Ecosystem Services 73 (2025) 101730

Contents lists available at ScienceDirect

Ecosystem Services

journal homepage: www.elsevier.com/locate/ecoser

Review Paper

Global impacts of glacier retreat on ecosystem services provided by soil and vegetation in mountain Regions: A literature review

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ARTICLE INFO

Keywords:
Biodiversity change
Climate change impacts
Ecosystem functioning
High-mountain environments
Nature's contributions

ABSTRACT

Glacier retreat in mountain regions is driving profound ecological transformations with significant implications for biodiversity and socio-economic activities. However, the impacts of these ecological changes on ecosystem functioning and service provision remain poorly understood. This systematic literature review synthesises existing knowledge on the impacts of glacier retreat on ecosystem services provided by soil and vegetation in high-mountain regions worldwide. We identified 11 ecosystem services from 383 papers showing that the roles of plants and soil in providing ecosystem services shift over space and time as glaciers retreat. Regulating services, such as climate regulation and soil erosion mitigation, generally increased with glacier retreat, while supporting services, such as nutrient cycling, showed idiosyncratic responses that depended on the local context. Additionally, certain ecosystem services, such as the provision of biochemical and genetic resources, occurred only in areas near glacier fronts and have not been recorded elsewhere. These shifting patterns highlight potential trade-offs and win–win conditions in ecosystem service provision between vegetation and soil as well as within different plant communities. We conclude by emphasising the need for conservation and management strategies that account for both gains and losses of ecosystem services as well as for changes in biodiversity that sustain these services. Understanding the consequences of biodiversity change for ecosystem service dynamics is crucial for informing sustainability efforts and ensuring the resilience of high-mountain ecosystems in the face of ongoing glacier extinction.

1. Introduction

Mountains are among the fastest-changing and most impacted environments by climate change (Beniston, 2012). Over the past forty years, temperatures in mountain regions have risen three times faster than the global average, resulting in rapid glacier mass loss (Albrich et al., 2020; Gao et al., 2016; Lamprecht et al., 2018; Pepin et al., 2015). Current estimates predict that glaciers could lose between 18 % and 36 % of their mass globally by 2100 (IPCC, 2019; Dussaillant et al., 2019; Sommer et al., 2020). Despite the significant impact that glacier retreat is already having on the livelihoods and well-being of mountain communities worldwide, it is estimated that the retreat could expose approximately 149,000 ± 55,000 km^2 of land (an area the size of Nepal) by 2100 (Cook et al., 2023). This could create new opportunities for ecosystems to develop in these newly exposed landscapes (Bosson et al., 2023; Carey et al., 2017; Cauve-Fraunié et a 2016; Cauve-Fraunié and Dangles, 2019; Motschmann et al., 2020; Ranzani et al., 2018). Thus, while glacier loss poses a serious challenge to human societies and economies—given their heavy reliance on the ecosystem services provided by mountain glaciers—the development of new post-glacial landscapes may also offer new ecosystem functions and therefore benefits to human societies.

Glacier retreat exposes barren terrains referred to as proglacial habitats, which expand over time and undergo ecological and physical changes (Erschbamer & Caccianiga, 2016). Proglacial regions progress through various stages, each marked by distinct physical features and vegetation communities (Erschbamer & Caccianiga, 2016; Losapio et al., 2021; Marcante et al., 2009; Ficetola et al., 2021). These rapidly

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https://doi.org/10.1016/j.ecoser.2025.101730
Received 24 October 2024; Received in revised form 11 April 2025; Accepted 12 April 2025
Available online 24 April 2025
2212-0416/

evolving environments have drawn significant scientific interest, with proglacial mountain regions increasingly seen as "living laboratories" for studying how ecosystems develop following climate change (Fickert, 2020). While much research has focused on vegetation and soil development, there remains a crucial gap in understanding how these affect ecological processes and services. Ecosystem services (ES)—defined as the direct or indirect contributions of ecosystems to human well-being (De Groot et al., 2002; Millennium Ecosystem Assessment, 2005)—are crucial for understanding both the ecological dimension of climate change and biodiversity change as well as the socio-economic and policy dimension of climate and ecological actions (Palomo, 2017). Understanding how ES shift with glacier retreat and biodiversity change is key to assessing ecosystem gains, losses, and effective strategies.

Although the concept of ES has been defined multiple times, sometimes with contradicting terminology (Boyd and Banzhaf, 2007), this concept continues to be very useful, in particular for regions which are highly vulnerable to climate change and where the supply of natural resources is intertwined with the socio-economic development of the local communities (Garmendia et al., 2022; Grêt-Regamey et al., 2012). High-mountain regions are home to over 671 million people, and more than half of the global population depends—directly or indirectly—on mountain-related ES, which have been considered of high value in global ES evaluations (Duan et al., 2017; Jones & O'Neill, 2016; Huber et al., 2013; Zhang et al., 2019). Furthermore, mountain ecosystems contribute directly to several United Nations Sustainable Development Goals (SDGs) (UN, 2015). In particular, they play a key role in water regulation and sanitation, food production, biodiversity maintenance, and climate regulation (Bolch, 2017; Clason et al., 2022; Cook et al., 2021; Immerzeel et al., 2020; Zhang et al., 2019).

Although the demand for ES provided by mountain ecosystems, particularly those with agriculture practices, has been widely studied across various disciplines (Grêt-Regamey et al., 2020; Locatelli et al., 2017; Palomo et al., 2017), far less attention has been given to the current and future supply of ES emerging after glacier retreat in less accessed, high-mountain regions. Consequently, the role of these newly formed ecosystems in contributing to various Sustainable Development Goals (SDGs) remains poorly understood. Given the rapid pace of glacier melt worldwide, understanding these emerging ecosystems and their potential future impacts is crucial. Zimmer et al. (2022) emphasise the urgent need for research and responsible management of these newly exposed landscapes.

Despite the growing body of research on ecological succession in proglacial environments, a comprehensive synthesis of the ES emerging in these landscapes remains lacking. To address this gap, this study systematically reviews existing literature to: (1) Identify the ES provided by soil and vegetation after glacier retreat, (2) Analyse how the provision of these ES changes over time and space as glaciers retreat, and 3) Demonstrate the importance of examining ES through measured ecological indicators, even when ES terminology was not explicitly used, as a way to address knowledge gaps in this field. To achieve these objectives, this study addresses the following research questions: (1) What ES provided by soil and vegetation in recently deglaciated areas can be identified based on the existing literature? (2) What roles do plants and soil play in delivering these services at different stages of glacier retreat, and how do these roles and their interactions shift over time as the ecosystem develops? (3) What key knowledge gaps exist in the study of ES in recently deglaciated landscapes?

Through a comprehensive global systematic review of current literature, we assess how glacier retreat influences ES while examining how biodiversity change influences multi-dimensional ES responses. Our study offers a synthesis of the dynamic changes of ES, highlighting how some services diminish or disappear as glaciers recede while new ES emerge and others are transformed. The results of this literature review are divided into two parts: (1) the identification of ES and (2) how they change with glacier retreat. In the discussion, we examine overarching trends, exceptions, and the role of plant–soil interactions in mediating these changes, highlighting their functions and roles in socio-ecological systems. We conclude by highlighting critical gaps where empirical research is still lacking, offering insights for both ecological theory and applied conservation and management policies.

2. Materials and methods

2.1. Search strategy

We conducted the literature search using the following keywords: TITLE-ABS-KEY ((plant* OR vegetation OR flora OR "vascular plant" OR "plant community" OR "plant succession" OR "vegetation cover") OR (soil OR topsoil OR "soil formation" OR "soil properties" OR " soil organic matter" OR "soil fertility" OR "soil microbial" OR "soil community") AND ("glacier retreat" OR deglaciation OR "glacier recession" OR "post-glacial" OR "glacier foreland") OR "mountain glacier" OR "time since deglaciation")) AND PUB YEAR > 2005 AND (LIMIT-TO (DOCTYPE, "ar")). Given the limited knowledge and small number of published research studies on ES in proglacial environments, we intentionally avoided using terms specific to individual ES types such as "climate regulation" to prevent excluding studies that did not explicitly use ES terminology but nevertheless investigated plant and soil functioning that has been previously linked to ecosystem benefits. This approach ensured that studies examining regulatory, provisioning and cultural services were included, even if they did not directly label these functions as "ecosystem services." This strategy enabled us to capture a comprehensive range of studies on plant and soil functions for ES in recently deglaciated areas.

We performed the search in December 2024 using the Scopus and Web of Science databases, covering publications from 2006 to 2024. We chose studies published from 2006 onward to ensure that our findings reflect research conducted after the release of the *Millennium Ecosystem Assessment* (MEA) 2005 framework, which established a common classification and framework for assessing ES across diverse systems.

2.2. Selection of studies

To identify the ES provided by plants and soil in recently deglaciated mountain areas, a systematic literature search was conducted following the *Preferred Reporting Items for Systematic Reviews and Meta-Analyses* (PRISMA) guidelines (Moher et al., 2015) to ensure a rigorous and transparent identification and reporting of the selected studies (Fig. 1).

We applied strict inclusion and exclusion criteria to refine our selection of studies. We excluded studies focusing on glacier environments rather than proglacial areas, such as glacier ice, ice debris, or glacier-fed rivers. Although reference sites beyond the successional stages are not strictly located within proglacial regions, they were included to provide insights into how post-glacial landscapes develop without direct glacier influence. Studies on historical glacier, mountain or proglacial reconstructions were only considered if they examined plant- or soil-driven geomorphological changes. We limited the timescale to research conducted on landscapes that emerged during and after the Little Ice Age, excluding studies on glacier dynamics from earlier times such as the Pleistocene glaciations. These criteria ensured a targeted analysis of plant-driven ecosystem processes in proglacial environments.

Our selection only included studies on primary succession driven by glacier retreat, excluding those on fire-induced succession or other drivers. We included studies which measured physical, chemical or biological aspects of vascular plants and soil, including biological soil crusts (biocrusts) and all soil horizons. Studies focusing on animals or non-vascular plants were excluded, except when assessing soil or plant contributions to their diversity or interactions.

This study also included review papers that, while not focused specifically on our topic, provided crucial insights for our study. These reviews were included to help us identify relevant references, contextualise our findings within broader research trends, and ensure a

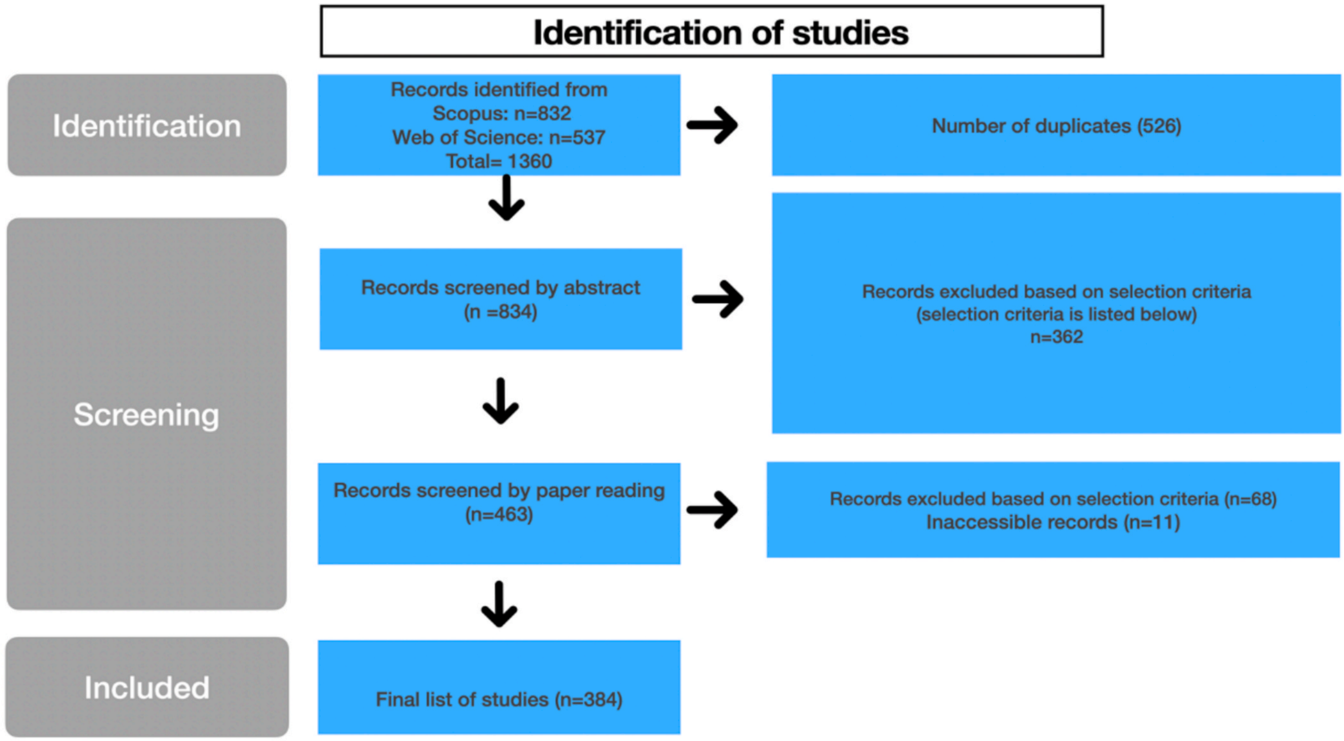

Fig. 1. ***Preferred Reporting Items for Systematic Reviews and Meta-Analyses*** **(PRISMA) flow diagram illustrating the study selection process.** The initial search identified 1,360 records from Scopus (n = 832) and Web of Science (n = 537). After removing 526 duplicate records, 834 records remained for abstract screening. Based on predefined selection criteria, 362 records were excluded, leaving 463 records for full-text review. An additional 79 records were excluded (68 based on selection criteria and 11 due to inaccessibility), resulting in a final inclusion of 383 studies for analysis.

comprehensive synthesis of existing knowledge. By including them, we aimed to cross-check our bibliography and integrate key perspectives that might have otherwise been overlooked. Any papers that were already part of our original dataset were excluded. We then screened the remaining papers using the same PRISMA flowchart and applied the same selection criteria to them (Fig. 1). All papers that met the inclusion criteria were subsequently added to our original list (n = 41). Our final list contained 383 studies.

For each of the 383 retained studies, we extracted information on: (i) the country of the study; (ii) the glacier name(s); (iii) the temporal scale (s) of the chronosequence(s) evaluated (a chronosequence being the succession of ecological stages following glacier retreat); (vi) the ES identified in the study; (iv) the measured ES indicator(s); (v) the reported stage(s) of the chronosequence (early, mid, late stage) (see Fig. 3); (vi) the ES trend(s) associated with glacier retreat and the number of papers supporting this trend.

2.3. Ecosystem service identification

We used the Millennium Ecosystem Assessment (MA) classification framework, which divides ES into four broad categories: (i) regulating, (ii) provisioning, (iii) cultural and (iv) supporting services (MA, 2005). We categorised each study based on the ES it measured.

If a study did not explicitly mention ES, we identified the ES based on the study's scope and the indicators measured. We assigned the ES category based on indicators that have been used as proxies for ES supply in other studies or used to measure ecosystem processes and functions linked with ES (Drobnik et al., 2018; Fu et al., 2013; Miedema and Anand, 2022). Studies could fall under multiple ES categories if they measured different indicators or used an indicator that has been linked to multiple ES (Greiner et al., 2017). For example, studies measuring soil carbon content were linked to both carbon regulation and nutrient cycling.

To assess ES trends associated with glacier retreat, we categorised studies based on the stage of the chronosequence at which the ES was observed. Given that glacier retreat rates vary globally due to differences in topography and microclimate, the studies were grouped into three stages based on vegetation community structure and development, rather than the age of deglaciation (see Fig. 3). Following the principles of ecological succession, proglacial regions were divided into stages. Stage 1 encompasses the proglacial zones closest to the glacier, characterised by barren deposits and pioneer plant species. Stage 2 represents a transitional phase and Stage 3 includes the oldest, most established communities, dominated by competitive species typically referred to as "climax" vegetation (van Andel et al., 1993; Meiners et al., 2015).

We classified ES trend directions as positive when ES-related indicators increased over time and negative when they declined as the glacier retreated. For studies that did not track changes over time or space–time, we recorded only the identified ES and the observed stage. To quantify the most consistent trends recorded for each indicator, the number of studies supporting each trend were counted and then compared with the total number of studies measuring the same indicator. Indicators that were only found in one study were not recorded for comparison. For studies evaluating trends across multiple glaciers, we recorded each glacier's trend individually.

3. Results

3.1. Geographic distribution of ES studies

Out of the 383 selected studies, 125 were conducted in China, with most of these taking place on the Hailuogou Glacier, which has experienced rapid retreat primarily due to the influence of a changing monsoonal temperate climate. The second-most reported country was Switzerland with 75 studies carried out, the majority of which on the

Damma Glacier. Norway accounted for 95 studies, of which the majority were conducted in Svalbard, specifically in the Midtre Lovénbreen proglacial region.

3.2. ES recorded in proglacial zones

On average, each study measured 2.12 ES. Provisioning services were the most measured (n = 309) followed by supporting services (n = 300). In contrast, regulatory services were measured by 203 studies, while no studies measured any indicators that could be linked to plant and soil contribution to cultural services in proglacial regions (Fig. 2). All 11 ES were reported across all successional stages, regardless of the geographical location of the study site.

3.2.1. Regulating services

Six different regulating ES were recorded in proglacial regions: climate regulation (n = 147), soil erosion regulation (n = 8), water regulation (n = 32), air quality regulation (n = 7), pollination (n = 8) and disease regulation (n = 1). Of the 147 studies on climate regulation, most focused on the contribution of plants and soil to carbon storage, identifying proglacial zones as important carbon sinks with potential for climate change mitigation. Other studies investigated the role of plants and soil as CO_2 emitters in these emerging ecosystems (Thomazini et al., 2014; Wang et al., 2020).

Overall, proglacial regions were found to act as both carbon sinks and sources at different stages of ecosystem development (Chiri et al., 2015; Conen et al., 2017; Li et al., 2022). The melting and flowering seasons also influenced climate regulation, with all stages storing soil for brief periods or throughout the year (n = 125) (Li et al., 2022; Vilmundardóttir et al., 2017). In addition to their role in climate regulation, soil–plant interactions contributed to erosion regulation and slope stability in specific areas of proglacial zones (n = 8) (Ohler et al., 2023; Musso et al., 2020). Studies measuring slope stabilisation further linked geomorphic stabilisation with changes in plant functional traits with glacier retreat (Eichel et al. 2016; Haselberg et al., 2024). Plants also contributed to disease regulation by shaping the spread of antibiotic-resistant genes (ARGs) (Li et al., 2023). Their role in regulating atmospheric pollutants was measured by analysing the concentrations of heavy metals in plant tissues (Chen et al., 2023). Water regulation, identified as a soil contribution following glacier retreat, was also significant, with soils acting as water storage systems and subsurface flow paths across different stages (n = 34) (Hagedorn et al., 2015; Hartmann et al., 2022; Strauss et al., 2009).

3.2.2. Supporting services

This review also highlights the significant role of supporting services in proglacial regions. Most studies investigating nutrient cycling in these areas identified the key contributions of plants and soil to the nitrogen, carbon and phosphorus cycles, with nutrient storage being the most measured indicator in the studies (n = 175) (Nash et al., 2018; Ren et al., 2022). In addition to nutrient storage, soil and plants also played a role in nutrient cycling through key processes such as nutrient fixation and denitrification either directly or indirectly (Bai et al., 2020; Khan et al.,2023; Perez et al., 2023; Sun et al., 2023). These processes were primarily studied by analysing microbial gene expression, enzyme activity, plant functional traits and plant–microbe interactions (Bhattacharya et al., 2022; Kandeler et al., 2006; Zeng et al., 2015; Yang et al., 2021).

Microbes contributed to soil formation by driving both physical and chemical weathering (n = 13), as well as by serving as a source of soil organic matter accumulation (n = 47) (D'Amico et al., 2014; Frey et al., 2010; Rzepa et al., 2019). Other indicators of soil chemical weathering

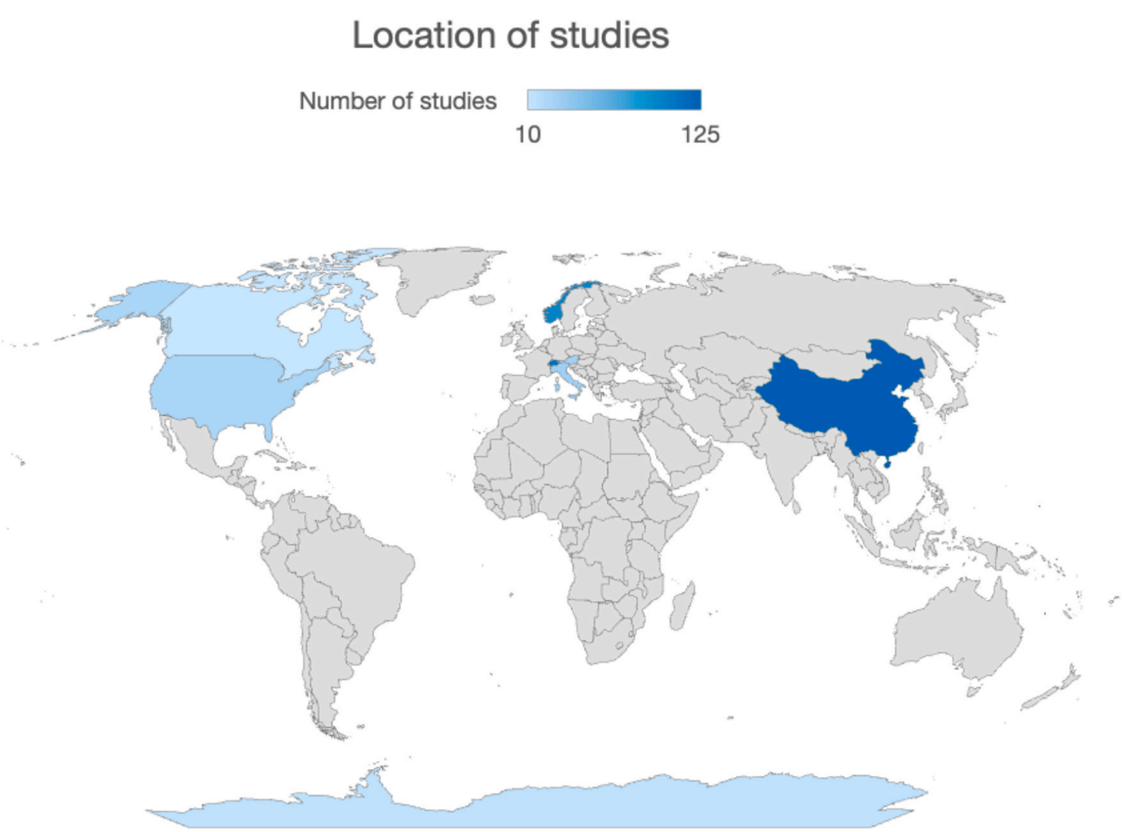

Fig. 2. Geographic distribution of studies included in the review. This global map illustrates the countries where more than ten studies from the review were conducted. Countries and regions with fewer than ten studies are listed separately: Greenland (5), Chile (7), New Zealand (5), Bolivia (2), India (2), Nepal (2), Peru (4), Argentina (2), Kyrgyzstan (2), Australia (1), Colombia (1), Ecuador (1), Iceland (1) Georgia (1), Kyrgyzstan (2), Mexico (1), Russia (1), Tanzania (1), and Venezuela (1).

were also used to measure soil accumulation rates with time (Dahms et al., 2012). In contrast, plants primarily contributed to soil formation through organic matter accumulation from plant litter decomposition (D'Amico et al., 2014). Along with an increase in plant litter, an increase in plant biomass, photosynthetic rate and vegetation cover contributed to the ES of primary production (Wei et al., 2021). Primary production was seen to also support other ES such as climate regulation, food provision, raw materials and oxygen production (Muraoka et al., 2008).

3.2.3. Provisional services

This review also identified the significant role that soil, plants and their interactions play in contributing to genetic resources in proglacial regions (n = 309). Proglacial regions also show a shift between the ES genetic resources for animals, microbes and plants with glacier retreat (Cantera et al., 2024; Insam et al., 2017). Most studies measured different indices of biodiversity across various communities, with the majority focusing on species richness and vegetation cover (Fischer et al., 2019; Wei et al., 2021). Within these studies, the changes in

Table 1

Changes in ecosystem services (ES) provided by soil with glacier retreat. This table summarises the ES delivered by soil in proglacial areas, including the indicators used to measure each service, the trend in ES provision over time following glacier retreat, and the stage (early, mid, or late) where each ES was reported to be most prominent. The trend selected for each ES was the one most frequently reported in the literature. The confidence level reflects the number of studies that observed these trends relative to the total number of studies that identified a trend in the specific indicator. Indicators measured by only one study were not included in the table.

Category	Ecosystem service	Indicator	General trend	Peak stage	Number of studies following trend	Examples
Regulating services	**Climate regulation**	Carbon fluxes	↗	Late	8/8	Bradley et al., 2016; Guelland et al., 2013
		Soil organic carbon storage	↗	Late	80/90	Insam et al., 2017; Montagnani et al., 2019; Wietrzyk-Pełka et al., 2020
		Carbon use efficiency	↘	Early	2/3	Guelland et al.,2013; Venkatachalam et al., 2021
		Carbon accumulation rates	↘	Early	2/3	Guelland et al; 2013; Egli et al., 2012
		Labile carbon content	↘	Early	4/4	Khedim et al., 2021; Ma et al., 2023
		Recalcitrant/stable carbon content	↗	Late	2/2	Jílková et al. 2021; Ma et al., 2023
		Methanotrophic activity	↗	Late	2/2	Mateos-Rivera et al., 2018; Yun et al., 2023
	Water regulation	Soil water content	↗	Late	11/14	Li et al., 2022; Pessi et al., 2019; Noll and Wellinger, 2006.
	Erosion regulation	Soil erosion rates	↘	Early	3/3	Eichel et al., 2013; Musso et al., 2020
Supporting services	**Soil formation**	Soil formation rates	↘	Early	2/3	Dahms et al., 2012
		Soil organic matter (SOM)	↗	Late	28/30	Krauze et al., 2021; Pessi et al., 2019; Schweizer et al. 2018
		Weathering	↘	Early	3/7	Burga et al., 2010
	Nutrient cycling	Carbon use efficiency	↗	Late	2/3	Guelland et al.,2013; Ma et al., 2023; Venkatachalam et al., 2021
		Nitrogen fixation activity	↘	Early	3/5	Brankatschk et al., 2011; Schmidt et al., 2016; Turpin-Jelfs et al., 2018
		Mineralisation activity	↗	Late	2/2	Brankatschk R et al., 2019; van Leeuwen et al, 2021
		Denitrification and nitrification activity	↗	Late	9/10	Brankatschk et al.,2011;Perez et al., 2022
		Nitrogen content	↗	Late	54/62	Alfaro et al., 2020; Dong et al., 2022; Huang et al., 2023; Ma et al., 2013
		Phosphorus content	↘	Intermediate	8/18	Bai et al., 2019; Huang et al., 2023; Greinwald et al.,2023
		Bioavailable phosphorus content	↗	Late	4/9	Huang et al., 2013; Jiang et al., Wang et al., 2020
Provisioning services	**Genetic resources**	Microbial diversity/ biomass	↗	Late	55/87	Yao et al., 2023; Yoshitake et al., 2018; Pessi et al., 2019;
		Diazotrophic diversity	↘	Late	3/4	Bradley et al.,2016; Egli et al., 2012; Frey et al.,2013
		Bacteria: fungi relative abundance ratio	↘	Early	3/5	Alfaro et al., 2020; Bardgett 2007;
		Copiotrophs: oligotrophs relative abundance ratio	↘	Early	2/2	Kim et al., 2017; Ma et al., 2023

distribution of endemic and non-endemic plant species near the glacier terminus, along with the presence of rare taxa and key ecosystem engineers in the glacier foreland were recorded (n = 6) (Anthelme et al., 2022). Other studies analysed functional diversity to better understand underlying ecological changes with glacier retreat (Haselberg et al., 2024; Khelidj et al., 2024; Lei et al., 2021; Losapio et al., 2021). In addition to the provision of genetic resources, plants and soil were recorded to provide biochemical services. While fungi used for biochemical purposes were found in the glacier forefield by one of the studies, plants that could serve as contamination biomarkers were found across all stages (Bing et al., 2016; Calvillo-Medina et al., 2020). Investigations into the role of soil and plants in animal diversity mainly focused on invertebrates (n = 17) (Doblas-Miranda et al., 2011; Lei et al., 2015; Schlegel and Riesen, 2014).

3.3. Ecosystem service provision trends with time since glacier retreat

3.3.1. Trends of ecosystem services provided by soil

All measured ES delivered by proglacial soils were impacted by glacier retreat (see Table 1). Soil's provision of supporting services showed an overall increase in soil formation, with changes in the rate of formation based on bioclimate, parent materials and geomorphological properties (D'Amico et al., 2015). Despite soil organic matter accumulation, soil weathering rates have been shown to decrease further from the glacier while specialised soil fungi have been seen to promote granite weathering near the glacier terminus (Brunnel et al., 2016). Newly developed soils also contribute to the establishment of plants through soil–plant interactions, which further increases organic matter in the ecosystem (Sun et al., 2023; Charles et al., 2025). Trends of soil's delivery of the ES nutrient cycling were also documented, but patterns varied based on the nutrients and the processes within the cycle that were being studied (Brankatschk et al., 2011). For instance, nutrient storage tended to increase with glacier retreat for carbon and nitrogen pools but peaked in the intermediate levels for total and available phosphorus content (Bai et al., 2019; Jiang et al., 2018). Other aspects of the nutrient cycle, including nutrient fixation, mineralisation and nitrification, were observed at all stages; however, their patterns varied across different chronosequences (Perez et al., 2022).

Contrasting trends were also observed within each ES category based on the ecological indicators being measured by each study. For regulating services, climate regulation showed contrasting trends as microbial carbon emissions and carbon storage increased with time, but carbon sequestration rates and soil carbon thermal stability decreased with glacier retreat in some sites (Guelland et al., 2013; Egli et al., 2012). Additionally, the contribution of soil to the regulation of toxic materials included the absorption and release of heavy metals such as mercury and cadmium across the chronosequences (Chen et al., 2023). Soil's delivery of water regulation was measured through water storage, soil moisture and water holding capacity, all of which generally increased with glacier retreat (Liu et al., 2012; Pessi et al., 2019).

Glacier retreat also influenced the delivery of provisioning services by soil. As glaciers receded, microbial diversity, biomass and activity generally increased (Bardgett et al., 2007). However, some studies noticed a shift in the composition of microbial communities and therefore a change in the provision of ES (Alfaro et al., 2020; Bardett et al., 2007). Bacteria were more dominant near the glacier terminus, while fungi became more prominent in the later stages of retreat (Alfaro et al., 2020). Similarly, a shift in microbial dominance towards oligotrophy with glacier retreat was recorded by several studies (Ma et al., 2023). Other studies focused on microbial groups, such as cyanobacteria abundance patterns and diversity, which generally showed different patterns in different glaciers, with a few studies showing a decrease with glacier retreat (Bradley et al., 2016; Egli et al., 2012; Frey et al., 2013).

3.3.2. Trends of ecosystem services provided by plants

Similarly to soil, all ES provided by plants were impacted by glacier retreat, showing loss, gains and shifting trends across the proglacial chronosequence. For the provisioning services of genetic resources, plant diversity generally increased with glacier retreat. However, relative abundances showed that endemic and specialised plant species were negatively affected by the fast development of emerging ecosystems. Beta diversity generally showed a change in plant communities with glacier retreat accompanied by changes in functional traits (Khelidj et al., 2024; Losapio et al., 2021). Changes in functional traits further mediated the role of plants in delivering different ES (Haselberger et al., 2024). Certain leaf and bark traits, such as high metal accumulation capacity, enhance the ability of specific plant species to uptake contaminants, making them more effective biomarkers for tracing metal pollution, especially in regions impacted by glacier retreat (Bing et al., 2016).

Successional changes in plant communities increased soil erosion control and climate regulation (Eichel et al., 2018; Musso et al., 2020). Most studies linking erosion regulation to glacier retreat have identified interactions between vegetation and geomorphic processes and changes in plant functional diversity as two of the main mechanisms through which plants reduce soil erosion (Eichel et al., 2016; Ohler et al., 2023). An increase in vegetation biomass, vegetation cover and photosynthetic activity increased plants' contribution to climate regulation, as well as their role in nutrient cycling (Feng et al., 2019; Muraoka et al., 2008). Although plants involved in nitrogen fixation were more prevalent near glacier forefronts, non-nodulating plants increased with glacier retreat, which in turn impacted nitrogen cycling (Zhang et al., 2023).

When comparing trends of ES provision by soil and plants (Tables 1 and 2), a shift in the drivers of soil formation emerged. In the early stages near glacier forefronts, soil formation was primarily driven by microbial weathering processes such as the use of ancient carbon and apatite for soil formation (Bardgett et al., 2007; Wu et al., 2014). With glacier retreat, plant litter and microbial biomass became key sources of soil carbon (Conen et al., 2007). Despite the increase of these ES with glacier retreat, plant accumulation of harmful substances for humans, such as the presence of antibiotic-resistant genes (ARGs) as well as heavy metals, also increased with glacier retreat, showing the trade-offs of vegetation development (Li et al., 2023).

4. Discussion

This literature review highlights the complex relationships between plant and soil development and the provision of ecosystem services (ES) in proglacial ecosystems following glacier retreat. Given the high sensitivity of mountain ecosystems to glacier retreat, newly emerging ecosystems are expected to expand in the future (Ficetola et al., 2024; Bosson et al., 2023), which will have a direct impact on the functioning of these ecosystems and thus the services they provide (Khelidj et al., 2025). Our findings highlight the crucial role of plants and soil in providing supporting and regulating services in proglacial regions, particularly climate regulation and nutrient cycling, while services like pollination and bioremediation remain less studied (Tu et al., 2024). Our findings also reveal that ES provision is highly context-dependent within glacier forelands, influenced by both biodiversity change and environmental gradients (Cauvy-Fraunié et al., 2016, 2020). Importantly, single ES types do not shift in isolation: we identified clear trade-offs and co-benefits.

Glacier retreat simultaneously enhances carbon sequestration potential in newly vegetated landscapes while reducing hydrological stability and associated aquatic services such as sediment transport and water quality regulation (Cauvy-Fraunié et al., 2016). These interactions must be incorporated into predictive and mechanistic models to better anticipate ES trajectories under climate change. We further highlight that species composition as well as richness plays a crucial role in maintaining multi-functionality. This aligns with recent experimental and observational studies (Isbell et al., 2017; Cauvy-Fraunié et al., 2020) suggesting that future conservation efforts must prioritise functional

Table 2
Changes in ecosystem services (ES) provided by plants with glacier retreat. This table summarises the ES delivered by plants in proglacial areas, including the indicators used to measure each service, the trend of ES provision over time following glacier retreat, and the stage (early, mid, or late) where each ES was reported to be most prominent. The trend selected for each ES was the one most frequently reported in the literature. Studies measuring only one indicator were not included in the table.

Category	Ecosystem service	Indicator	General trend	Peak stage	N. supporting studies	Examples
Regulating services	**Climate regulation**	Carbon content	↗	Late	5/8	Montagnani et al., 2019; Wei et al., 2021
	Air quality regulation	Atmospheric heavy metals content	↗	Late	3/4	Chen et al., 2023; Wang et al., 2021; Wang et al., 2020
	Erosion control	Slope stability	↗	Late	5/7	Ohler et al., 2023; Eichel et al., 2023; He et al., 2023
	Disease regulation	Spread antibiotic resistance genes (ARGs)	↘	Early	1/1	Li et al., 2023
	Pollination	Species richness of pollinators and pollinating plants	↗	Late	2/3	Albrecht et al., 2010; Losapio et al., 2016; Tu et al., 2024
Supporting services	**Soil formation**	Input from plant litter	↗	Late	5/7	D'Amico et al., 2014; White et al., 2007
	Nutrient cycling	Nitrogen content in vegetation	↗	Late	6/11	Lei et al., 2021; Montagnani et al., 2019; Sun et al., 2022; Wei et al., 2021
		Phosphorus content in vegetation	↘	Early	3/6	Krauze et al., 2021
	Primary production	Vegetation cover	↗	Late	35/35	Ohler et al., 2023; Szymański et al., 2019; Varolo et al., 2015;Wei et al., 2021
		Plant biomass	↗	Late	9/10	Chen et al., 2023; Greinwald et al., 2023; Jiang et al., 2018;
Provisional services	**Genetic resources**	Plant alpha diversity	↗	Late	37/47	Fischer et al., 2019; Breen and Levesque, 2006;Wei et al., 2021
		Diversity of N2-fixing plants	↘	Early and intermediate	2/2	Zhang et al., 2021
	Biochemicals, bioremedies and biomarkers	Biomarkers for trace metal contamination	↗		1/1	Bing et al., 2016

diversity over simple species counts to safeguard key services.

Our review also identified critical knowledge gaps and biases in the literature addressing ES provision by plants and soil in proglacial areas. First, there is a clear geographic—and likely environmental—bias in existing research, with 50 % of studies concentrated in a few proglacial areas, primarily in China and Switzerland, whereas proglacial zones in tropical regions such as Andes are underrepresented, and the provision of cultural ES in all areas remains largely unexplored. Second, the scaling of ES from local to regional levels and the long-term stability of service provisioning under extreme climatic events and glacier extinction remain difficult to quantify. These gaps highlight the need for expanded research on glacier retreat and monitoring of biodiversity and ES both in underrepresented regions and across a broader range of ES categories. Future research must move toward interdisciplinary models that integrate biodiversity shifts with socio-ecological feedback, providing a more predictive and policy-relevant framework for managing ES in a changing world.

4.1. Regulating services

Climate regulation

Our review highlights that one of the key ES provided by soil and plants in proglacial zones is climate regulation through carbon storage. In the early stages near glacier forelands (Fig. 3), studies have observed specialised microbes that utilise both atmospheric carbon dioxide and ancient carbon from the glacier foreland as their primary sources of carbon uptake (Bardgett et al., 2007; Liu et al., 2016). This initial carbon accumulation paves the way for plant growth, which then becomes crucial for soil carbon accumulation (Yoshitake et al., 2011). Some studies in our review also reported symbiotic relationships between fungi and plants that enhance soil carbon uptake via root associations (Wutkowska et al., 2021). In the later stages, an increase in plant biomass and photosynthetic activity boosts carbon storage in plants, while the decomposition of plant litter becomes a vital carbon source for soil microbes (Yu et al., 2023) (Fig. 4kheli

Results of our review align with previous findings showing that climax communities store more carbon than initial pioneer communities (Bautista-Cruz and del Castillo, 2005). Forests at higher elevations have a greater soil carbon density than those in lowland areas, making them a more significant global carbon store than previously thought (Spracklen & Righelato, 2014; Yu et al., 2014). Mountain grasslands and forests act as carbon sinks, helping to mitigate climate change and supporting the goal of net-zero emissions in the coming decades (Bai and Cotrufo, 2022; Rockström et al., 2021; Sun & Liu, 2020).

While plants contribute to carbon storage in later stages, soil has a maximum carbon storage capacity. Once this saturation point is reached, carbon storage slows down and may even diminish (Jørgensen et al., 2013; Wang et al., 2023). Carbon sources also influence whether climate regulation in proglacial regions is seen as an ES or disservice. Ancient carbon, for example, affects the characteristics of stored carbon and emission rates. Ma et al. (2023) found that as glaciers retreat, soil carbon transitions from labile to recalcitrant forms. Labile carbon decomposes quickly, providing energy for microbes, while recalcitrant carbon decomposes slowly, promoting long-term storage and improving soil stability (Shi et al., 2023). Our review indicates a general decline in labile carbon and a rise in recalcitrant carbon as glaciers retreat (Khedim et al., 2021). However, soil carbon sequestration stability declines with glacier retreat due to increased interactions with microaggregates in

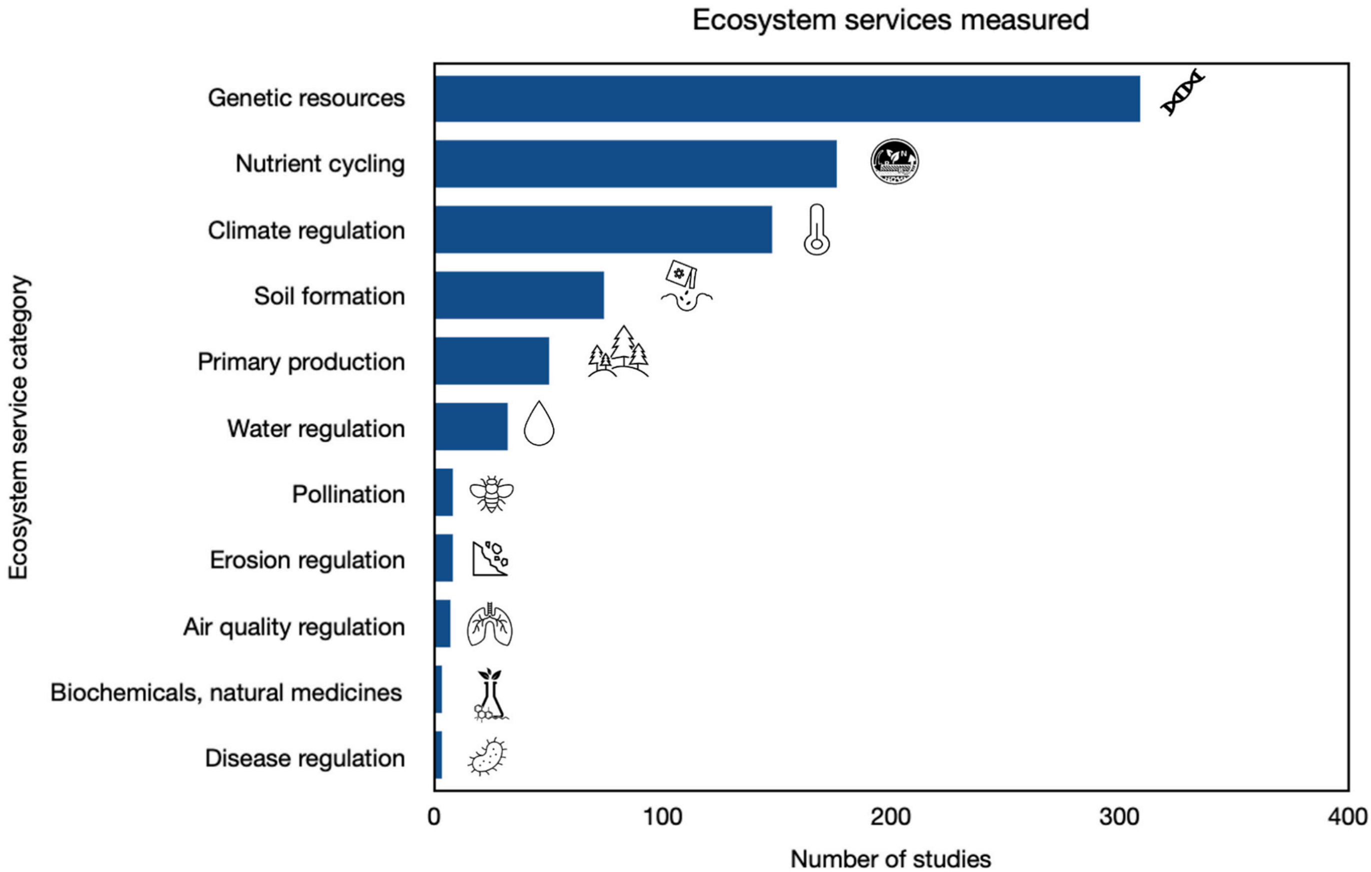

Fig. 3. Frequency of ecosystem services measured in proglacial regions. This graph displays the most frequently measured ES in proglacial regions according to the literature, along with the number of studies that assessed each ES. Note that individual studies usually measured multiple ES. The average of investigated ES per study was of 2.12.

later stages (Jílková et al., 2021; Khedim et al., 2021). Thus, determining the soil carbon saturation point and identifying carbon sources for specific chronosequences can provide better insights into soil's long-term role in climate regulation.

Soil erosion and water regulation

Our review also shows that soil microbial community structure, plant functional traits and an increase in vegetation cover play a key role in reducing soil erosion (He et al., 2023, Eichel et al., 2023; Ohler et al., 2023; Musso et al., 2020). Recent papers outside this review have proposed that another way in which soil–plant relationship contributes to geomorphic regulation is via the symbiotic interactions formed between plant roots and soil microbial communities (Qiu et al., 2024; Yan et al., 2020). Our review also shows how soil–plant interactions contribute to soil erosion control, accumulation of soil organic matter and water content retention via increasing diversity of root systems with glacier retreat (Borchardt et al., 2019; Liu et al. 2012; Sun et al., 2016). Although freshwater regulation was not identified in plants by our review, research shows that different plant physiological traits such as leaf morphology, deep root systems and stomatal regulation help plants retain and regulate water content (Fan et al., 2017; Methany, 2017).

4.2. Supporting services

Soil formation

Most studies highlighted the significant role of proglacial zones in supporting soil formation through weathering and soil organic matter (SOM) accumulation (Klaar et al., 2015; Pessi et al., 2019; Sun et al., 2016; Wu et al., 2015). Soil microbes capable of breaking down apatite and other weathering products have been identified in proglacial regions worldwide (Górniak et al., 2017; Zhou et al., 2018; Jones and Oburger, 2011). Notably, weathering genes were abundant in bacteria along the Damma Glacier forefield, supporting the evidence of their key role in rock weathering during the initial stages of soil development (Feng et al., 2023; Lapanje et al., 2012). Plants also actively contribute to soil formation by facilitating weathering and providing organic matter (D'Amico et al., 2014). This suggests that both pioneer microbial communities, specialising in soil formation and nutrient fixation, and early-stage plants near glacier forefronts (as shown in Fig. 3) contribute simultaneously to soil development through distinct mechanisms.

With glacier retreat, increasing biomass and vegetation cover enhance plant contributions to soil organic matter (SOM) through litter decomposition, accelerating soil formation (D'Amico et al., 2014). A notable exception is the Hailuogou Glacier chronosequence, where SOM peaked after 80 years before gradually declining (Schurig et al., 2013; Schweizer et al., 2018; Zhou et al., 2013; Wu et al., 2014). This shift in plant-driven soil formation suggests that while some ES are provided consistently through the same mechanisms across proglacial chronosequences, certain drivers evolve over time, carrying important implications for conservation strategies in these areas.

Nutrient cycling

Similarly, both plants and soil are crucial to nutrient cycling in glacier forelands. While nutrient cycling was observed at all stages in our review, distinct shifts emerged in the contributions of plants and soil microbes, as well as in the patterns across the chronosequence. Notably, our review revealed distinct trends in diazotrophic abundance, with some activity peaking at mid and later stages while other studies found higher abundances closer to the glacier (Bai et al., 2019; Pérez et al., 2022; Wang et al., 2021). Research on nutrient-poor soils shows that specialised microbial species, such as nitrogen-fixing bacteria (e.g., cyanobacteria), which capture atmospheric nitrogen and convert it into

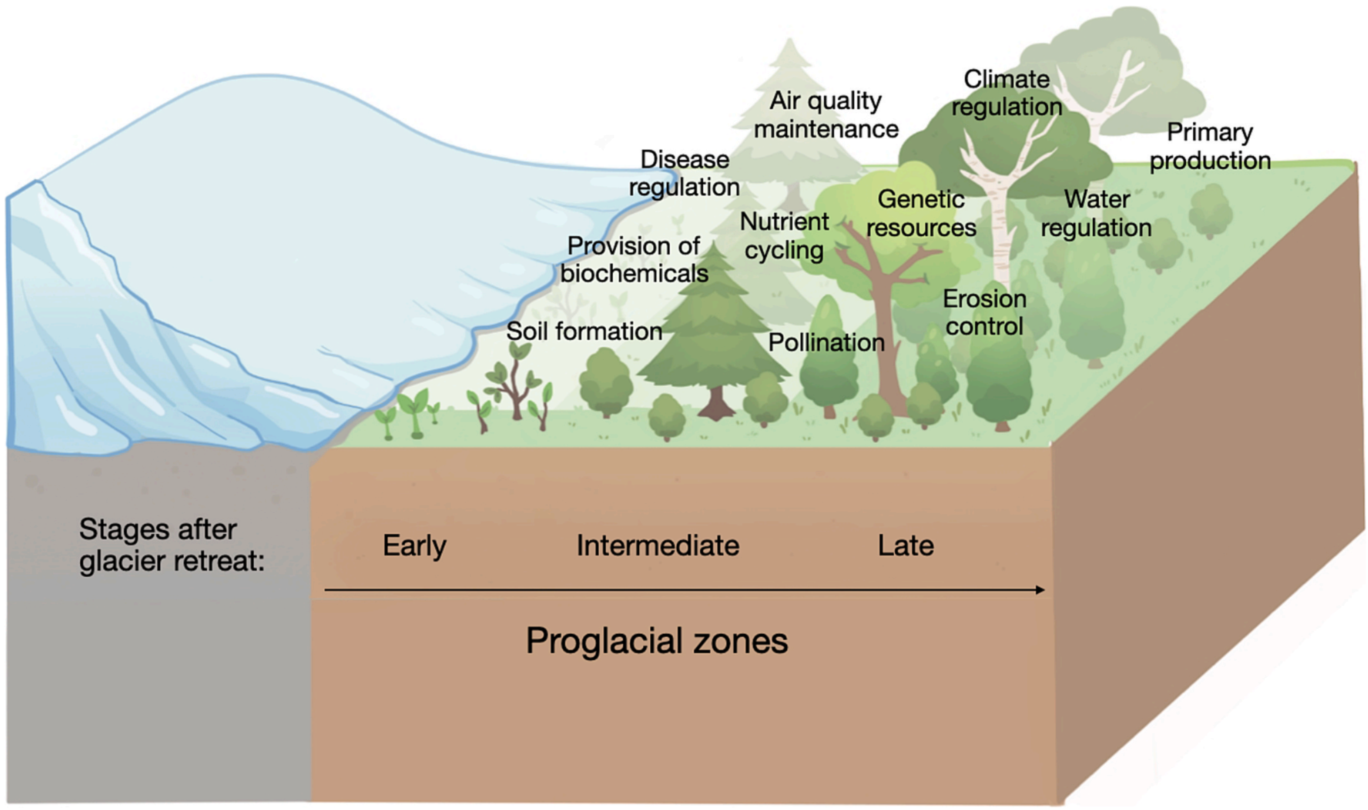

Fig. 4. Summary of ecosystem services (ES) reported in proglacial regions based on the reviewed literature. The ES labels are positioned in areas where their supply was noted to be highest. For more detailed data on specific ES and their spatial distribution, please refer to the corresponding tables in the results section.

usable organic compounds, are abundant in early stages of succession (Bai et al., 2020; Huang et al., 2023; Wietrzyk et al., 2018).

On the other hand, heterotrophic nitrogen-fixing bacteria played a major role during the later stages of glacier retreat (Wang et al., 2021). Despite the nutrient limitations in newly formed soils, pioneer plants can establish themselves through specialised nutrient allocation strategies and symbiotic relationships with these microbes (Lei et al., 2022; Sun et al., 2022). Nodulating plant species showed a peak in mid stages, while non-nodulating species increased with distance from the glacier (Zhang et al., 2023). Overall, these findings provide insight into how nitrogen fixation dynamics shift during primary succession, influencing nitrogen availability in post-glacial landscapes, while also altering the roles and mechanisms by which plants and soil contribute to nitrogen cycling individually.

Carbon dynamics and glacier retreat also played an important role in mediating the contribution of soil to the phosphorus cycle (Wang et al., 2016). Total phosphorus soil content typically peaked in intermediate stages while organic and inorganic phosphorus showed different trends with glacier retreat (Huang et al., 2023; Li et al., 2020; Wu et al., 2019). Studies in Svalbard have attributed this pattern to changes in plant and soil composition. Microbial pioneer colonisers promote phosphorus availability through rock weathering, leading to an increase in soil phosphorus. Additionally, plant and microbial residues have shown to contribute to available phosphorus in the top layers of soil (Zhou et al., 2019).

Some studies recorded both available and total phosphorus content to peak at mid stages of the chronosequences (Bai et al.,2020; Huang et al., 2023; Zhou et al., 2013). This might be a result of more established plant communities increasingly sequestering up phosphorus and phosphorus leaching out of the soil profile (Gao et al., 2024; Peltzer et al., 2010; Peng et al., 2024; Yu et al., 2022; Wang et al., 2020; Zhang et al., 2015). Other studies showed that phosphorus followed a similar pattern to carbon and nitrogen, showing an increase with glacier retreat (Borchhardt et al., 2019). These findings highlight the dynamic changes in the contributions of plants and soil to nutrient cycling during ecosystem development, underscoring the importance of understanding these processes for evaluating the shifting provision of ES with glacier retreat.

4.3. *Provisioning services*

Genetic resources

As glaciers retreated, the availability of plant genetic resources generally increased, with species richness, abundance and vegetation cover rising accordingly (Fischer et al., 2019; Wei et al., 2021). Studies on plant beta diversity, which reflects shifts in community composition and structure, also highlighted changes in functional traits associated with glacier retreat (He et al., 2023; Losapio et al., 2021; Jiang et al., 2018; Khelidj et al., 2024). Studies have demonstrated the link between functional traits and ES by showing how plant functional traits influence geomorphological processes, ultimately enhancing slope stability and reducing the risk of landslides (Eichel et al., 2016; He et al., 2023). Similar studies linking ecosystem functioning to plant functional traits, like wood density and plant height, show their association with stable, long-term biomass, which could ultimately lead to an increase in primary production and climate regulation (Baker et al., 2004).

Other studies show how plant functional traits influence carabid beetle communities during primary succession on deglaciated terrain in the Alps (Gobbi et al., 2010). The research highlights how early ruderal plant strategies and traits affect carabid species richness by regulating resource availability, and later, stress-tolerant plants support greater carabid diversity, linking plant strategies and functional traits to ES associated with biodiversity and habitat maintenance. Changes in plant functional diversity offer valuable insights into how ES evolve with glacier retreat and how they are mediated by plant communities beyond mere species richness.

Shifts in bacterial community structure and diversity reveals soil's contribution to genetic resources and their subsequent impact on other ES (Franzetti et al., 2020; Insam et al., 2017; Tian et al., 2023; Wojcik et al., 2018). A notable shift in relative abundances revealed a transition from a bacterial-dominant to a fungal-dominant microbial community (Bradley et al., 2016; Frey et al., 2013; Guerreri et al., 2024; Jiang et al., 2018). This change in community composition likely reflects broader shifts in functional diversity and ecosystem processes. Fungal communities, for example, are often associated with enhanced organic matter decomposition and nutrient turnover, while bacteria in proglacial zones have been shown to be key contributors of the nitrogen cycle, further reflecting the interdependence between different ES (Bai et al., 2019; Frey et al., 2013).

These community changes suggest that species near glacier fronts are negatively affected by glacier retreat, often being replaced by other communities. For instance, microbial keystone species in Svalbard's Midtre Lovenbreen glacier exhibit a decrease in diversity over time since deglaciation (Dong et al., 2022). Similarly, research in the Andes indicates a decline in endemic plants as glaciers retreat, with an increase in non-endemic species (Anthelme et al., 2022). Within 169 years of deglaciation, plant communities in the Andes lacked key endemic species, were colonised by non-native species and experienced a slow establishment of tropical alpine growth forms. These results underscore how deglaciation and climate change disrupt plant community composition and biodiversity, impacting the persistence of native species and genetic resources.

Changes in genetic resources could have broader implications beyond biodiversity loss, potentially affecting other crucial ES. Microbial communities also shift from copiotrophs to oligotrophs with glacier retreat, resulting in higher microbial carbon use efficiency in soils farther from the glacier (Kim et al., 2017; Ma et al., 2023; Zhu et al., 2020). Since microbial carbon use efficiency is a key factor in soil organic carbon storage and climate regulation (Tao et al., 2023), these shifts could affect biodiversity and other ES, such as climate regulation and nutrient cycling. Specifically, oligotrophs can reduce microbial-driven carbon losses and enhance carbon sequestration compared to copiotrophs (Feng et al., 2021; Ma et al., 2023). Other studies also show higher carbon metabolism with increasing time since glacier retreat, leading to increased CO_2 emissions from microbial activity (Zhu et al., 2020). As different microbial groups play specialised roles in ecosystem processes, these shifts signal changes not only in genetic resources but also in the provision of ES like nutrient cycling and climate regulation (Bai et al., 2019; Ma et al., 2023; Perez et al., 2019).

4.4. Limitations and recommendations for policy making

While our review serves as an initial step in identifying and researching how climate change affects ES in proglacial regions of high mountains, a more in-depth investigation into the supply and demand of these services is essential. The first step for the quantification and prediction of ES is the development of standardised direct measures of ES. Due to the current lack of direct measurements of ES, this study relied on indicators measuring ecosystem processes and functions that have been previously linked to ES, such as soil carbon content and plant nutrient content. Despite having to rely on indirect measurements to identify ES in proglacial ecosystems, we show the relevance of linking ecosystem processes with services and the importance of showing their interrelation when considering conservation management practices. Nevertheless, the importance of using standardised indicators and a comprehensive analysis of the effects of glacier retreat on ES continues to be imperative to understanding the impacts of climate change on livelihoods (Boyd and Banzhaf, 2007).

Despite the importance of tracking biodiversity for conservation efforts, we recommend that conservation plans not only focus on measuring different indicators of alpha diversity but also consider species' functions and the services they provide to people. This approach better captures the complexity of climate change's impacts not only on biodiversity but also on ES. Similarly, we found that while most studies focused on measuring common soil properties—primarily nutrient content and soil organic matter—only a few examined microbial-specific functions, soil–plant interactions, and the saturation points of soil water and nutrients with glacier retreat. Furthermore, by prioritising the measurement of ES in vulnerable ecosystems, a deeper understanding of their current and potential uses can inform policies for sustainable resource management.

5. Synopsis and Conclusion

This review highlights the crucial role of plants and soil in shaping proglacial regions beyond biodiversity by identifying the ecosystem services they provide and examining how climate change influences ES provision through the changing roles of plants and soil as glaciers retreat.

Pioneer soil microbial communities in poorly developed terrains contribute to soil formation after glacier retreat through the physical and chemical weathering of rocks and minerals, as well as by converting atmospheric and ancient carbon into organic forms that are stored in soil or used by plants. In doing so, pioneer soil microbial communities also play a key role in climate regulation and nutrient cycling by utilising different carbon sources and making nutrients accessible for plant use. As glaciers retreat, the role of soil in climate regulation and nutrient cycling becomes increasingly complex.

As soil and vegetation develop and biodiversity increases in the short term, soil's contribution to genetic resources grows as well. While microbial diversity increases soil organic carbon, it also leads to higher microbial activity, which increases soil carbon emissions, thus making its role in climate regulation more complex. As glaciers retreat, the development of plant communities enhances genetic diversity while altering functional traits that influence ecological processes and ES. Plants near the glacier tend to have ruderal traits, such as high specific leaf area (SLA) and low canopy height, enabling rapid growth that supports soil formation and primary production. Specialised structures like nodules enhance nutrient cycling by fixing atmospheric nitrogen. In contrast, late-successional plants display complex root systems and distinct bark traits, allowing them to regulate soil erosion, mitigate landslides and facilitate the uptake of nutrients and contaminants. These shifts in plant traits highlight how succession drives changes in ES, shaping landscape stability and ecosystem resilience.

We also demonstrated how glacier retreat impacts ES provision and identified different trends in ES provision. We expect that ongoing climate change will have a direct impact not only on mountain biodiversity but also on the ES provided by pioneer, rare or cold-adapted plant and microbial species. This novel understanding of the relationships between glacier retreat and ES provided by plants and soil can inform effective conservation and land-management strategies in these highly dynamic and unique areas.

CRediT authorship contribution statement

Laura Marcela Velasquez Casallas: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Nora Khelidj:** Writing – original draft, Investigation, Conceptualization. **Alejandra Morán-Ordóñez:** Writing – review & editing, Supervision. **Gianalberto Losapio:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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.

Acknowledgements

We thank the members of the Biodiversity Change group at University of Lausanne and University of Milan for fruitful discussions. We thank Daniel Velasquez for helping with drawing Fig. 3. We are grateful to the handling editor and three anonymous reviewers for commenting on an early version of our manuscript.

Data availability

Data are publicly and freely available on UNIMI Dataverse at https://doi.org/10.13130/RD_UNIMI/LWIOZV

Funding sources

This work was supported by the European Union, Next Generation EU, Italian Ministry of University and Research [CUP I13C22000360001; CUP G53D23006250001]; the Swiss National Science Foundation [grant number PZ00P3_202127]; and the European Biodiversity Partnership Biodiversa + [project PrioritIce, number 31BD30_209629].

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2025.101730.

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