guiding the implementation of effective ecological restoration measures. Different techniques can be used, from the analysis of aerial photographs, the use of soil erosion models and, at a more detailed scale, fingerprinting of sediments and their sources (Alewell et al. 2008; Walling, 2013; Hooke et al., 2017). Sediment fingerprinting is a methodology whereby sediment sources are identified based on distinctive soil properties, and has mainly been developed based on physicochemical and radionuclide signatures (Collins et al. 2020). After verifying that these signatures are present during erosion, water-mediated transportation and deposition, the identification of different sediment sources (e.g., lithological units, surface or subsurface soil) can then be performed (Haddadchi et al. 2013). When these sediment source categories can be related to specific areas in a catchment, soil erosion hotspots can be determined and their relative importance can be assessed. As such, sediment source fingerprinting provides field evidence to validate soil erosion modelling, or can be applied in areas where other methods fail. For example, remote sensing may not be applicable in areas dominated by diffuse erosion processes. Although several review papers have recently been published on sediment source fingerprinting and the associated difficulties (e.g. Laceby et al. 2017), as well as challenges for the future (e.g. Collins et al. 2020), most studies have been performed in agricultural settings and the use of these techniques in high mountain environments has received only limited attention. Although sediment source fingerprinting based on geochemical signatures is meaningful for discriminating between lithological sources, or those based on different soil types found across the drainage area of interest, it is less useful for identifying soils that originate under different types of vegetation, because vegetation alters geochemical soil properties only under specific circumstances (e.g., after a wildfire) (Stone et al. 2014). In high mountainous regions, as vegetation type is strongly linked to topography and microclimate (Scherrer & Körner 2011), being able to identify sediment originating from specific plant communities would enhance the fingerprinting method significantly and enable the detailed identification of soil erosion hotspots relative to land use and cover. Therefore, if current techniques are not yet robust enough to identify sediment sources from beneath specific types of vegetation, new methods must be sought that would permit a more targeted sediment source fingerprinting approach.

In this opinion paper, we argue that sediment source fingerprinting studies should combine current geochemical knowledge with novel techniques used in different disciplines. In particular, methods used in forensic science and freshwater ecology permit the identification and tracing of eroded soil through the implementation of molecular techniques (Tringe & Rubin, 2005). These emerging tools could be used to refine sediment provenance in mountainous regions, through the collection and identification of environmental DNA (eDNA), or DNA of organisms isolated from environmental samples (Pawlowski et al 2020), in sediment originating from beneath vascular plant communities. Such a method would enable stakeholders to pinpoint hotspots of soil erosion in a watershed, and should guide the implementation of effective mitigation actions, such as nature-based solutions, when restoring these fragile environments. In the next sections, we will start by reviewing applications of conventional sediment source fingerprinting methods in high mountain environments and how these methods contribute to identify hotspots of soil erosion. Then, we will consider sediment source fingerprints sensitive to vegetation and explore the relevance of eDNA for tracing. Next, sampling of sediments containing eDNA fingerprints will be discussed. The last section will reflect upon the contribution of eDNA fingerprinting to ecological restoration activities in high mountain environments where water erosion is severe and landslides occur frequently.

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Lessons learned from conventional sediment source fingerprinting applications

We performed a literature search to identify relevant publications on sediment source fingerprinting in high mountain environments (Methods given in the Online Resource, **Fig. S1**). Through our literature search, we selected 19 articles (Online Resource, **Table S1**). This small number of studies which were published since 2003 highlights the limited use of this technique for examining sediment provenance in high mountain environments, especially when compared to an annual average of 31 articles on sediment source fingerprinting, mainly considering lowland agricultural environments (Collins et al. 2020). Most of the research we found was conducted in the European Alps (n = 9, of which five were conducted in the same catchment), followed by the Elburz and Zagros Mountains (n = 5), the Rocky Mountains (n = 2), the Pyrenees (n = 1), Himalayas (n = 1), and the mountain ranges of Taiwan (n = 1) (**Fig. 2**). Land use and cover were dominated by forests, scrublands, or grasslands, and reflected the moisture regime (humid versus dry conditions), grazing pressure, and elevation range (below versus above the thermal treeline) of the region (Online Resource, **Table S1**). In catchments with varying surface areas, between <1 km² and >25 000 km², the number of sediment source categories varied between two and six. The most common source discrimination was conducted between lithological sources (and associated soil types) (n = 11), followed by surface and subsurface sources (n = 6), geomorphological domains (n = 1), and land use (2). The disentangling of contributions from different sub-catchments relied mainly on lithological homogeneity within the targeted sub-catchments. Fingerprinting was done based on geochemical properties (n = 11), environmental radionuclides (n = 6) (and a combination of both, n = 2), spectrocolorimetry (n = 2), or other tracing properties such as mineral magnetic signatures (n = 3) (Online Resource, **Fig. S2**).

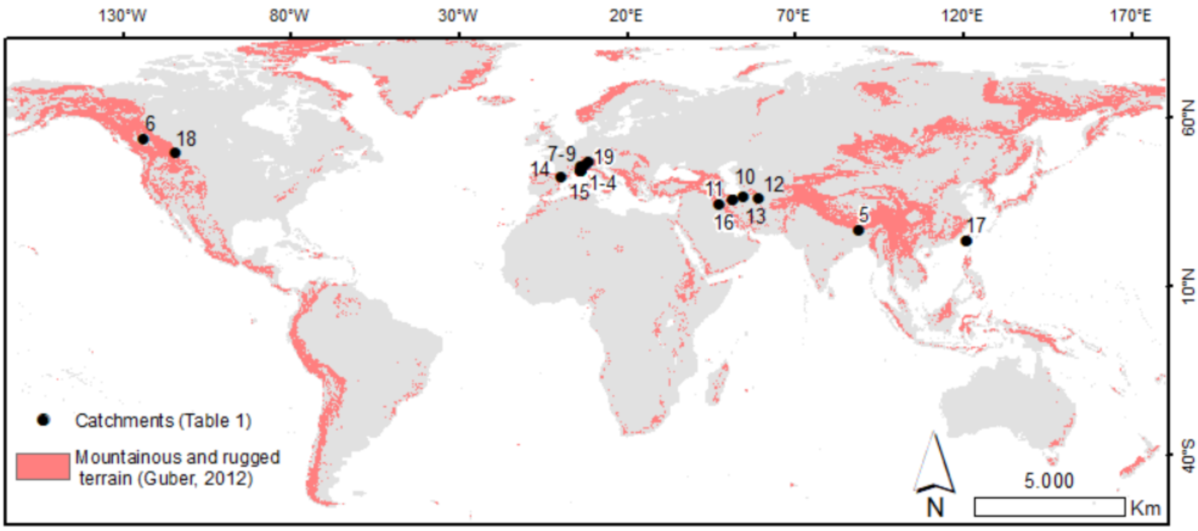


***Fig. 2** Location of the catchments where sediment source fingerprinting was applied in high mountain environments for which a high terrain ruggedness and thermal treeline are characteristic features. Ruggedness is an expression of the topographic heterogeneity based on the difference between maximum and minimum elevation over a given surface area (see Guber, 2012). References: (1) Battista et al. 2020, (2) Delunel et al. 2014, (3) Evrard et al. 2011, (4) Foster et al. 2003, (5) Froehlich and*

*Walling, 2006, (6) Gateuille et al. 2019, (7) Legout et al. 2013, Navratil et al. (8) 2012a, (9) 2012b; Nosrati and Collins, (10) 2019a, (11); Nosrati et al. (12) 2018a, (13) 2018b; 2019b; (14) Palazón et al. 2014; (15) Poulenard et al. 2012; (16) Raigani et al. 2019; (17) Resentini et al. 2017; (18) Stone et al. 2014; (19) Stutenbecker et al. 2019. Details in Online Resource, **Table S1**.*

Studies were able to discriminate sediment sources successfully based on lithology (and associated soil type) by measuring elemental geochemistry (including petrography/mineralogy), visible spectra or mineral magnetic properties (Online Resource, **Table S1**). Lithologies are often, but not always, associated with certain erosion features that characterise them, such as badlands on highly erodible black marls (Navratil et al. 2012a, b; Poulenard et al. 2012; Legout et al. 2013). As such, Evrard et al. (2011) were able to identify glaciogenic deposits and associated mass movements as the major sediment source. However, lithology-based source discrimination is of limited use in areas where the lithology is either too homogeneous or too heterogeneous (Chen et al. 2019; Ramon et al. 2020), and the latter is not uncommon in high mountain environments that have long and complex tectonic histories. Furthermore, for mixed deposits such as glacial till or slope colluvium, the sediment fingerprinting signal may be difficult to isolate, hampering source discrimination if based on lithology alone (Legout et al. 2013). Such mixed deposits often cover large fractions of high mountain environments. Discriminating between sources based on soil types alone, Palazón et al. (2014) could not account for poorly developed soils on steep slopes, although Leptosols covered approximately 13% of the catchment surface area.

To improve identification of sediment from mixed sources or topsoils, it is possible to quantify fallout radionuclides in sediments, such as the synthetic caesium-137 (^{137}Cs) associated with the testing of atomic weapons in the 1950s and 60s, or the natural geogenic or cosmogenic fallout radionuclides, such as excess lead-210 ($^{210}Pb_{ex}$) and beryllium-7 (^{7}Be), as they are independent of soil properties and leave a signature on exposed surfaces during the fallout period (Evrard et al. 2020). If fallout radionuclides are present in sediments, then it is an indicator that processes such as sheet erosion (irrespective of land use type and vegetation) have eroded topsoils uphill. However, rill and gully erosion, landslides or bank erosion, cause deeper soils to be translocated downhill. In sediments originating from these subsurface soils, the measurement of pulses of low ^{10}Be (a long-lived cosmogenic radionuclide used to determine catchment-wide denudation rates, Kober et al. 2019) was found to be successful for identifying the source of the sediment (Battista et al., 2020). In a separate study, ^{10}Be also allowed the differentiation of sediments originating from rock outcrops, glacial, periglacial and colluvial deposits (Delunel et al. 2014), but this technique does require a homogenous lithology in the study area. The distinction between surface and subsurface sediment sources has also been made using the geochemical properties of specific sources from roads and quarries (Nosrati and Collins 2019a, b). From our literature search, we found that erosion of subsurface soil layers dominates sediment production in high mountain environments (Online Resource, **Table S1**). These subsurface sediments mainly originate from landslides affecting both slopes and channel banks. Erosion from unpaved footpaths and roads can also significantly contribute to catchment sediment export (Nosrati and Collins, 2019b).

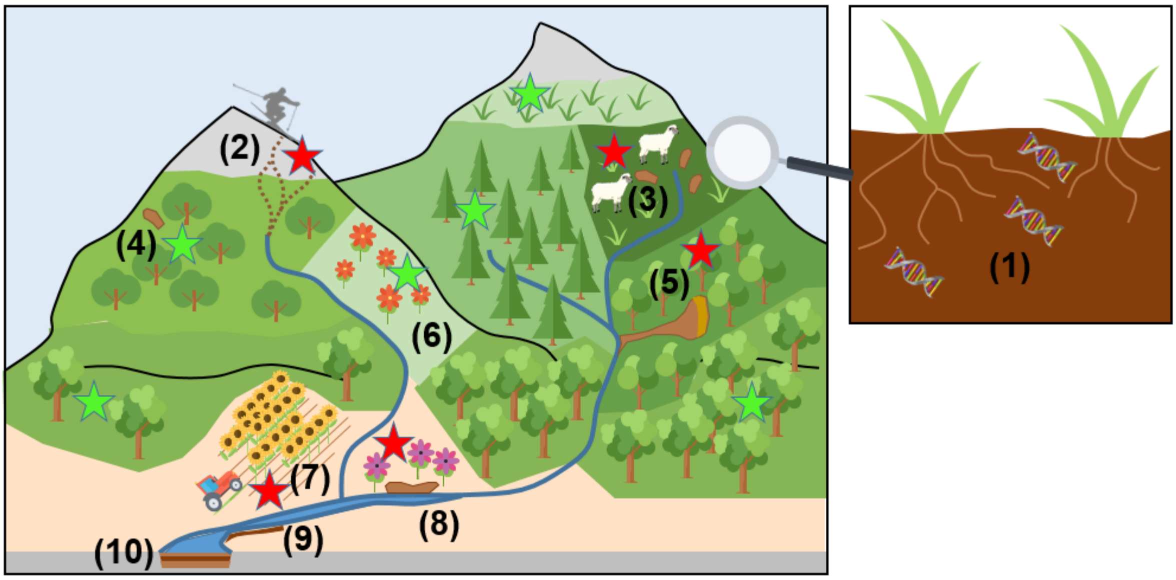
For land use and vegetation type, geochemical properties allowed a rough discrimination between the main land-use types (such as forest and agricultural land) producing surface erosion (Gateuille et al. 2019). In addition, Stone et al. (2014) used geochemical alterations caused by fire in logged subalpine forests and distinguished between unburned, burned and burned-salvaged areas. Of the three categories, burned areas produced the most sediment, which was mainly attributed to sheet erosion.

Sediment source fingerprints sensitive to vegetation

Sediments originating from beneath different types of vegetation can be identified, and the most successful techniques include the measurement of total soil organic carbon (TOC) and nitrogen (TN) elemental concentrations, along with their stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) (e.g., Huon et al. 2013; Gourdin et al. 2015; Laceby et al. 2016). However, these methods have largely been performed in agricultural catchments, and their discriminating power remains limited to differentiating between different crops, particularly in zones that comprise a mixture of C_3 and C_4 plants (Evrard et al. 2013). Novel tools have, however, been developed to increase the discrimination potential between different plant types, such as the analysis of compound-specific stable isotopes (CSSI, Gibbs 2008). CSSI analysis of plant-derived biomarkers (e.g., alkanes or fatty acids), can provide more detailed information on sediment origin from cultivated land versus forests in catchments dominated by C_3 plants in Switzerland (Alewell et al. 2016), or native forests (*Nothofagus alessandrii* and *Pitavia punctata*) versus plantations (*Pinus radiata* and/or *Eucalyptus nitens*) in Chile (Bravo-Linares et al. 2018). Nevertheless, debate remains regarding which biomarkers should be prioritised (Reiffarth et al. 2016), as well as how they are conserved, during sediment transfer across landscapes (Koiter et al. 2013; Hirave et al. 2020). Also, there is a need to replicate sampling over time to integrate temporal changes in biomarker signatures to improve the accuracy of results (Reiffarth et al. 2019).
Recently, environmental DNA (eDNA) has been considered as a marker that could be used for fingerprinting soils and sediments (e.g., Giguet-Covex et al. 2019; Foucher et al. 2020) (**Fig. 3**). Developed initially for biodiversity studies (Taberlet et al. 2007; Thomsen et al. 2012), the measurement of eDNA is now widely performed and allows the successful discrimination of DNA originating from plants, mammals, bacteria, fungi and worms (e.g., Giguet-Covex et al. 2014; Pedersen et al. 2015; Parducci et al. 2017). The persistence of eDNA in sediments obtained from lake deposits (also called sedDNA, or sedaDNA for ancient deposits), has allowed for paleoecological reconstructions as far back as the Pleistocene (e.g., Willerslev et al. 2003; Willerslev and Cooper 2005). Importantly, recent advances in high-throughput sequencing have resulted in the development of DNA metabarcoding as a tracer technique, allowing the characterisation of whole plant communities to the family, genus or species level (Fahner et al. 2016). Although research on plant eDNA signatures in soils and sediments is limited, initial results are promising and indicate that eDNA could yield more accurate results than other sediment fingerprints that are sensitive to vegetation. Empirical studies indicate that although plants with a high surface cover and/or high vegetative biomass dominated the eDNA signal of soils and sediments, more sparse cover, as well as scattered and rare taxa, can also be detected (Yoccoz et al. 2012; Niemeyer et al. 2017; Alsos et al. 2018; Edwards et al. 2018; Capo et al. 2021). The eDNA signal thereby records a highly localized signal of vegetation. For soils, Edwards et al. (2018) demonstrated that eDNA records species within less than a meter from

sampling points, and hence several authors could distinguish between vegetation communities using eDNA, e.g. boreal heath and meadows in Norway (Yoccoz et al. 2012; Edwards et al. 2018), subalpine and alpine grassland, heath and meadows in France (Taberlet et al. 2012). Differences in vegetation communities were also distinguished based on eDNA signals derived from sediments, collected from lakes (e.g., Niemeyer et al. 2017) or streams (e.g., Evrard et al. 2019). Particularly relevant for the development of eDNA fingerprinting is that the diversity of taxa was better represented in eDNA signals from catchments with high water erosion rates and a high connectivity along the hydrographic network (Giguet-Covex et al. 2019). Although eDNA quantity in soils and sediments is sufficient to detect taxa, the detection rate may differ between plant growth forms. Yoccoz et al. (2012), for example, observed that the relationship between plant biomass and eDNA abundance in soils varied between woody plants, graminoids and forbs, and suggested that in addition to total plant biomass, biomass turnover rates must also be considered when interpreting soil eDNA.

One possible, yet unexplored avenue is the use of eRNA for fingerprinting (Tytgat et al., 2016). As RNA it is much less stable then DNA, it could serve as chronometers of sediment transfer in a similar way as ^{7}Be or $^{210}Pb_{ex}$ is being used (e.g., Evrard et al., 2016).



Sediment source areas identified from eDNA fingerprinting as ecological restoration priority (high soil mobilisation rates and high connectivity to the fluvial network).

Area not being a sediment source or poorly connected to the fluvial network and therefore not detectable from eDNA fingerprinting. Not considered an ecological restoration priority.

Fig. 3 As soils get mobilized by water erosion and landslides, particle-attached eDNA allows to define sediment provenance in terms of vegetation type. (1) Plant DNA is bound to fine mineral particles giving every soil a unique eDNA signature, (2) Highly degraded alpine grassland on ski run with gullies, (3) Overgrazed pasture with numerous shallow landslides, (4) Degraded shrubland with isolated shallow landslides, (5) Broadleaf forest with debris flow, (6) Ecologically restored subalpine grassland without erosion, (7) Cropland with sheet and rill erosion, (8) Exotic species on eroding riverbank, (9)-(10) Deposited sediment along the river or in a lake containing eDNA from sediment sources which are hydrologically connected to the fluvial network.

Understanding the quality and persistence time of eDNA fragments in soils and sediments is of utmost importance for the development of a tracing technique. However, our understanding of eDNA persistence times and the factors that control eDNA degradation is still limited (Pietramellara et al. 2009; Evrard et al. 2019; Foucher et al. 2020; Kanbar et al. 2020; Capo et al. 2021). In principle, the chemically-induced degradation of extracellular eDNA (i.e. DNA exuded from cells) starts immediately after its release (Nagler et al. 2018). However, extracellular eDNA is rapidly adsorbed onto fine mineral soil particles such as clay, which protects it from nuclease activity (Nagler et al. 2018). Factors that control eDNA persistence are DNA properties (e.g. molecule length and ionic strength), soil properties (e.g. mineralogy, exchangeable clay content and pH), environmental conditions (e.g. humidity and temperature), and microbial activity (Nagler et al. 2018; Taberlet et al. 2018; Giguet-Covex et al. 2019). The characterisation of eDNA signatures and their strength also varies with soil depth. Erosion of soil horizons enriched in organic material (mainly topsoils) provided greater amounts of eDNA as compared to erosion from mineral soil horizons (Giguet-Covex et al. 2019). Mineral soil horizons (i.e. subsoils) may yield eDNA signatures which result from the influx of water or soil particles from organic soil horizons, rendering in subsoils an eDNA signature that is weaker, yet similar to that of the topsoil. However, mineral soil horizons can also contain eDNA from root litter, and it has been suggested that this could result in deeper soil layers having a distinct eDNA signature (Andersen et al. 2012; Nagler et al. 2018). Furthermore, eDNA extracted from soil samples can include vascular plant taxa represented by both active and dormant tissues, seeds, pollen and litter, and may therefore not necessarily reflect the vegetation cover at the time of geomorphological activity, resulting in false positives in eDNA fingerprints (Fahner et al. 2016; Beng et al. 2021). Where soils are sparsely vegetated, i.e. those most susceptible to water erosion, belowground plant species richness may still allow the origin of soil to be identified from its eDNA signal (Hiiesalu et al. 2012). Overall, the persistence of eDNA from plants in soils requires more research and, more specifically, there is limited information on the cycling of eDNA and its signal strength in relation to chemical composition (e.g. lignin and cellulose content) and the (resulting) differential recalcitrance of plant tissues (such as roots compared to shoots) (Silver and Miya 2001; Levy-Booth et al. 2007). Empirical research indicates that plant species with traits favouring eDNA preservation (e.g., organs with a high quantity of cellulose), may leave high quality eDNA signals in soil for many decades (Yoccoz et al. 2012; Foucher et al. 2020). On the contrary, plants for which the DNA degrades relatively rapidly (such as for crops) may only allow the detection of changes in vegetation type over a period of several years (Foucher et al. 2020).

The persistence of eDNA in sediments during water-mediated transportation and deposition depends on an array of environmental properties such as microbial activity, oxygenation, ultraviolet (UV) penetration and pH, and has mainly been studied in relationship to eDNA burial in lakes and reservoirs (Capo et al. 2021). Once deposited in water bodies, (deep) burial in anoxic conditions favours long-term eDNA preservation (Giguet-Covex et al 2019). However, degradation processes continue to break eDNA strands into smaller fragments, reducing the quality of eDNA molecules for taxonomic classification (Valentini et al., 2009). From a mesocosm experiment simulating a stream environment, Nevers et al. (2020) demonstrated that fish eDNA signals in sediment (sand particles) degrade rapidly and may drop below detectable levels after two to three months. Furthermore, eDNA desorption from particles can also occur in sediment deposits (Capo et al. 2021).

In addition to the quality of eDNA signals in soils and sediments, the success of identifying plant species through eDNA also depends on the ability to extract, sequence and taxonomically identify the eDNA molecules (Capo et al. 2021). Optimizing the DNA extraction protocol depending on the physical and chemical properties of the sediment may for example improve the recovery of DNA originating from plants, and different extraction protocols may produce diverging results (Capo et al. 2021). For amplification based on polymerase chain reaction (PCR), plant-specific g-h primers (Taberlet et al. 2007) are commonly used to amplify short fragments of the P6 loop region of the chloroplast trnL (UAA) intron, which has allowed species-level identification for the large majority of amplified sequences but with some variability among plant families and functional groups (Taberlet et al. 2007; Alsos et al 2018; Niemeyer et al 2017; Edwards et a 2018; Giguet-covex 2019; Foucher et al. 2020; Stoof-Leichsenring et al; 2020). However, freshly deposited and well-preserved sediments may contain longer DNA segments, for which primers targeting the rbcL gene of chloroplast DNA and internal transcribed spacer (ITS) of nuclear DNA may increase the taxonomic resolution (Fahner et al. 2016). An alternative, yet so far unexplored approach for sediment source fingerprinting, is to combine short sequences from environmental metagenomes into longer taxonomic markers, as successfully done in an eDNA study in Arctic lake sediments (Pedersen et al. 2016). This approach allows the analysis of fragmented and hence poorly preserved DNA, but is at the same time more expensive and time consuming. The taxonomic resolution achieved is also limited by the extent of the taxonomic sequencing database. The number of species for example, differs significantly between reference libraries associated with genetic markers (Hollingsworth et al 2011). Therefore, reference databases (e.g., Barcode of Life Database) may need to be extended with DNA barcodes for plants from largely understudied regions, such as high mountains (Edwards et al. 2018).

Sediment sampling for eDNA fingerprinting

As eDNA fingerprinting is new method to sediment tracing, we discuss the major considerations when targeting specific sediment types, i.e. suspended sediment, lag deposits and lake/reservoir deposits (Online Resource, **Table S1**). A major point of attention is that the sampling equipment needs to be sterile to avoid eDNA contamination, leading to the creation of false positives in the data. For suspended sediments, sterilization can easily be achieved when collecting samples as snapshots (Deffersha et al., 2021), using recipients that are inserted in the stream only once. More challenging is the use of automatic samplers to collect suspended sediment, as the tubing should ideally be sterilised before collecting each individual sample.

Lag deposits on river beds or floodplains can be easily collected using sterile equipment and recipients, and are potentially highly suitable for eDNA fingerprinting. However, as lag deposits are exposed to the atmosphere, airborne contamination of the sediment by allochthonous eDNA may occur (Johnson et al. 2021; Lennartz et al. 2021). This type of contamination would probably produce weak eDNA signals in the sediment, which could be excluded from the data by defining a threshold below which detected species (including false positives) are not considered when identifying sediment sources. Another possible source of contamination relevant for sediments exposed to the atmosphere is allochthonous plant litter (Poté et al. 2009) or plant growth on the sediment deposits, as well as bioturbation. The time between sediment deposition and sampling should be kept as short as possible. Furthermore, as explained in the previous section, eDNA degrades with time when exposed to environmental conditions such as high temperature. Similar issues of imperfect sampling and eDNA persistence may apply when using sediments collected from time-integrated samplers (Gateuille et al., 2019).

Sediment deposits in lakes or reservoirs have eDNA signals that persists for long periods, conserving plant eDNA signals for thousands of years (Willerslev et al., 2003). However, these sources are also subjected to imperfect sampling (Beng et al., 2021; Capo et al. 2021), reducing the accuracy of soil erosion hotspot identification. Overall, eDNA fingerprinting is a very promising tool to trace sediments, but more research is needed in the context of soil erosion studies and the environments in which samples are collected.

The contribution of eDNA fingerprinting to ecological restoration activities

Mitigating erosion, mass movements, and geological hazards in high mountains is increasingly conceived within frameworks of ecological restoration, i.e., recovering the form and function of ecosystems that have been damaged by degradation (Hubble et al. 2017). In a high mountain environment, ecological restoration activities can also comprise the prevention and control of slope and riverbank instabilities as well as the confinement of runoff and sediment regimes to the capacity river channels. In this regard, the practice of soil and water bioengineering is rapidly emerging as a short-term hazard control that can enable long-term ecological recovery (Rey et al. 2019). This practice includes a myriad of nature-based solutions that are co-designed by practitioners and researchers (Stokes et al. 2014). However, the application of soil and water bioengineering in high mountains can be limited by severe environmental conditions, such as strong, desiccating winds, high temperature fluctuations, prolonged snow cover, the presence of shallow and nutrient-poor soils and exposure to events that generate extreme runoff. Therefore, plant establishment and ecological recovery times are slow in high mountains (Dupin et al. 2019). Consequently, interventions are often only partially successful or suffer from high failure rates.

High mountain environments are characterised by biogeographic units along altitudinal gradients that show a strong differentiation in vegetation communities. High-resolution vegetation maps of these units are increasingly available (e.g., Dirnböck et al. 2003; Dobrowski et al. 2008; Zhang et al. 2020), and usually include typical indicator species per vegetation community. Furthermore, topographically-controlled micro-climatic conditions are associated with local plant species distribution (Scherrer and Körner 2011). Because there are strong relationships between vegetation types and geomorphological processes in high mountain environments (Geertsema and Pojar 2007; Giaccone et al. 2019; Lizaga et al. 2019; Shu et al. 2019), the use of eDNA to track erosion sources would provide information to the species level and be able to determine changes in vegetation over short timescales. Furthermore, eDNA signals in sediments will mainly originate from areas experiencing higher erosion rates and which are highly connected with the hydrographic network (**Fig. 3**).

The use of eDNA sediment source fingerprinting would allow the investigation of complex and often poorly understood relationships between vegetation cover, restoration activities, and geomorphological response at the catchment scale. In many regions, long-term land use has strongly modified the vegetation communities of biogeographic belts, with impacts on soil hydrology, erodibility, stability, and catchment hydrogeomorphological responses (e.g., Bajard et al. 2020). Agro-pastoralist practices specific to high mountains have shaped vegetation and soils over centuries, depending on the type and intensity of mowing, grazing, fertilization and irrigation (Tasser and Tappeiner, 2002; Bajard et al. 2017). In recent decades, the abandonment of these practices around the world has caused the rewilding of high mountain areas (e.g., Nyssen et al. 2014). Secondary vegetation succession has, however, not necessarily reduced erosion or mass movements. The restoration of slope stability with vegetation is far from straightforward (Kim et al. 2017; Lan et al. 2020), and relies much on information about root distribution and mechanical traits (Stokes et al. 2009; Rossi et al. 2017). Recent studies have also stressed the particular importance of diverse plant communities and associated traits for the stabilization of slopes (Kobayashi and Mori 2017; Wessels 2017). Source discrimination in sediment fingerprinting should, therefore, be based on catchment properties that allow the highest discrimination potential, i.e. eDNA, and are directly linked to restoration efforts. To improve the success rates of restoration activities, collaboration between scientists and stakeholders can accelerate technology transfer rates (Stokes et al. 2014; Frankl et al., 2016; Giupponi et al. 2019; Rey et al. 2019). However, time and budget constraints often hamper in-situ monitoring of soil and water bioengineering applications, and very few monitoring programs exist (Giupponi et al. 2019). Knowledge of success rates is, however, essential for restoration (Frankl et al. 2021). To this end, sediment source fingerprinting has been shown to provide a valid framework for supporting soil restoration activities (Mukundan et al. 2012; Walling, 2013). Environmental DNA has already been used to successfully monitor restoration programs, but with a focus on fungal species (Yan et al., 2018). To identify vulnerable locations in which interventions are urgently needed, the use of riverbed lag deposits collected after major hydro-climatic events could be the most valid approach (Sellier et al. 2020). With the growth of plant DNA barcoding databases, taxonomic information can be derived directly from primers relevant to vascular plants (ITS2 and rbcL; Yan et al., 2018). The scope of applications is not limited to the identification of present-day sediment sources, but can be expanded to investigations of human-environment interactions over longer times scales (for example, when applied to lake sediments) (**Fig. 3**). Expanding the spectrum of eDNA signals to microbiological communities could also allow the exploration of the importance of the soil microbiome in ecological restoration (e.g., Burri et al. 2009), and yield an indicator of catchment biodiversity (Taberlet et al. 2018).

Conclusions

In high mountain environments, biogeographical zones are characterised by unique vegetation communities that are adapted to prevailing environmental conditions and where geomorphological processes are closely related to vegetation type and cover. As sediment source fingerprinting research should rely on catchment characteristics that yield the highest source discrimination potential, we argue that this characteristic should be the type of vegetation. This opinion is supported by the challenges that land managers encounter in the restoration of ecosystems. We emphasise that eDNA source fingerprinting should be further developed, in combination with conventional approaches, in order to understand geomorphological dynamics in high mountain environments and their relationships with ecological restoration because:

- Strong associations exist between geomorphological processes and vegetation, and thus, a sediment fingerprinting technique that is sensitive to vegetation would allow the monitoring and evaluation of soil and water bioengineering applications.
- eDNA signals in soils and sediments allow discrimination between plant species. This information can be linked to vegetation maps to create a novel sediment fingerprinting approach and identify erosion hotspots at unprecedented resolutions.

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Supplementary Information

Literature search: In December 2020, we retrieved papers from a database of peer-reviewed literature (https://www.scopus.com/) and processed them in a reference management system (https://www.mendeley.com/), as specified in **Fig. S1**. Articles dealing specifically with high mountain environments were selected based on the following three criteria:

1. Study areas must overlap, at least partially, with a mountain area, as defined by terrain ruggedness (Gruber 2012), and in reference to the mapped mountain regions in the 2019 IPCC Special Report on the Ocean and Cryosphere in a Changing Climate.
2. Studies should reference the environmental characteristics that define subalpine and alpine vegetation belts in high mountains. This was confirmed by looking for terms such as "ice", "snow" and "alpine" in the full articles.
3. Studies should focus on multiple sediment sources from high mountain environments. This excluded studies of large-scale provenance in which (i) high mountain regions were only considered as one source type, or (ii) only major units of mountain belts were considered (as the scale of such studies is not relevant for ecological restoration).

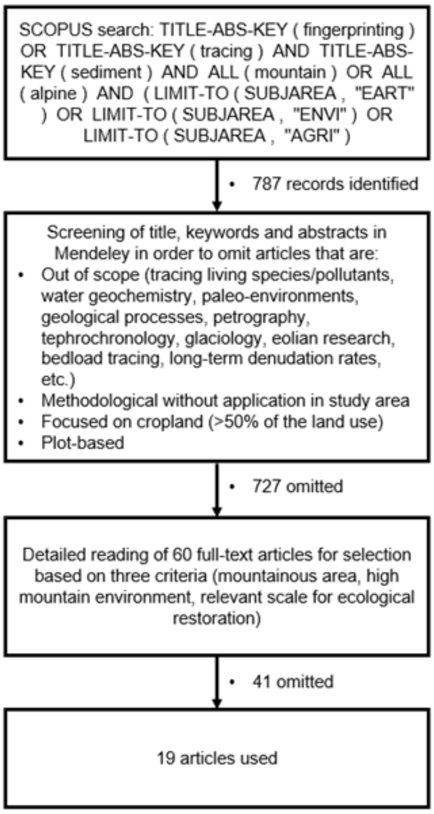

Fig. S1 Flowchart for selecting peer-reviewed papers on sediment source fingerprinting specific to high mountain environments.

The 19 used articles were read and their information was synthesised and used according to the variables of Table S1.

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Data retrieved from the literature search

Table 1 Studies on sediment source fingerprinting in high mountain environments

Reference	Country (Mountain range)	Lat., Long.*	Surface area (km²)	Altitude range (m a.s.l.)	Tracing properties considered	Source type	Sources (#)	Dominant land use
Gateuille et al. (2019)	Canada (Rocky Mts.)	54.014°, -124.013°	25200	c. 650 - c. 1100	Geochemical properties	Land use + surface / subsurface	3	Forest
Stone et al. (2014)	Canada (Rocky Mts.)	49.519°, -114.507°	715	1100 - 3100	Geochemical properties	Sub-catchments / Land use	3	Conifer forests
Legout et al. (2013)	France (Alps)	44.093°, 6.231°	22	c. 700 - c. 1900	Physical characteristics (spectral)	Lithology	4	Forest and grassland
Navratil et al. (2012b)	France (Alps)	44.093°, 6.231°	905	405 - 2961	Geochemical properties	Lithology	4	Forest (44%)
Navratil et al. (2012a)	France (Alps)	44.093°, 6.231°	905	405 - 2927	Geochemical properties	Lithology	4	Forest (44%)

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Evrard et al. (2011)	France (Alps)	44.093°, 6.231°	905	405 - 2960	Geochemical properties, Environmental radionuclides	Lithology and erosion processes	4+2	Forest (44%)
Poulenard et al. (2012)	France (Alps)	44.093°, 6.231°	22	c. 700 - c. 1900	Physical characteristics (spectral)	Lithology	4	Grassland (67%)
Delunel et al. (2014)	France (Alps)	44.91°, 6.26°	14	c. 1600 - 3564	Environmental radionuclides	Geomorphic domains	4	
Foster et al. (2003)	France (Alps)	45.8°, 6.133°	26.5	c. 447 - 2351	Mineral magnetic properties	Lithology and soil type	4	Conifer forest and grassland
Froehlich and Walling (2006)	India (Himalaya)	26.528°, 88.754°	c. 6500	c. 80 - 8585	Environmental radionuclides	Surface / subsurface	2	
Raigani et al. (2019)	Iran (Zagros Mts.)	34.248°, 47.496°	308	1300 - 2600	Geochemical properties	Sub-catchments / Lithology	3	Rangeland (43%)
Nosrati et al. (2018a)	Iran (Kopet Dag Mts.)	36.317°, 58.917°	228	1213 - 3262	Geochemical properties	Sub-catchments / Lithology	3	Rangelands, woodlands (70%)

Nosrati et al. (2018b)	Iran (Elburz Mts.)	36.677°, 54.439°	78	550 - 2950	Geochemical properties, Environmental radionuclides	Surface / subsurface	3	Forest (66.7%)
Nosrati and Collins (2019b)	Iran (Elburz Mts.)	35.803°, 51.358°	292	1721 - 2793	Geochemical properties	Surface / subsurface	3	Grazing land (97.4%)
Nosrati and Collins (2019a)	Iran (Elburz Mts.)	35.808°, 51.326°	< 1	c. 1800 - c.2500	Geochemical properties	Surface / subsurface	3	Grazing land (72%)
Palazón et al. (2014)	Spain (Pyrenees)	42.583°, 0.483°	283	1039 - 3404	Mineral magnetic and environmental radionuclides	Lithology and soil type	3	
Stutenbecker et al. (2019)	Switzerland (Alps)	46.233°, 7.406°	385	492 - 4346	Geochemical properties	Sub-catchments / Lithology	3	> 50% little or no vegetation, followed by shrub, herbaceous vegetation (c. 22%)
Battista et al. (2020)	Switzerland (Alps)	47.067°, 8.283°	477	c. 440 - c. 2100	Environmental radionuclides	Surface / subsurface	2	
Resentini et al. (2017)	Taiwan	23.698°, 120.961°	approx. range 200 - 2000	0 - 3952	petrographic and mineralogical fingerprint	Lithology	2-3	

* As reported or obtained from Google Earth using the catchment name or place names mentioned. The coordinates can refer to the outlet of the catchment or to a location within the study area.

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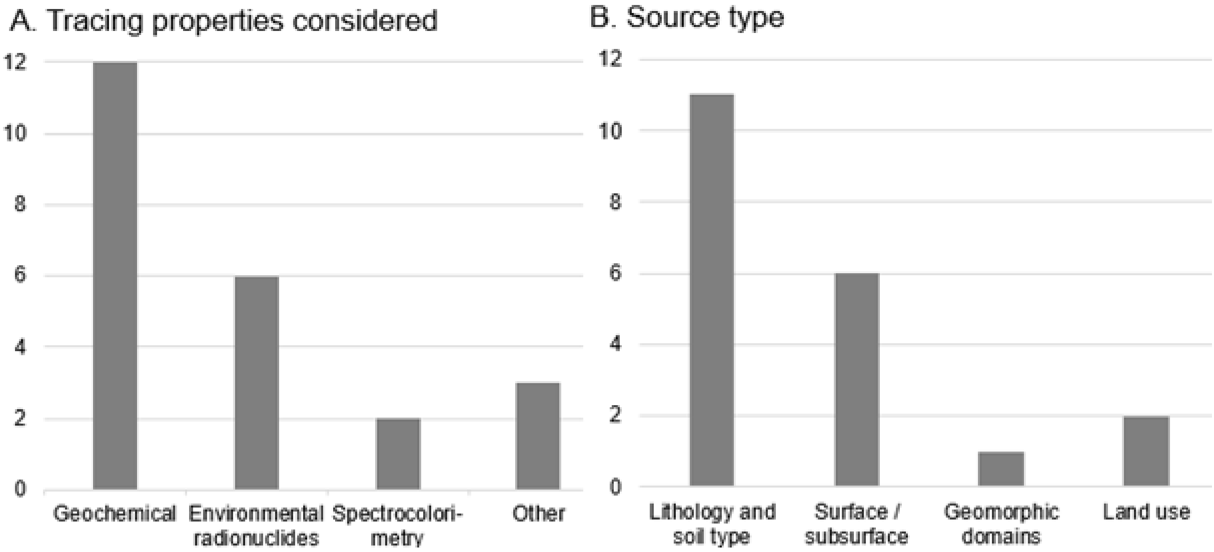

Fig. S2 Number of studies relevant to the major discriminating characteristics (A) and source types (B)